Diversity of gall-forming rusts (Uromycladium, Pucciniales) on Acacia in Australia

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Key words
cryptic species
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systematics
taxonomy
16 new taxa

Abstract  Uromycladium tepperianum has been reported on over 100 species of Acacia, as well as on the closely related plant genera, Falcataria, Racocperma and Paraserianthes. Previous studies have indicated that U. tepperianum may represent a complex of host-specific, cryptic species. The phylogenetic relationships between 79 specimens of Uromycladium were determined based on a concatenated dataset of the Small Subunit, the Internal Transcribed Spacer and the Large Subunit regions of nuclear ribosomal DNA, and the mitochondrial cytochrome c oxidase subunit 3. This study showed that the host range of U. tepperianum s.str. was restricted to species of Acacia in the ‘A. bivenosa group’ sensu Chapman & Maslin (1992). An epitype of U. tepperianum on A. ligulata is designated to create a stable taxonomy for the application of this name. Sixteen novel species of Uromycladium are described, based on host preference, morphology and a phylogenetic species concept.

INTRODUCTION

McAlpine (1905) established Uromycladium for rust fungi (Pucciniales) on species of Acacia (Fabaceae) in Australia that were characterised by single-celled teliospores on branched and septate pedicels. Five species were described by McAlpine (1905) as new, namely, U. alpinum, U. bisporum (syn. U. acaciae fide Sydow & Sydow 1915), U. maritimum, U. robinsonii and U. simplex. McAlpine (1905) additionally recombined Uromyces tepperianus and Ureda nobilis as Uromycladium tepperianum and Uromycladium notabile, respectively. Since then, three additional species of Uromycladium have been described, namely, U. fusisporum (Savile 1971), U. naracootensis (Berndt 2010) and U. falcataeriae (type on Falcataria moluccana, Doungsa-ard et al. 2015).

Uromycladium tepperianum s.lat. causes prominent galls on the stems, phyllodes, inflorescences and pods of over 100 species of Acacia (Morris 1991, Berndt 2010). Uromycladium tepperianum s.str. has also been recorded on Paraserianthes lophantha subsp. lophantha in Western Australia (Gathe 1971, Morris 1987), and Paraserianthes lophantha subsp. montana in Indonesia (Manser 1892, Boedin 1959). Severe infection may lead to the death of host plants (Gathe 1971, Morris 1997, Wood & Morris 2007), and for this reason, U. tepperianum was introduced as a biological control agent for the control of A. saligna in the Eastern and Western Cape provinces of South Africa (Morris 1991, Wood & Morris 2007, Wood 2012).

Samuel (1924) first suggested that U. tepperianum may be divisible into a number of biological species, each adapted to a different host. Several authors have supported this hypothesis based on observations of host range and intraspecific molecular variation (Burges 1934, Walker 1983, Morris 1987, Berndt 2010, Doungsa-ard et al. 2015). Morris (1987) inoculated isolates of U. tepperianum from different host species onto a range of species of Acacia and found there were host specific genotypes. Doungsa-ard et al. (2015) used a molecular phylogenetic approach to show that the rust on Falcataria moluccana, which had been attributed to U. tepperianum (Braza 1997, Old & Cristovao 2003, Rahayu et al. 2010, Rahayu 2011, Widyastuti et al. 2013), was a distinct species, U. falcataeriae, and that there was intraspecific variation within U. tepperianum s.lat.

This study investigated the diversity of Uromycladium spp. that produce three teliospores per pedicel and form galls on their hosts. The purpose of the study was to define U. tepperianum in the strict sense, and resolve closely related species by a combined biological (host range), morphological and phylogenetic species concept. Four gene regions from ribosomal (rDNA) and mitochondrial DNA were analysed, together with morphological characters, for 74 specimens on Acacia, two on Falcataria and three on Paraserianthes lophantha.

MATERIALS AND METHODS

Specimen selection and morphological examination

During 2012–2015, specimens of Uromycladium spp. on species of Acacia and P. lophantha were collected from various locations in Australia (Table 1). All specimens were preserved in the Plant Pathology Herbarium, Department of Agriculture and Fisheries, Queensland (BRIP).

Rust spores were mounted on glass slides in 100 % lactic acid and gently heated to boiling before microscopic examination. Ranges were expressed as either min.–max., or (min.–) mean – SD – mean + SD (–max.) with values rounded to 0.5 μm.
| Taxon                      | Accession number | Host                     | State/ Country | GenBank accession |
|---------------------------|------------------|--------------------------|----------------|-------------------|
| **Uromycladium brachycarpae** | BRIP 58595       | Acacia brachycarpa       | Qld, Australia | KR994685           |
|                           | BRIP 57477       | Falcataelia moluccana    | Laguana, Philippines | JX032973           |
|                           | BRIP 57990       | F. moluccana             | Timor Leste     | KJ132974           |
| **U. farinosae**          | BRIP 58154       | A. farinosa              | SA, Australia   | KR994866           |
|                           | BRIP 59385       | A. flavescens            | Qld, Australia | KR994867           |
|                           | BRIP 57923       | A. glaucia               | Qld, Australia | KR994784           |
| **U. fusissporum**        | BRIP 57526       | A. salicin              | Qld, Australia | JX032971           |
| **U. holosporicae**       | BRIP 56538       | A. holosporicae          | NT, Australia   | KR994869           |
|                           | BRIP 56641       | A. holosporicae          | NT, Australia   | JX033004           |
|                           | BRIP 56543       | A. holosporicae          | NT, Australia   | KR994870           |
| **U. impexae**            | BRIP 57655       | A. impexixe              | Qld, Australia | KR994861           |
|                           | BRIP 57513       | A. impexixe              | Vic, Australia | KR994934           |
|                           | BRIP 57508       | A. impexixe              | NSW, Australia | KR994963           |
|                           | BRIP 57509       | A. impexixe              | NSW, Australia | JX033015           |
|                           | BRIP 57528       | A. impexixe              | NSW, Australia | KR994745           |
| **U. leioalyx**           | BRIP 57626       | A. leioalyx              | NSW, Australia | KR994696           |
|                           | BRIP 57626       | A. leioalyx              | NSW, Australia | JX033018           |
|                           | BRIP 57582       | A. leioalyx              | NSW, Australia | KR994748           |
|                           | BRIP 59926       | A. leioalyx              | Qld, Australia | KR994868           |
| **U. ligustrinae**        | BRIP 55385       | A. ligustrinae           | WA, Australia   | KR994869           |
|                           | BRIP 56567       | A. acuminata             | WA, Australia   | KR994700           |
|                           | BRIP 57070       | A. acuminata             | WA, Australia   | KR994701           |
| **U. malnini**            | BRIP 57700       | A. acuminata             | WA, Australia   | KR994701           |
|                           | BRIP 57700       | A. acuminata             | WA, Australia   | KR994701           |
|                           | BRIP 57700       | A. acuminata             | WA, Australia   | KR994977           |
|                           | BRIP 57700       | A. acuminata             | WA, Australia   | JX033023           |
| **U. mori**               | BRIP 57700       | A. morii                 | WA, Australia   | KR994978           |
|                           | BRIP 57700       | A. morii                 | WA, Australia   | JX033024           |
| **U. paradoxa**           | BRIP 56435       | A. paradoxa              | WA, Australia   | KR994840           |
|                           | BRIP 58602       | A. paradoxa              | WA, Australia   | KR994844           |
| **U. paradoxa**           | BRIP 57924       | A. deblata               | Tas, Australia  | KR994972           |
|                           | BRIP 57629       | A. diattia               | NSW, Australia  | KR994829           |
| **U. mori**               | BRIP 57924       | A. murphy                | Tas, Australia  | KR994972           |
|                           | BRIP 57629       | A. diattia               | NSW, Australia  | KR994830           |
| **U. paradoxa**           | BRIP 57858       | A. elata                 | NSW, Australia  | KR994830           |
|                           | BRIP 57879       | A. eumarsi               | NSW, Australia  | KR994831           |
|                           | BRIP 58300       | A. rubitta               | NSW, Australia  | KR994832           |
| **U. paradoxa**           | BRIP 59219       | A. deblata               | Vic, Australia  | KR994834           |
|                           | BRIP 59233       | A. murphy                | Vic, Australia  | KR994835           |
| **U. paradoxa**           | BRIP 59235       | A. leioalyx              | Vic, Australia  | KR994971           |
|                           | BRIP 57873       | A. scirpifolia            | WA, Australia   | KR994971           |
| **U. simplex**            | BRIP 57827       | A. scirpifolia            | WA, Australia   | KR994971           |
| **U. tepperianum**        | BRIP 57307       | A. tepperianum           | WA, Australia   | KR994719           |
|                           | BRIP 57596       | A. tepperianum           | WA, Australia   | KR994720           |
|                           | BRIP 57707       | A. rostellifera          | WA, Australia   | KR994721           |
|                           | BRIP 57742       | A. cupularis             | WA, Australia   | KR994723           |
|                           | BRIP 57816       | A. cupularis             | WA, Australia   | KR994876           |
|                           | BRIP 58146       | A. cupularis             | SA, Australia   | KR994972           |
|                           | BRIP 58147       | A. cupularis             | SA, Australia   | KR994972           |
|                           | BRIP 58160       | A. cupularis             | SA, Australia   | KR994972           |
|                           | BRIP 59439       | A. xanthina             | WA, Australia   | KR994728           |
|                           | BRIP 59895       | A. xanthina             | WA, Australia   | KR994729           |
|                           | BRIP 59499       | A. xanthina             | WA, Australia   | KR994822           |
|                           | BRIP 56126       | A. scorodera              | WA, Australia   | KR994731           |
| **U. tetragonaphyllea**    | BRIP 57748       | A. tetragonaphyllea      | WA, Australia   | KR994732           |
|                           | BRIP 59403       | A. parasenis the tophartha | WA, Australia   | KR994879           |
|                           | BRIP 62249       | P. lopannahtha           | WA, Australia   | KR994704           |
| **U. woodii**             | DAR 52969       | P. lopannahtha           | WA, Australia   | KR994735           |

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* NSW = New South Wales, NT = Northern Territory, Qld = Queensland, SA = South Australia, Tas = Tasmania, Vic = Victoria, WA = Western Australia.  
* Dougsa-ar et al. (2015).
Fig. 1 Phylogram obtained in a maximum likelihood search in RAxML of concatenated SSU, ITS, LSU and CO3 gene regions. Bootstrap support values (≥ 70 %) from 1000 replicates above nodes. Posterior probabilities (≥ 0.95) summarised from 30,000 converged trees obtained in a Bayesian search are shown below nodes.
Means and standard deviations (SD) were made from at least 30 measurements. Images were captured with a Leica DFC 500 camera attached to a Leica DMLB compound microscope with Normarski differential interference contrast.

**DNA extraction, PCR amplification and DNA sequencing**

DNA was extracted as described by Doungsa-ard et al. (2015). High fidelity Phusion® DNA Polymerase (New England Biolabs, MA, USA) was used in PCR as per the manufacturer-specified cycling and reaction conditions. The internal transcribed spacer (ITS) region was amplified with ITS1F/ITS4B (Gardes & Bruns 1993). The large subunit (LSU) region was amplified with the primers Rust2inv (Aime 2006)/LR7 (Vilgalys & Hester 1990) and nested with the primers LROR/LR6 (Vilgalys & Hester 1990). The small subunit (SSU) region was amplified with the primers NS1 (White et al. 1990)/Rust 18SR (Aime 2006). Cytochrome c oxidase subunit 3 (CO3) in the mitochondrial genome was amplified with the primers CO3_F1/CO3_R1 (Vialle et al. 2009). Annealing temperatures were: 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 purification and direct sequencing. Contigs were made from sequence trace files with Sequencher v. 5.0 (Gene Codes Corporation, Ann Arbor, Michigan).

**Phylogenetic analyses**

The LSU, ITS, SSU and CO3 sequences were aligned in SATe v. 1.2 (Liu et al. 2012) with the MAFFT and MUSCLE algorithms (Katoh & Toh 2008). DNA sequences were deposited in GenBank with the accession numbers listed in Table 1 and the final alignment and trees were deposited in TreeBASE (http://purl.org/phylo/treebase/phylows/study/TB2:S18219). The sequences from each locus were concatenated and run as a partitioned dataset with maximum likelihood (ML) and Bayesian inference as phylogenetic criteria. GTRGAMMA was specified as the model of evolution for nucleotide sequence data for both Maximum likelihood and Bayesian analyses were run four times to test accuracy. 30,000 trees were summarized to create a consensus tree. The ML and Bayesian analyses were run four times to test accuracy. The cold chain was heated 2003). Four runs, each consisting of four chains, were implemented for 10 million generations. The cold chain was heated 2003). Four runs, each consisting of four chains, were implemented for 10 million generations. The cold chain was heated.

**RESULTS**

**Phylogenetic relationships obtained with nuclear rDNA and mitochondrial loci**

Maximum likelihood and Bayesian inference recovered congruent topologies (Fig. 1). The phylogenetic analyses recovered 18 species that could be differentiated from each other by host range and a phylogenetic species concept. All species with three, striate teliospores per pedicel were recovered in a monophyletic group, and this character is considered a synapomorphy for this clade, which represents *U. tepperianum* s.lat. *Uromycladium tepperianum* s.str., which was first described on *A. salicina* (Saccardo 1889) in the ‘*A. bivenosa* group’ sensu Chapman & Maslin (1992), was sister to other species of *Uromycladium* with three, striate teliospores per pedicel. *Uromycladium falcatae* was distinguished from other gall-forming species in the *U. tepperianum* s.lat. complex, by the number of striae per spore (Doungsa-ard et al. 2015), but this character was not informative for the remaining species. Based on host range and a phylogenetic species concept from the analysis of DNA sequences from four genes, 16 new species of *Uromycladium* are described. Species obtained from holotype specimens were submitted to GenBank, and taxonomic novelties were deposited in MycoBank (www.MycoBank.org; Crous et al. 2004). The taxonomy of all species of *Uromycladium* with three spores per pedicel is discussed below.

**TAXONOMY**

*Uromycladium brachycarpae* Doungsa-ard, McTaggart, Geering & R.G. Shivas, sp. nov. — MycoBank MB818526; Fig. 2

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

**Type.** **Australia**, Queensland, Girraween (−28.8275, 151.9375), on *A. brachycarpa*, 6 Mar. 2012, C. Doungsa-ard, D.J. Aster & A.R. McTaggart (holotype BRIP 58999), SSU, ITS and CO3 sequences GenBank KR94781, KR994736, KR994685 and KR994866.

Galls along branches and stems, up to 7 cm long and 1 cm diam. *Spermogonia* subepidermal, associated with telia. *Telia* cinnamon brown, powdery. *Teliospores* in clusters of three, depressed globose or subglobose, at first hyaline, later cinnamon brown, with 37–44 equatorial striae and 25–31 striae.

**Fig. 2** *Uromycladium brachycarpae* on *Acacia brachycarpa* (BRIP 58999). a–b. Galls on branch; c. pedicellate teliospores; d. teliospores (equatorial view); e. teliospores (surface view). — Scale bars: b = 1 mm; c–e = 10 μm.
convergent at the apex, margin crenulate in equatorial view, (14–)15–17 (–18) × (18–)19–20 (–22) μm, apical germ pore 4–5.5 μm diam, deciduous or with a fragment of the pedicel attached; wall 2.5–3.5 μm, thickened at the apex (2–)3–4 μm; pedicel branched, with a long axis (34–)38–57 (–58) × 4–5 μm and two shorter lateral branches, pedicel wall 1 μm thick at sides, septum situated near and above the basal branch and about 8–11 (–12) μm below the top fertile cell, hyaline.

On stems of *A. brachycarpa*.

Notes — *Uromycladium brachycarpae* is only known from one specimen on *A. brachycarpa* in Queensland. *Acacia brachycarpa* is a member of the ‘Acacia ulicifolia group’, which includes *A. asparagoides*, *A. brownii*, *A. echnula*, *A. gunnii*, *A. saxicola* and *A. ulicifolia* (Maslin et al. 2001). None of these other species of *Acacia* are recorded in Australian herbaria with gall rust. *Uromycladium brachycarpae* was recovered as sister to all other species of *U. tepperianum* s.lat. on *Acacia*.

*Uromycladium falcatariae* Doungsa-ard, McTaggart, Geering & R.G. Shivis (as *falcatariurn*), Australas. Pl. Pathol. 44: 28. 2015

**Type.** **PHILIPPINES**, Magaysay, Siniloan Laguna, University of the Philippines Los Baños, Laguna-Quezon Land Grant, on *Falcataria moluccana*, 6 July 2012, K.L. Lancetta, T.A. Felices, T.U. Dalisay, A.I. Llano, A.R. McTaggart, M.D.E. & R.G. Shivis (holotype BRIP 58154), SSU, ITS, LSU and CO3 sequences GenBank KR994782, KR994737, KR994866 and KR994987.

Galls on swollen distorted stems, up to 20 cm long and 2 cm wide, sometimes forming witches’ brooms. *Spermatogonia* globose, ellipsoid or obovoid, hyaline, 3–4 × 3–7 μm. *Telia* yellowish brown, powdery. *Teliospores* globose or subglobose, yellowish brown, (13–)15–19 (–21) × (17–)18–22 (–24) μm, in clusters of three on branched and septate pedicels, with 25–32 striae converging at a solitary apical germ pore 2.5–4 μm diam, deciduous; wall 1.5–2.5 μm thick at sides and 2–3.5 μm at apex; pedicel persistent, branched, with a long axis 36–44 × 4–6 μm and two shorter lateral branches, pedicel wall 1–1.5 μm thick at sides, septum situated near and above the basal branch and about 14–16 μm below the upper fertile cell, hyaline.

On stems of *F. moluccana* (tribe *Ingeae*).

Additional material examined. **TINOR LESTE**, on *F. moluccana*, Mar. 2011, J.D. Ray & G. Soares, BRIP 57990, SSU, ITS, LSU and CO3 sequences GenBank KJ633014, KJ632994, KJ632974 and KJ639060.

Notes — *Uromycladium falcatariae* occurs on *F. moluccana* in the tribe *Ingeae*, which is a sister group to Australian *Acacia* (Brown et al. 2011). Doungsa-ard et al. (2015) suggested that *U. falcataeae* speciated by a host jump from *Acacia* (tribe *Acacieae*) to *Falcata* (as *Paraserianthes*) (tribe *Ingeae*), rather than by coevolution on related host species.

*Uromycladium farinosae* Doungsa-ard, McTaggart, Geering & R.G. Shivis, *sp. nov.* — MycoBank MB818527; Fig. 3

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

**Type.** **AUSTRALIA**, South Australia, Warramboo, Nantuma Road, next to railway line, 110 m from intersection with Tod Highway (-33.2967, 135.6261), on *A. farinosa*, 24 Dec. 2012, A.D.W. Geering (holotype BRIP 58154), SSU, ITS, LSU and CO3 sequences GenBank KR994782, KR994737, KR994866 and KR994987.

Galls on stems and phyllodes, up to 3 cm diam or confluent to 7 cm long. *Spermatogonia* subepidermal, embedded or associated with telia, scattered, reddish brown to dark brown, depressed globose, 200–220 μm wide and 80–110 μm high. *Telia* scattered, young telia pale and velvet to powdery when mature, cinnamon brown. *Teliospores* in clusters of three, depressed globose, at first hyaline, later cinnamon brown, with 31–40 equatorial striae and 22–25 striae convergent at the apex, margin crenulate in equatorial view, 13–17 × (16–)17–20 (–21) μm, apical germ pore 4–5 μm diam, deciduous or sometimes with a fragment of the pedicel attached; wall 1.5–2.5 (–3) μm, thickened at the apex 2.5–4 μm; pedicel branched, with a long axis 33–39 (–43) × 4–5 μm and two shorter lateral branches, pedicel wall 1–1.5 μm thick at sides, septum situated near and above the basal branch and about 13–15 μm below the upper fertile cell, hyaline.

On phyllodes of *A. farinosa*.

Notes — *Uromycladium farinosae* is known from one specimen on *A. farinosa* in South Australia. It was recovered as sister to *U. ligustrinae* and *U. merrallii* in the phylogenetic analyses.

*Uromycladium flavescens* Doungsa-ard, McTaggart, Geering & R.G. Shivis, *sp. nov.* — MycoBank MB818528; Fig. 4

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

**Type.** **AUSTRALIA**, Queensland, Teewah, on *A. flavescens*, 6 Mar. 2012, A.R. McTaggart (holotype BRIP 55385), SSU, ITS, LSU and CO3 sequences GenBank KR994783, KR994730, KR994867 and KR994988.

Galls on stems and trunks, up to 10 cm long and 2 cm wide. *Spermatogonia* subepidermal, associated with telia, scattered, reddish brown, depressed globose, 180–240 μm wide and 80–110 μm high. *Spermatia* hyaline, ellipsoid to obovoid, (2.5–)3–4 × 4–6 μm. 
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Telia cinnamon brown, powdery. Teliospores in clusters of three, vesicle absent, depressed globose or subglobose, at first hyaline, later cinnamon brown, with 35–45 equatorial striae and 24–28 striae convergent at the apex, margin crenulate in equatorial view, (15–)16–18–(19) × (19–)20–23(–24) μm, apical germ pore 5–5.5(–6) μm diam, deciduous; wall 2–3 μm diam; pedicels not seen.

On stems and trunks of A. flavescens.

Additional material examined. AUSTRALIA, Queensland, Noosa Heads (−26.3789, 153.1069), on A. flavescens, 9 June 2012, C. Doungsa-ard, M.D.E. & R.G. Shivas, BRIP 57283, SSU, ITS, LSU and CO3 sequences GenBank KR994784, KR994739, KR994688 and KR994989.

Notes — Uromycladium flavescentis is specific to A. flavescens in subclade Plurinerves. It was sister to U. holosericeae on A. holosericea in subclade Juliflorae. This may indicate speciation occurred by a host shift of a recent common ancestor between sympatric subclades of Acacia.

Uromycladium holosericeae Doungsa-ard, McTaggart, Geering & R.G. Shivas, sp. nov. — MycoBank MB818529; Fig. 5

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

Type. AUSTRALIA, Queensland, Bowen, summit of Flagstaff Hill (−20.0172, 148.2666), on A. holosericea, 21 Sept. 2013, M.D.E. & R.G. Shivas (holotype BRIP 59653), SSU, ITS, LSU and CO3 sequences GenBank KJ633028, KJ632998, KJ632986 and KJ639062.

Galls on stems and phyllodes, up to 5 cm long and 3 cm wide. Spermogonia subepidermal, associated with telia, scattered, reddish brown, depressed globose, Telia erumpent, cinnamon brown, powdery. Teliospores in clusters of three, vesicle absent, depressed globose or subglobose, at first hyaline, later cinnamon brown, with 35–40 equatorial striae and 24–27 striae convergent at the apex, margin crenulate in equatorial view, (16–)17–19–(20) × (18–)20–24 μm, apical germ pore 4–5.5 μm diam, deciduous; wall (1.5–)2–2.5(–3) μm, thickened at the apex (2–)2.5–3.5(–4) μm; pedicel branched, with a long axis, 55–80 × 4–5 μm, and two shorter lateral branches, pedicel wall 1–2 μm thick at sides, septum situated near and above the basal branch and about 14–16 μm below the top fertile cell, hyaline.

On stems of A. holosericea.

Additional materials examined. AUSTRALIA, Northern Territory, Nitmiluk, near Katherine Gorge (−14.3172, 132.4258), on A. holosericea, 20 Apr. 2012, C. Doungsa-ard, A.R. McTaggart, R. Berndt, V. Faust-Berndt, M.D.E. & R.G. Shivas, BRIP 56543, SSU, ITS, LSU and CO3 sequences GenBank KJ633020, KJ633004, KJ632987 and KJ639061; Northern Territory, Nitmiluk (−14.3105, 132.4217), on A. holosericea, 20 Apr. 2012, C. Doungsa-ard, A.R. McTaggart, R. Berndt, V. Faust-Berndt, M.D.E. & R.G. Shivas, BRIP 56543, SSU, ITS, LSU and CO3 sequences GenBank KR994786, KR994741, KR994690 and KR994991; Queensland, Laura, Peninsula Developmental Road (−15.4394, 144.2114), on A. holosericea, 13 May 2014, W. Khemmuk & A.D.W. Geering, BRIP 61544, SSU, ITS, LSU and CO3 sequences GenBank KR994787, KR994742, KR994969 and KR994992.

Notes — There was intraspecific variation in the ITS and LSU regions between isolates of U. holosericeae from the Northern Territory and Queensland. The main distribution of A. holosericea extends from Derby, Western Australia eastwards.
across the Kimberley Region and Northern Territory to eastern Queensland (Doran & Turnbull 1997). The variation observed in rDNA may reflect genetic diversity of *U. holosericeae* across the geographic range of *A. holosericea*.

**Uromycladium implexae** Doungsa-ard, McTaggart, Geering & R.G. Shivas, *sp*. *nov.* — MycoBank MB818530; Fig. 6

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

*Type.* **AUSTRALIA**, Victoria, Euroa (-36.7742, 145.5139), on *A. implexa*, 12 May 2013, C. Doungsa-ard, W. Khemmuk & A.D.W. Geering (holotype BRIP 59220), SSU, ITS, LSU and CO3 sequences GenBank KJ633016, KJ633008, KJ632984 and KJ639071.

Galls on branches, stems and phyllodes, confluent up to 50 cm long, variable in shape and size. *Spermogonia* subepidermal, associated with telia, reddish brown, depressed globose, 200–240 μm wide and 100–110 μm high. *Spermatia* hyaline, ellipsoid, (2–)3–4(–5) × 4–5(–6) μm. *Telia* erumpent, cinnamon brown, powdery. *Teliocystes* in clusters of three, vesicle absent, depressed globose or subglobose, at first hyaline, later cinnamon brown, with 32–39 equatorial striae and 21–27 striae convergent at the apex, margin crenulate in equatorial view, (12–)13–16(–17) × (16–)17–20(–21) μm, apical germ pore 3.5–4.5 μm diam, deciduous; pedicel branched, with a long axis (42–)51–70 × 4–5 μm and two shorter lateral branches, pedicel wall 1.0 μm thick at sides, septum situated near and above the basal branch and about (15–)19–26(–27) μm below the top fertile cell, hyaline.

On stems, branches and phyllodes of *A. implexa*.

**Additional materials examined.** **AUSTRALIA**, New South Wales, Rookhurst, Thunderbolts Way (-31.8681, 151.8628), on *A. implexa*, 13 June 2012, A.J. Carnegie, BRIP 57508, SSU, ITS, LSU and CO3 sequences GenBank KR994789, KR994744, KR994693 and KR994994; New South Wales, Stroud Road, Buckets Way (-32.3439, 151.9278), on *A. implexa*, 13 July 2012, A.J. Carnegie, BRIP 57509, SSU, ITS, LSU and CO3 sequences GenBank KJ633015, KJ633007, KJ632983 and KJ639072; New South Wales, Blaxland, Great Western Highway, on *A. implexa*, 23 Aug. 2012, A.J. Carnegie, BRIP 57626, SSU, ITS, LSU and CO3 sequences GenBank KR994790, KR994745, KR994694 and KR994995; Victoria, Melbourne, along the Merri Creek Trail between Glenlyon Road and Blyth Street-Separation Street, East Brunswick, on *A. implexa*, 18 June 2012, J. Edwards, BRIP 57313, SSU, ITS, LSU and CO3 sequences GenBank KR994788, KR994743, KR994692 and KR994993.

Notes — *Uromycladium implexae* occurs on *A. implexa* in subclade *Plurinerves*. The host is similar in morphology to *A. melanoxylon*, from which it is distinguished by the colour of the funicle, time of flowering and phyllode shape (Gowers 1990). Records of *U. tepperianum* s.lat. on *A. melanoxylon* (McAlpine 1905, Burges 1934) were unable to be verified as gall rust was not found on *A. melanoxylon* in the present study.

**Uromycladium leiocalycis** Doungsa-ard, McTaggart, Geering & R.G. Shivas, *sp*. *nov.* — MycoBank MB818533; Fig. 7

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

*Type.* **AUSTRALIA**, Queensland, Seventeen Mile Rocks, 308 Seventeen Mile Rocks Road, next to iSEE Church (-27.5497, 152.9581), on *A. leiocalyx*, 29 Nov. 2013, C. Doungsa-ard & A.D.W. Geering (holotype BRIP 59926), SSU, ITS, LSU and CO3 sequences GenBank KR994794, KR994749, KR994698 and KR994999.

**Fig. 6** *Uromycladium implexae* on *Acacia implexa* (BRIP 59220). a–b. Galls on branches and phyllodes; c. teliospores (equatorial view); d. teliospores (surface view). — Scale bars: c–d = 10 μm.

**Fig. 7** *Uromycladium leiocalycis* on *Acacia leiocalyx*. a. Galls on branch (BRIP 57536); b. galls on inflorescences (BRIP 59926); c. young pedicellate teliospores (BRIP 59926); d. teliospores (equatorial view) (BRIP 59926); e. teliospores (surface view) (BRIP 59926). — Scale bars: b = 1 cm; c–e = 10 μm.
Galls on branches, stems, phyllodes and inflorescences, globose to irregular, up to 5 cm diam. Spermogonia subepidermal, associated with telia, scattered, dark brown to black, depressed globose, 200–240 μm wide and 80–110 μm high. Spermatia hyaline, ellipsoidal, 4–5 × 3–4 μm. Telia on branches, erumpent, cinnamon brown, powdery. Teliospores in clusters of three, vesicle absent, depressed globose or subglobose, at first hyaline, later cinnamon brown, with 27–44 equatorial striae and 24–28 striae convergent at the apex, margin crenulate in equatorial view, (14–)16–18(–20) × (14–)19–23(–26) μm, apical germ pore 4–5 μm diam, deciduous or with a fragment of the pedicel attached; wall 2–3 μm thick through the apex; pedicel branched, with a long axis (26–)28–50(–53) × 4–5 μm and two shorter lateral branches, pedicel wall 1 μm thick at sides, septum situated near and above the basal branch and about 13–17(–18) μm below the top fertile cell, hyaline.

On branches, stems, phyllodes and inflorescences of A. leiocalyx.

Additional materials examined. Australia, Queensland, Wavell Heights, end of Bilsen Road near Downfall Creek (–27.382475, 153.053798), on A. leiocalyx, 15 July 2012, C. Doungsa-ard & R.G. Shivas, BRIP 56928, SSU, ITS, LSU and CO3 sequences GenBank KR994791, KR994746, KR994695 and KR994998; Queensland, Mount Cooloon (–26.5622, 153.0942), on LSU and CO3 sequences GenBank KR994791, KR994746, KR994695 and KR994996; Queensland, Mount Airlie, 12 Aug. 2012, C. Doungsa-ard & A.R. McTaggart, BRIP 57511, SSU, ITS, LSU and CO3 sequences GenBank KJ633016, KJ633006, KJ632982 and KJ639074; Queensland, Mount Airlie, Mount Airlie Road (–28.0717, 152.5742), on A. leiocalyx, 1 Aug. 2012, C. Doungsa-ard, A.R. McTaggart, A.D.W. Geering & R.G. Shivas, BRIP 57536, SSU, ITS, LSU and CO3 sequences GenBank KR994792, KR994747, KR994696 and KR994997; New South Wales, Maclean, Wharf Street approaching Highland Ridge (–29.4589, 152.2111), on A. leiocalyx, 12 Aug. 2012, C. Doungsa-ard, A.R. McTaggart & A.M. Young, BRIP 57582, SSU, ITS, LSU and CO3 sequences GenBank KR994793, KR994748, KR994697 and KR994998.

Notes — There was intraspecific variation in the ITS and LSU regions of U. leiocalycis. These differences may reflect genetic diversity of U. leiocalycis on A. leiocalyx, which contains two subspecies, namely A. leiocalyx subsp. leiocalyx and subsp. herveyensis (Pedley 1978).

Uromycladium ligustrinae Doungsa-ard, McTaggart, Geering & R.G. Shivas, sp. nov. — MycoBank MB818537; Fig. 8

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

Type. Australia, Western Australia, Koekey, Southern Branch Road approaching Great Southern Highway (–32.2289, 116.9892), on A. ligustrina, 1 Oct. 2012, C. Doungsa-ard, A.R. McTaggart, A.D.W. Geering, Y.M. Li, M.D.E. & R.G. Shivas (holotype BRIP 57708), SSU, ITS, LSU and CO3 sequences GenBank KR994795, KR994750, KR994699 and KR995000.

Galls on branches and phyllodes, up to 1 cm diam or conflu-ent to 4 cm. Spermogonia subepidermal, associated with telia, scattered, dark brown to black, depressed globose, 200–250 μm wide and 80–120 μm high. Telia erumpent, cinnamon brown, powdery. Teliospores in clusters of three, vesicle absent, depressed globose or subglobose, at first hyaline, later cinnamon brown, with 27–44 equatorial striae and 24–28 striae convergent at the apex, margin crenulate in equatorial view, (14–)16–18(–20) × (14–)19–23(–26) μm, apical germ pore 4–5 μm diam, deciduous or with a fragment of the pedicel attached; wall 2–3(–3.5) μm, thickened at the apex (2.5–)3–3.5(–4) μm; pedicel branched, with a long axis (48–)51–75(–84) × 4–6 μm and two shorter lateral branches, pedicel wall 1 μm thick at sides, septum situated near and above the basal branch and about (13–)18–23 μm below the top fertile cell, hyaline.

On branches and phyllodes of A. ligustrina.

Notes — Uromycladium ligustrinae is known only from the type specimen. The phylogenetic analyses showed that it was sister to U. merrallii, which occurs on A. merrallii. Acacia ligustrina is closely related to A. merrallii and both are classified in sect. Phyllodineae (Maslin 2013).

Fig. 8 Uromycladium ligustrinae on Acacia ligustrina (BRIP 57708). a–c. Galls on branches; d. teliospores (equatorial view); e. teliospores (surface view). — Scale bars: c = 1 cm; d–e = 10 μm.
On branches and phyllodes of A. acuminata, A. burkittii, A. coolgardienesi, A. cyclops, A. gibbosa, A. incognita, A. latior, A. patagiata, A. resinimarginea, A. sibina and A. yorokrankinesis.

Additional materials examined. AUSTRALIA, Western Australia, Yalgoo, 2 km north of Tambellup, Great Southern Highway (-33.9331, 117.6456), on A. merrallii, 29 Sept. 2012, C. Doungsa-ard & A.R. McTaggart, BRIP 57970, SSU, ITS, LSU and CO3 sequences GenBank KR994790, KR994759, KR995009; Western Australia, Broomehill West, Mount Magnet Road (-28.3811, 116.3182), on A. coolgardienesi, sequences GenBank CO3, 28 Sept. 2012, C. Doungsa-ard & R.G. Shivas, BRIP 57697, LSU and CO3 sequences GenBank KR994798, KR994759, KR994795, KR995002; Western Australia, Mount Burges, southern Goldfields, Mount Burges station, site 292 north of the Transline (-30.6925, 120.8192), on A. burkittii, 3 Dec. 2013, A.A. Mitchell & P.J. Waddell, BRIP 61549, SSU, ITS, LSU and CO3 sequences GenBank KR994802, KR994756, KR994710 and KR995010.

Notes — Uromycladium maslinii is restricted to Western Australian endemic species of Acacia. Uromycladium maslinii was found on A. acuminata, A. burkittii, A. coolgardienesi, A. cyclops, A. gibbosa, A. incognita, A. latior, A. patagiata, A. resinimarginea, A. sibina and A. yorokrankinesis. There was intra-specific variation in the ITS region of U. maslinii from specimens on different species of Acacia, indicating it may represent a complex of cryptic species.

Uromycladium merrallii Doungsa-ard, McTaggart, Geering & R.G. Shivas, sp. nov. — MycobeinMB 2818545; Fig. 10

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

Type. AUSTRALIA, South Australia, Warrambro, Nantuma Road, next to railway line, 110 m from intersection with Tod Highway (-33.2946, 135.6261), on A. merrallii, 24 Dec. 2012, A.D.W. Geering (holotype BRIP 58153), SSU, ITS, LSU and CO3 sequences GenBank KR994803, KR994757, KR994711 and KR995011.

Galls on stems and branches, up to 3 cm diam or confluent to 7 cm along branches. Spermogonia subepidermal, deformed globose, associated with telia, scattered. Telia erumpent, cinna-mon brown, powdery. Teliospores in clusters of three, vesicle absent, deformed globose or subglobous, at first hyaline, later cinnamon brown, with 33–43 equatorial striae and 24–30 striae concurrent at the apex, margin crenulate in equatorial view, (13.5–15–17.5–18) μm × (16.5–20–24–26) μm, apical germ pore 4–5.5 μm diam, deciduous or with a fragment of the pedicel attached; wall (2–2.5–3–3.5) μm, thickened at the apex 2.5–3.5–(4–5) μm; pedicel branched, with a long axis (37–)42–71–(72) μm × (5–)5.5–6.5–(7–) μm and two shorter lateral branches, pedicel wall 1–2 μm thick at sides, septum situated near and above the basal branch and about (15.5–)16.5–20 (21–) μm below the top fertile cell, hyaline.

On branches of A. merrallii.

Notes — Uromycladium merrallii is only known from the type specimen on A. merrallii. Uromycladium merrallii was sister to U. ligustrinae, which occurs on A. ligustrina, a close relative of A. merrallii (Maslin 2013).
Uromycladium mitchellii Doungsa-ard, McTaggart, Geering & R.G. Shivas, sp. nov. — MycoBank MB818549; Fig. 11

Etymology. Named after the indefatigable Australian botanist, Andrew A. Mitchell, who has collected many rust and smut fungi in Australia, including this rust on A. trudgeniana.

Type. AUSTRALIA, Western Australia, Fortescue, West Pilbara, about 5 km west of Yarraloola Station Homestead on Old Main Road (-21.5778, 115.8636), on A. trudgeniana, 8 June 2013, A.A. Mitchell, (holotype BRIP 59355), SSU, ITS, LSU and CO3 sequences GenBank KR994845, KR994836, KR994827 and KR995036.

Galls on stems, swollen or distorted, up to 5 cm diam. Spermogonia subepidermal, dark brown to black, scattered, associated with telia, 150–200 μm wide and 100–150 μm high. Spermatia hyaline, ovate or ellipsoid, 2–3(–4) × 2(–)2.5–3.5 μm. Telia powdery on gall and persistent when mature. Teliospores in clusters of three, subglobose to depressed globose, at first hyaline, later yellowish brown to cinnamon brown, densely covered in randomly arranged warts, 13–17(–20) × (13–)15–18(–20) μm, apical germ pore 3–4.5 μm diam; wall 2–3 μm, thickened at the apex 2–4.5 μm; pedicel branched, with a long axis 55–70 × 4.5–7.5 μm and two shorter lateral branches, pedicel wall 1–1.5 μm thick at sides, septum situated near and above the basal branch and about 13–16 μm below the top fertile cell, hyaline.

On branches of A. trudgeniana.

Notes — Uromycladium mitchellii was sister to another species (described below as U. morrissii sp. nov.) and together formed a monophyletic group with a shared derived character of three warded teliospores per pedicel. It is known from a single specimen on A. trudgeniana in Western Australia. Acacia trudgeniana belongs to a group of closely related species in sect. Phyllocladinae, referred to as the ‘A. pyrifolia group’ (Maslin 2013), which is sister to the ‘A. victoriae group’ (Murphy et al. 2010, Maslin 2013). Uromycladium mitchellii is the first rust found on a host in this phylogenetic group and it is hypothesized that collections of Uromycladium found on species of Acacia in the A. victoriae and A. pyrifolia clade sensu Murphy et al. (2010), will be closely related to each other.

Uromycladium morrissii Doungsa-ard, McTaggart, Geering & R.G. Shivas, sp. nov. — MycoBank MB818550; Fig. 12

Etymology. Named after Dr Michael J. Morris, a South African plant pathologist who introduced this rust into South Africa in 1987 as a biological control agent for A. saligna, where it has significantly helped to bring this species under control.

Type. AUSTRALIA, Western Australia, Perth, 5 km north of The Vines Resort (-31.7543, 116.0167), on A. saligna, 24 May 2012, R.G. Shivas (holotype BRIP 56962), SSU, ITS, LSU and CO3 sequences GenBank KJ633021, KJ632996, KJ632985 and KJ639063.

Galls on branches, stems, inflorescences, pods and phyllodes, irregular, up to 20 cm in length or forming witches’ brooms up to 40 cm diam. Spermogonia subepidermal, depressed globose, associated with telia, scattered, reddish brown, 200–250 μm wide and 100–120 μm high. Spermatia hyaline, ellipsoid, (3.5–) 4–6(–7) × (2–)3–4(–5) μm. Telia erumpent, cinnamon brown, powdery. Teliospores in clusters of three, depressed globose
or subglobose, at first hyaline, later cinnamon brown, with 33–40 equatorial striae and 27–35 striae convergent at the apex, margin crenulate in equatorial view, (11–)14–18–(20) × (17–)18–22–(26) μm, apical germ pore 4–5.5 μm diam, deci- duous or with a fragment of the pedicel attached; wall 2–3 μm, thickened at the apex, (2–)2.5–3.5–(4) μm; pedicel branched, with a long axis (40–)42–58–(65) × 4.5–6.5 μm and two shorter lateral branches, pedicel wall 1–1.5 μm thick at sides, septum situated near and above the basal branch and about (15–)16–24 μm below the top fertile cell, hyaline. On stems, branches, phyllodes, inflorescences or pods of A. saligna.

Additional materials examined. AUSTRALIA, Western Australia, Bailup, Toodyay Road, on A. saligna, 24 May 2012, R.G. Shivas, BRIP 56963, SSU, ITS, LSU and CO3 sequences GenBank KJ632997, KJ632980 and KJ639064; Western Australia, Two Rocks, 4 km south of Breakwater Drive (-31.5016, 115.6109), on A. saligna, 27 Sept. 2012, A.D.W. Geering, Y.M. Li, M.D.E. & R.G. Shivas, BRIP 57860, SSU, ITS, LSU and CO3 sequences GenBank KJ633027, KJ632995, KJ632988 and KJ639069.

Notes — Uromycladium morrisii is highly destructive on A. saligna in south-western Western Australia (Morris 1987 as U. tepperianum). It was introduced as a biocontrol agent in South Africa, where A. saligna is a noxious weed (Morris 1997, Wood 2012). Experimental inoculations of 23 Australian species of Acacia demonstrated gall formation only on A. saligna, which indicated strong host-pathogen specificity (Morris 1987). Intraspecific variation in the ITS region of U. morrisii may reflect genetic variation of this pathogen on A. saligna, of which there are at least four subspecies (Millar & Byrne 2007, Millar et al. 2008, 2011).

Uromycladium morrisii Doungsa-ard, McTaggart, Geering & R.G. Shivas, sp. nov. — MycoBank MB824917; Fig. 13

Etymology. Named after Dr Daniel J. Murphy, an Australian botanist and molecular systematist, who has focused much of his research on the taxonomy, classification and biogeography of Acacia.

Type. AUSTRALIA, Victoria, Mount Macedon, 409 Cameron Drive (-37.3722, 144.5964), on A. dealbata, 12 May 2013, C. Doungsa-ard, W. Khemmuk & A.D.W. Geering (holotype BRIP 59219), SSU, ITS, LSU and CO3 sequences GenBank KR994850, KR994843, KR994834 and KR995043.

Galls on branches, stems, phyllodes, leaves and pods, swollen or distorted with proliferating lobes up to 5 cm diam. Spermogonia subepidermal, associated with telia, 160–240 μm wide and 100–170 μm high, punctiform, black, scattered. Spermatia hyaline, ovate or ellipsoid, 2–3 × 4 μm. Telia powdery. Teliospores in clusters of three, subglobose to depressed globose, yellowish brown to cinnamon, with 35–44 equatorial striae composed of warts that converge and become indistinct towards the apex, margin verruculose in equatorial view, (15–)16–20–(23) × (21–)22–25–(30) μm, apical germ pore 5–6.5 μm diam; wall 1–4 μm at sides, thickened at apex 3–5.5 μm; pedicel branched, with a long axis, 30–50 × 3.5–6 μm, and two shorter lateral branches, pedicel wall 1–1.5 μm thick at sides, septum situated near and above the basal branch and about 13–18 μm below the top fertile cell, hyaline.

On branches, stems, phyllodes, inflorescences and pods of A. dealbata, A. decurrens, A. elata, A. mearnsii, A. penninervis and A. rubida.

Additional materials examined. AUSTRALIA, New South Wales, Blackheath, Blue Mountains, Grand Canyon, on A. elata, 16 Mar. 2012, R. Berndt &
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V. Faust-Berndt, BRIP 55674, ITS, LSU and CO3 sequences GenBank KR994837, KR994828 and KR995037; New South Wales, Mount Colah, Foxglove, on A. decurrens, 25 Aug. 2012, A.J. Carnegie, BRIP 57629, SSU, ITS, LSU and CO3 sequences GenBank KR994846, KR994838, KR994829 and KR995038; New South Wales, Captains Flat, Parkers Gap Road (~35.6061, 149.7581), on A. elata, 6 Oct. 2012, A.J. Carnegie, BRIP 57878, SSU, ITS, LSU and CO3 sequences GenBank KR994847, KR994839, KR994830 and KR995039; New South Wales, Calga, Peats Ridge (~33.3128, 151.2654), on A. mearnsii, 6 Oct. 2012, A.J. Carnegie, BRIP 57879, ITS, LSU and CO3 sequences GenBank KR994840, KR994831 and KR995040; New South Wales, Jerangle, Bredbo-Jerangle Road (~35.9189, 149.2569), on A. rubida, 6 Oct. 2012, A.J. Carnegie, BRIP 57929, ITS, LSU and CO3 sequences GenBank KR994848, KR994841, KR994832 and KR995041; New South Wales, Riamukka, Brackendale Road (~31.4289, 151.6508), on A. penninervis, 16 Oct. 2012, A.J. Carnegie, BRIP 58300, SSU, ITS, LSU and CO3 sequences GenBank KR994849, KR994842, KR994833 and KR995042; Victoria, Kergunyah (~36.3333, 147.0333), on A. dealbata, 30 Apr. 1905, G.H. Robinson, VPRI 5831; Tasmania, Berriedale, Museum of Old and New Art (~42.8122, 147.2619), on A. mearnsii, 12 May 2013, J. Edwards, BRIP 59233, SSU, ITS, LSU and CO3 sequences GenBank KR994851, KR994844, KR994835 and KR995044; Tasmania, Tinderbox (~43.0347, 147.3325), on A. dealbata, 2 Dec. 2012, M. Glenn, BRIP 59234, SSU, ITS, LSU and CO3 sequences GenBank KJ633030, KJ633011, KJ632992 and KJ639076.

Notes — Uromycladium murphyi differs from other gall-forming species of Uromycladium by having teleospores with striations comprised of warts rather than distinct striae as in U. tepperianum (McAlpine 1905). Uromycladium murphyi was identified on six species of Acacia in the Botrycephalae subclade sensu Murphy et al. (2010). Many earlier records of this rust species were likely identified as U. notabile, e.g., on A. dealbata (McAlpine 1905, 1906, Barry 2003, Berndt 2010), A. pruinosa (McAlpine 1905, 1906) and A. mearnsii (Barry 2003, Berndt 2010). However, the name Uromycladium notabile is a synonym for another rust Endoraecium digitatum (Fig. 14), which is a nomenclatural consequence of McAlpine (1905) basing his description of Uromycladium notabile on a mixed collection of urediniospores of Endoraecium and teliospores of Uromycladium. Berndt (2011) first recognised that McAlpine’s (1905) description of Uromycladium notabile was based on a mixed collection when he synonymised Uredo notabilis with Endoraecium digitatum.

Intraspecific molecular diversity (single nucleotide polymorphisms (SNPs) and/or indel sites in the ITS and LSU regions) was found amongst isolates of U. murphyi. It is possible that further species diversity exists within U. murphyi. However, this was not resolved with the species criteria used in the present study and more sampling is needed to determine whether there are cryptic species in this group.

Uromycladium paradoxae Doungsa-ard, McTaggart, Geering & R.G. Shivas, sp. nov. — MycoBank MB818551; Fig. 15

Etymology. Name refers to one of the hosts, Acacia paradoxa, on which it was found.

Type. AUSTRALIA, Victoria, Tarrawinge (~36.3858, 146.4233), on A. paradoxa, 12 May 2013, C. Doungsa-ard, W. Khemmuk & A.D.W. Geering (holotype BRIP 59204), SSU, ITS, LSU and CO3 sequences GenBank KR994806, KR994760, KR994714 and KR995014.

Fig. 14 Uredo notabilis. a. Illustration of holotype showing host symptoms (III a) on A. notabilis and urediniospore ornamentation (III b, c, d) (Ludwig 1890); b. galls on phyllodes of A. notabilis (isotype MEL 1054135); c. urediniospore showing reticulate surface. — Scale bar: c = 10 μm.

Fig. 15 Uromycladium paradoxae on Acacia paradoxa (BRIP 59204). a–b. Galls on branches; c. teliospores (equatorial view); d. teliospores (surface view). — Scale bars: b = 1 cm; c–d = 10 μm.
Galls globose on stems and branches, up to 3 cm diam, confluent along stems. Spermogonia subepidermal, associated with telia, scattered, dark brown, hyaline, cigar-shaped, depressed globose, 200–240 μm wide and 100–120 μm high. Spermatia hyaline, ellipsoid, (3–)3.5–4.5(–5.5) × (3–)3.5–6(–7.5) μm. Telia erumpent, cinnamon brown, powdery. Teliospores in clusters of three, depressed globose or subglobose, at first hyaline, later cinnamon brown, with 36–44 equatorial striae and 26–32 striae convergent at the apex, margin crenulate in equatorial view, (14–)15.5–19.5(–20) × (19.5–)20–23(–26) μm, apical germ pore 4.5–6 μm diam, deciduous or with a fragment of the pedicel attached; wall 2–3 μm thickened at the apex (2.5–)3–4(–5) μm; pedicel branched, with a long axis (25–)33–75(–80) × 4.5–6 μm and two shorter lateral branches, pedicel wall 1–2 μm thick at sides, septum situated near and above the basal branch and about (10–)11–17(–18.5) μm below the top fertile cell, hyaline.

On branches and stems of A. montana, A. paradoxa, A. stricta and A. verniciflua.

Additional specimens examined. AUSTRALIA, South Australia, Belair, Belair National Park, Queen Jubilee Drive (-35.0075, 138.6428), on A. paradoxa, 20 Dec. 2012, A.D.W. Geering, BRIP 58152; Queensland, Girraween, Girraween National Park, Pyramid Park (-28.8278, 151.5626), on A. stricta, 6 Mar. 2013, C. Doungsa-ard & A.R. McTaggart, BRIP 58602; SSU, ITS, LSU and CO3 sequences GenBank KR994804, KR994758, KR994712 and KR995012; Victoria, Inglisston, Werribee Gorge State Park, 138 Myers Road (-37.6556, 144.3650), on A. verniciflua, 28 Sept. 2012, C. Doungsa-ard, W. Khemmuk & A.D.W. Geering, BRIP 59221; SSU, ITS, LSU and CO3 sequences GenBank KR994810, KR994764, KR994718 and KR995018.

Notes — There was intraspecific variation from SNPs and indels in the ITS and LSU regions of U. paradoxa from five specimens on four host species, namely A. montana, A. paradoxa, A. stricta and A. verniciflua. This intraspecific variation in U. paradoxa may correspond to host variation or location.

Uromycladium scirpifoliae Doungsa-ard, McTaggart, Geering & R.G. Shivas, sp. nov. — MycoBank MB818552, Fig. 16

Etymology. Name refers to one of hosts, Acacia scirpifolia, on which it was found.

Type. AUSTRALIA, Western Australia, Boothendarra, Watheroo National Park (-30.3178, 115.8197), on A. scirpifolia, 28 Sept. 2012, C. Doungsa-ard & A.R. McTaggart (holotype BRIP 57817); SSU, ITS, LSU and CO3 sequences GenBank KR994809, KR994763, KR994717 and KR995017.

Galls on stems and branches, up to 8 cm long and 4 cm wide. Spermogonia subepidermal, associated with telia, scattered, reddish brown, depressed globose, 180–220 μm wide and 80–110 μm high. Spermatia hyaline, ellipsoid, (2.5–)3–4.5(–5.5) × 4.5–7(–7.5) μm. Telia erumpent, cinnamon brown, powdery. Teliospores in clusters of three, vesicle absent, depressed globose or subglobose, at first hyaline, later cinnamon brown, with 36–44 equatorial striae and 26–32 striae convergent at the apex, margin crenulate in equatorial view, (14–)15.5–19.5(–20) × (19.5–)20–23(–26) μm, apical germ pore 4.5–6 μm diam, deciduous or with a fragment of the pedicel attached; wall 2–3 μm thickened at the apex (2.5–)3–4(–5) μm; pedicel branched, with a long axis (25–)33–75(–80) × 4.5–6 μm and two shorter lateral branches, pedicel wall 1—2 μm thick at sides, septum situated near and above the basal branch and about (15–)17–23(–24) μm below the top fertile cell, hyaline.

On branches and stem of A. scirpifolia.

Additional specimen examined. AUSTRALIA, Western Australia, Coorow, Midlands Road, 200 m north of Coorow Train Station (-29.8817, 116.0206), on A. scirpifolia, 28 Sept. 2012, C. Doungsa-ard & A.R. McTaggart, BRIP 57827; SSU, ITS, LSU and CO3 sequences GenBank KR994810, KR994764, KR994718 and KR995018.

Note — Uromycladium scirpifoliae occurs on A. scirpifolia in Western Australia and is sister to U. morrisii. These two species together form a sister clade to U. maslinii, which are all restricted to Western Australia.

Uromycladium tepperianum (Sacc.) McAlpine, Ann. Mycol. 3: 310. 1905. emend. (s.str.) Doungsa-ard, McTaggart, Geering & R.G. Shivas — MycoBank MBT373119, Fig. 17

Basionym. Uromyces tepperianus Sacc., Hedwigia 28: 126. 1889.

Synonym. Caeomurus tepperianus (Sacc.) Kuntze, Revis. Gen. Pl. 3: 451. 1898.

Type. AUSTRALIA, South Australia, on Acacia salicina s.lat., 1889, J.G.O. Tepper, holotype PAD; South Australia, Black Hill, Sandy Creek, on A. salicina s.lat., 1889, J.G.O. Tepper (MEL 2070213 presumed isotype); South Australia, Walker Flat, Angas Valley Road (-34.7569, 139.5531); on A. ligulata, 22 Nov. 2013, A.D.W. Geering (BRIP 59895 here designated as epitype), SSU, ITS, LSU and CO3 sequences GenBank KR994821, KR994775, KR994729 and KR995029.

Galls on stems and branches, up to 15 cm long and 3–5 cm wide, elongated, confluent. Spermogonia subepidermal, associated with telia, scattered, reddish brown, depressed globose, 220–240 μm wide and 80–110 μm high. Spermatia hyaline, ellipsoid, 3–3.5 × 2–2.5 μm. Telia cinnamon brown, powdery. Teliospores in clusters of three, vesicle absent, depressed globose or subglobose, at first hyaline, later cinnamon brown, with 28–44 equatorial striae and 22–26 striae convergent at the apex, margin crenulate in equatorial view, (14–)15.5–19.5(–20) × (19.5–)20–23(–26) μm, apical germ pore 4.5–6 μm diam, deciduous or with a fragment of the pedicel attached; wall 2–3 μm thickened at the apex (2.5–)3–4(–5) μm; pedicel branched, with a long axis (25–)33–75(–80) × 4.5–6 μm and two shorter lateral branches, pedicel wall 1–2 μm thick at sides, septum situated near and above the basal branch and about (15–)17–23(–24) μm below the top fertile cell, hyaline.

On branches and stem of A. scirpifolia.
the apex, margin crenulate in equatorial view, 14–16(–17) × 18–23(–35) μm, apical germ pore 4–5 μm diam; wall 1.5–2.5(–3) μm, thickened at the apex (2.5–)3–4 μm; pedicel branched, with a long axis (23–)29–55(–70) × 4–5 μm and two shorter lateral branches, pedicel wall 0.5–1 μm thick at sides, septum above the basal branch, hyaline.

On stems or branches of *A. cupularis*, *A. ligulata*, *A. rostellifera*, *A. sclerosperma* and *A. xanthina* (‘A. bivenosa group’).

Additional materials examined. **AUSTRALIA**, Western Australia, Leonora (-29.5431, 122.4828), on *A. ligulata*, 1 Nov. 2011, A.A. Mitchell, A.M. Holm & A.L. Payne, BRIP 57307, SSU, ITS, LSU and CO3 sequences GenBank KR994811, KR994765, KR994719 and KR995019; Western Australia, Kookynie, Lake Rebecca (-30.0517, 122.2992), on *A. ligulata*, 27 July 2012, A.A. Mitchell & A.M. Holm, BRIP 57596, SSU, ITS, LSU and CO3 sequences GenBank KR994812, KR994766, KR994770 and KR995020; Western Australia, Mullewa, Geraldton-Mount Magnet Road (-28.5479, 115.5001), on *A. rostellifera*, 29 Sept. 2012, A.D.W. Geering, Y.M. Li, M.D.E. & R.G. Shivis, BRIP 57707, SSU, ITS, LSU and CO3 sequences GenBank KR994813, KR994767, KR994721 and KR995021; Western Australia, Mullewa, Geraldton-Mount Magnet Road (-28.5763, 115.4503), on *A. rostellifera*, 29 Sept. 2012, C. Doungaas-ard & A.R. McTaggart, BRIP 57714, SSU, ITS, LSU and CO3 sequences GenBank KR994814, KR994768, KR994722 and KR995022; Western Australia, Amelup (-34.2531, 118.2092), on *A. cupularis*, 2 Oct. 2012, C. Doungaas-ard, A.R. McTaggart, A.D.W. Geering, Y.M. Li, M.D.E. & R.G. Shivis, BRIP 57742, SSU, ITS, LSU and CO3 sequences GenBank KR994815, KR994769, KR994723 and KR995023; Western Australia, Amelup (-34.2550, 118.2075), on *A. cupularis*, 2 Oct. 2012, C. Doungaas-ard, A.R. McTaggart, A.D.W. Geering, Y.M. Li, M.D.E. & R.G. Shivis, BRIP 57816, SSU, ITS, LSU and CO3 sequences GenBank KR994816, KR994770, KR994724 and KR995024; Western Australia, Hamilton Hill, Manning Park (-32.0908, 115.7689), on *A. xanthina*, 23 July 2013, A.A. Mitchell, BRIP 59439, SSU, ITS, LSU and CO3 sequences GenBank KR994820, KR994774, KR994728 and KR995028; Western Australia, Capricorn, Great Northern Highway (-23.9925, 119.5664), on *A. sclerosperma*, 20 Apr. 2014, A.A. Mitchell, BRIP 61265, SSU, ITS, LSU and CO3 sequences GenBank KR994823, KR994777, KR994731 and KR995031; South Australia, Port Lincoln, Cape Baron PI (-34.7472, 135.8861), on *A. cupularis*, 20 Dec. 2012, A.D.W. Geering, BRIP 58146, SSU, ITS, LSU and CO3 sequences GenBank KR994817, KR994771, KR994725 and KR995025; South Australia, Muringda (-33.7408, 135.7067), on *A. cupularis*, 24 Dec. 2012, A.D.W. Geering, BRIP 58160, SSU, ITS, LSU and CO3 sequences GenBank KR994819, KR994772, KR994726 and KR995026; South Australia, Muringda (-33.7408, 135.7067), on *A. cupularis*, 24 Dec. 2012, A.D.W. Geering, BRIP 58160, SSU, ITS, LSU and CO3 sequences GenBank KR994819, KR994772, KR994773 and KR995027; South Australia, Hallett Cove, Hallett Cove Conservation Park (-35.0764, 138.4975), on *A. xanthina*, 2 Nov. 2013, A.D.W. Geering, BRIP 59899, SSU, ITS, LSU and CO3 sequences GenBank KR994822, KR994776, KR994730 and KR995030.

Notes — The holotype of *Uromyces tepperianus* was collected on *Acacia salicina* in South Australia by J.G.O. Tepper and described by Saccardo (1889). McAlpine (1905) transferred this rust to *Uromycladium*. The holotype of *U. tepperianum* is located in Saccardo’s collection at PAD (University of Padova, Italy). This specimen was examined by John Walker (pers. comm.), who observed that the teliospores had 22–26 striae that converged at the apex. A presumed isotype (MEL 2070213) of this specimen was examined in the present study and had similar morphology to the description given by Saccardo (1889). An attempt was made to extract DNA from this specimen, but PCR amplifications were unsuccessful.
Acacia salicina, the originally labelled host of the holotype of *U. tepperianum*, belongs to the ‘A. bivenosa group’ of closely related plant species, which also includes *A. ampliceps*, *A. bivenosa*, *A. cupularis*, *A. didyma*, *A. ligulata*, *A. rostellifera*, *A. scleropera*, *A. startii*, *A. telmica*, *A. tysonii* and *A. xanthina* (Chapman & Maslin 1992, Joseph et al. 2013a, b). *Acacia ligulata* has been historically confused with *A. salicina* (Chapman & Maslin 1992) and at the time of the original fungal description, the two were considered conspecific. The original members of the ‘A. bivenosa group’ that were recognised in the systematic census of Australian plants by Baron Ferdinand von Mueller were *A. salicina* and *A. rostellifera* (Von Mueller 1889). Specimens of *Uromycladium* were examined on five species in the ‘A. bivenosa group’, namely *A. cupularis*, *A. ligulata*, *A. rostellifera*, *A. scleropera* and *A. xanthina*. Both *A. ligulata* and *A. salicina* occur in the type locality, i.e., the Black Hill region near the Murray River in South Australia, but only *A. ligulata* was observed with gall rust (A.D.W. Geering, unpubl. data). Gall rust was not found on *A. salicina* at any other location during the course of this study.

Saccardo (1889) described and illustrated *Uromyces tepperianus* as having teliospores with prominent longitudinal striae, formed on unbranched pedicels. McAlpine (1906) observed that pedicels of *Uromyces tepperianus* were branched with three teliospores in a head. McAlpine (1906) transferred this species to *Uromycladium*, which he established for rust fungi on *Acacia* with teliospores in heads, i.e., on branched pedicels.

The specimen of gall rust on *A. ligulata* at the type locality (BRIP 57748) had teliospores in agreement with the descriptions and illustrations made by Saccardo (1889), McAlpine (1906) and observed by John Walker (unpubl. data). Saccardo (1889) illustrated a phylloide of the host of *Uromycladium tepperianum* (Fig. 17a). The phylloide length in *A. ligulata* is 3–10 cm (Chapman & Maslin 1992, Tame 1992), which overlaps with that for *A. salicina* (4–18 cm) (Simmons 1981, Tame 1992). Saccardo (1889) also illustrated *Uromycladium tepperianum* on an elongated stem gall (Fig. 17a), which is similar to the gall seen on *A. ligulata* in the type locality. The teliospores of *Uromycladium tepperianum* illustrated by Saccardo (1889) are similar in shape (depressed globose) and surface ornamentation (42–44 equatorial striae) (Fig. 17c) to the rust on *A. ligulata*. We conclude that the holotype of *Uromycladium tepperianum* was actually collected from *A. ligulata*. DNA sequence data has been obtained from a recent South Australian collection (BRIP 59895), which is a suitable epitype of *U. tepperianum* in order to provide nomenclatural stability.

*Uromycladium tepperianum* is distinct from other species in the genus as it infects hosts in the ‘A. bivenosa group’. Further, *U. tepperianum* has elongated galls along stems and branches rather than galls that are globose or with proliferating lobes. *Uromycladium tepperianum* s.str. is known only from Western Australia and South Australia.

**Fig. 18.** *Uromycladium tetragonophyllae* on *Acacia tetragonophylla* (BRIP 57748). a–b. Galls on branches; c. teliospores (equatorial view); d. teliospores (surface view). — Scale bars: b = 1 cm; c–d = 10 μm.
Galls on stems and branches, round to elongated, up to 3 cm diam. Spermatogonia subepidermal, associated with telia, scattered, reddish brown, depressed globose, 200–240 μm wide and 100–110 μm high. Spermatia hyaline, ellipsoid, (2–) 2.5–3.5(–4) × (3–)3.5–5(–6) μm. Telia erumpent, cinnamon brown, powdery. Teliospores in clusters of three, vesicle absent, depressed globose or subglobose, at first hyaline, later cinnamon brown, with 35–45 equatorial striae and 22–35 striae convergent at the apex, margin crenulate in equatorial view, (15.5–)17–20(–21) × (21–)22–25(–27) μm, apical germ pore 3.5–5.5 μm diam, deciduous or with a fragment of the pedicel attached; wall 2–2.5(–3) μm, thickened at the apex (2.5–)3–4.5(–5) μm; pedicel branched, hyaline, with a long axis (20–)29–80(–95) × 4–5.5 μm and two shorter lateral branches, pedicel wall 0.5–1 μm thick at sides, septum situated near and above the basal branch and about 10–23(–27) μm below the apical spore.

On stems of Paraserianthes lophantha (tribe Ingeae)

Additional materials examined. AUSTRALIA, Western Australia, Porongurup, on P. lophantha. July 2010, L. Braun (spores harvested by A.R. Wood on 28 Aug. 2014, from inoculated plants maintained at ARC-PPRI). BRIP 62249, SSU, ITS, LSU and CO3 sequences GenBank KR994826, KR994780, KR994734 and KR995034; Western Australia, Gloucester National Park, near Gloucester Tree, on P. lophantha, 1985, M.J. Morris (from rust maintained on inoculated plants at Commonwealth Scientific and Industrial Research Organisation (CSIRO), Australian Capital Territory), DAR 52697, LSU and CO3 sequences GenBank KR994735 and KR995035.

Notes — Uromycladium woodii is highly specific to P. lophantha ssp. lophantha (Morris 1987), which is an endemic Western Australian species that has become weedy in South Africa (Impson et al. 2011). This rust was collected from the Porongurup Ranges, Western Australia and maintained on living plants at CSIRO, Australia and the Agricultural Research – Council Plant Protection Research Institute, South Africa, where it was studied as a potential biological control agent (Burges 1934) and Morris (1987) that U. tepperianum was a species complex on multiple hosts, and a new taxonomy has been proposed. Uromycladium tepperianum s.lat. was divided into 16 species, which are formally described here. This takes the number of rust fungi in Australia to over 370 reported species (Shivas et al. 2014). Doungsa-ard (2015) determined that the presence of three teliospores on branched pedicels with striate telosporic walls was synapomorphic for U. tepperianum s.lat., and this finding was supported by the present study. At the species level, the morphology of spore characters is not useful to separate many of these taxa with three, striate teliospores per pedicel.

Phylogenetic analyses of genes from nuclear rDNA and mitochondrial DNA showed that the majority of these new species of Uromycladium were host specific on a single species of Acacia. There were four exceptions, namely U. maslinii, U. murphyi, U. paradoxae and U. tepperianum s.str., which occurred on more than one closely-related host species of Acacia. Molecular evidence from the ITS region indicated there was intraspecific diversity in U. holosericeae, U. morrisi, U. murphyi and U. paradoxae. This may reflect the intraspecific diversity of their host species, such as in A. saligna for U. morrisi (Thompson 2012) and species of the Botrycephaleae clade sensu Murphy et al. (2010) for U. murphyi.

The identification of species of Uromycladium in the proposed taxonomy depends on accurate identification of the host species. The host range of taxa with three, striate teliospores per pedicel in Uromycladium includes species of Acacia in sections Phyllodineae, Plurinerves, Juliflorae, and the Pulchelloidea clade, referred to in traditional classifications (Maslin 2013). Based on recent systematic studies of Acacia, A. saligna (host of U. morrisii) was transferred from sect. Phyllodineae and placed in the Pulchelloidea clade sensu Murphy et al. (2010), which also contains species of Acacia in sections Alatae, Lyco-podifoliae and Pulchellae (Murphy et al. 2010). It is interesting that species of Uromycladium with three, striate teliospores per pedicel have not otherwise been recorded on host species in these three sections.

McTaggart et al. (2016) determined that host jumps, followed by shifts and coevolution, shaped the extant diversity of rust
fungi in the last 115 million years. *Uromycladium* diversified approximately 16 million years ago, with the three-celled species of *Uromycladium* younger than 10 million years old. The present study showed that *Uromycladium* diversified on *Acacia*, with *U. falcataeae* and *U. woodii* as result of two independent host jumps from *Acacia* to the tribe *Ingeae* (Doungsa-ard et al. 2015). The evolutionary history of the 16 new species on *Acacia* is still uncertain and warrants future study. For instance, *U. maslinii* occurs on hosts in two closely related sections, namely *Juliflorae* and *Plurinerves* (Murphy et al. 2010). We hypothesize that the host range of *U. maslinii* across different sections of *Acacia* may be the result of host jumps. On the other hand, coevolution or shifts to closely related host species may have occurred in species such as *U. paradoxae* and *U. morrisii*, which occur on multiple species or subspecies of *Acacia* that are closely related (Thompson 2012, Maslin 2013). Similarly, coevolution or host shifts explained much of the observed species diversity in *Endoreaeum*, another genus of rust fungi on *Acacia* (McTaggart et al. 2015). Further species diversity of *Uromycladium* may be discovered when the numerous rusts that produce galls on *Acacia* and closely related genera are examined with a phylogenetic approach, considered together with host range.

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