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RESEARCH ARTICLE

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

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Key words

cryptic species
Pucciniales
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*, *Racosperma* 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.

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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 *Uredo notabilis* as *Uromycladium tepperianum* and *Uromycladium notabile*, respectively. Since then, three additional species of *Uromycladium* have been described, namely, *U. fusisporum* (Savile 1971), *U. naracoortensis* (Berndt 2010) and *U. falcatariae* (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* has also been recorded on *Paraserianthes lophantha* subsp. *lophantha* in Western Australia (Gathe 1971, Morris 1987), and *Paraserianthes lophantha* subsp. *montana* in Indonesia (Magnus 1892, Boedjin 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. falcatariae*, 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.

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Table 1 List of rust specimens included in this study.

Taxon	Accession number	Host	State[c], Country	GenBank accession			
				LSU	ITS	SSU	*CO3*
Uromycladium brachycarpae	BRIP[a] 58599	*Acacia brachycarpa*	Qld, Australia	KR994685	KR994736	KR994781	KR994986
U. falcatariae	BRIP 57477	*Falcataria moluccana*	Laguna, Philippines	KJ632973[d]	KJ633013[d]	KJ632993[d]	KJ639059[d]
	BRIP 57990	*F. moluccana*	Timor Leste	KJ632974[d]	KJ633014[d]	KJ632994[d]	KJ639060[d]
U. farinosae	BRIP 58154	*A. farinosa*	SA, Australia	KR994686	KR994737	KR994782	KR994987
U. flavescentis	BRIP 55385	*A. flavescens*	Qld, Australia	KR994687	KR994738	KR994783	KR994988
	BRIP 57283	*A. flavescens*	Qld, Australia	KR994688	KR994739	KR994784	KR994989
U. fusisporum	BRIP 57526	*A. salicina*	Qld, Australia	KJ632991[d]	KJ633031[d]	KJ633009[d]	KJ639075[d]
U. holosericeae	BRIP 56538	*A. holosericea*	NT, Australia	KR994689	KR994740	KR994785	KR994990
	BRIP 56541	*A. holosericea*	NT, Australia	KJ632987[d]	KJ633020[d]	KJ633004[d]	KJ639061[d]
	BRIP 56543	*A. holosericea*	NT, Australia	KR994690	KR994741	KR994786	KR994991
	BRIP 59653	*A. holosericea*	Qld, Australia	KJ632986[d]	KJ633028[d]	KJ632998[d]	KJ639062[d]
	BRIP 61544	*A. holosericea*	Qld, Australia	KR994691	KR994742	KR994787	KR994992
U. implexae	BRIP 57313	*A. implexa*	Vic, Australia	KR994692	KR994743	KR994788	KR994993
	BRIP 57508	*A. implexa*	NSW, Australia	KR994693	KR994744	KR994789	KR994994
	BRIP 57509	*A. implexa*	NSW, Australia	KJ632983[d]	KJ633015[d]	KJ633007[d]	KJ639072[d]
	BRIP 57628	*A. implexa*	NSW, Australia	KR994694	KR994745	KR994790	KR994995
	BRIP 59220	*A. implexa*	Vic, Australia	KJ632984[d]	KJ633016[d]	KJ633008[d]	KJ639071[d]
U. leiocalycis	BRIP 56928	*A. leiocalyx*	Qld, Australia	KJ632981[d]	KJ633017[d]	KJ633005[d]	KJ639073[d]
	BRIP 57285	*A. leiocalyx*	Qld, Australia	KR994695	KR994746	KR994791	KR994996
	BRIP 57511	*A. leiocalyx*	Qld, Australia	KJ632982[d]	KJ633018[d]	KJ633006[d]	KJ639074[d]
	BRIP 57536	*A. leiocalyx*	Qld, Australia	KR994696	KR994747	KR994792	KR994997
	BRIP 57582	*A. leiocalyx*	NSW, Australia	KR994697	KR994748	KR994793	KR994998
	BRIP 59926	*A. leiocalyx*	Qld, Australia	KR994698	KR994749	KR994794	KR994999
U. ligustrinae	BRIP 57708	*A. ligustrina*	WA, Australia	KR994699	KR994750	KR994795	KR995000
U. maslinii	BRIP 57697	*A. acuminata*	WA, Australia	KR994700	KR994751	KR994796	KR995001
	BRIP 57700	*A. acuminata*	WA, Australia	KR994701	KR994752	KR994797	KR995002
	BRIP 57703	*A. latior*	WA, Australia	KJ632975[d]	KJ632999[d]	KJ633023[d]	KJ639065[d]
	BRIP 57704	*A. incognita*	WA, Australia	KR994702	N/A	N/A	N/A
	BRIP 57743	*A. resinimarginea*	WA, Australia	KR994703	N/A	N/A	KR995003
	BRIP 57744	*A. gibbosa*	WA, Australia	KR994704	N/A	N/A	KR995004
	BRIP 57749	*A. coolgardiensis*	WA, Australia	KJ632976[d]	KJ633024[d]	KJ633003[d]	KJ639066[d]
	BRIP 57751	*A. acuminata*	WA, Australia	KR994705	KR994753	KR994798	KR995005
	BRIP 57755	*A. acuminata*	WA, Australia	KR994706	KR994754	KR994799	KR995006
	BRIP 57756	*A. acuminata*	WA, Australia	KJ632977[d]	KJ633025[d]	KJ633000[d]	KJ639067[d]
	BRIP 57819	*A. acuminata*	WA, Australia	KJ632978[d]	KJ633026[d]	KJ633001[d]	KJ639068[d]
	BRIP 57825	*A. yorkrakinensis*	WA, Australia	KR994707	N/A	KR994800	KR995007
	BRIP 57869	*A. sibina*	WA, Australia	KJ632979[d]	KJ633019[d]	KJ633002[d]	KJ639070[d]
	BRIP 57871	*A. patagiata*	WA, Australia	KR994708	N/A	N/A	KR995008
	BRIP 57873	*A. cyclops*	WA, Australia	KR994709	KR994755	KR994801	KR995009
	BRIP 61549	*A. burkittii*	WA, Australia	KR994710	KR994756	KR994802	KR995010
U. merrallii	BRIP 58153	*A. merrallii*	SA, Australia	KR994711	KR994757	KR994803	KR995011
U. mitchellii	BRIP 59355	*A. trudgeniana*	WA, Australia	KR994827	KR994836	KR994845	KR995036
U. morrisii	BRIP 56962	*A. saligna*	WA, Australia	KJ632985[d]	KJ633021[d]	KJ632996[d]	KJ639063[d]
	BRIP 56963	*A. saligna*	WA, Australia	KJ632980[d]	KJ633022[d]	KJ632997[d]	KJ639064[d]
	BRIP 57860	*A. saligna*	WA, Australia	KJ632988[d]	KJ633027[d]	KJ632995[d]	KJ639069[d]
U. murphyi	BRIP 59234	*A. dealbata*	Tas, Australia	KJ632992[d]	KJ633030[d]	KJ633011[d]	KJ639076[d]
	BRIP 55674	*A. elata*	NSW, Australia	KR994828[d]	KR994837[d]	N/A	KR995037[d]
	BRIP 57629	*A. deccurens*	NSW, Australia	KR994829[d]	KR994838[d]	KR994846[d]	KR995038[d]
	BRIP 57858	*A. elata*	NSW, Australia	KR994830[d]	KR994839[d]	KR994847[d]	KR995039[d]
	BRIP 57879	*A. mearnsii*	NSW, Australia	KR994831[d]	KR994840[d]	N/A	KR995040[d]
	BRIP 57929	*A. rubida*	NSW, Australia	KR994832[d]	KR994841[d]	KR994848[d]	KR995041[d]
	BRIP 58300	*A. penninervis*	NSW, Australia	KR994833[d]	KR994842[d]	KR994849[d]	KR995042[d]
	BRIP 59219	*A. dealbata*	Vic, Australia	KR994834[d]	KR994843[d]	KR994850[d]	KR995043[d]
	BRIP 59233	*A. mearnsii*	Tas, Australia	KR994835[d]	KR994844[d]	KR994851[d]	KR995044[d]
U. paradoxae	BRIP 58152	*A. paradoxa*	SA, Australia	KR994712	KR994758	KR994804	KR995012
	BRIP 58602	*A. stricta*	Qld, Australia	KR994713	KR994759	KR994805	KR995013
	BRIP 59204	*A. paradoxa*	Vic, Australia	KR994714	KR994760	KR994806	KR995014
	BRIP 59221	*A. montana*	Vic, Australia	KR994715	KR994761	KR994807	KR995015
	BRIP 59235	*A. verniciflua*	Tas, Australia	KR994716	KR994762	KR994808	KR995016
U. scirpifoliae	BRIP 57817	*A. scirpifolia*	WA, Australia	KR994717	KR994763	KR994809	KR995017
	BRIP 57827	*A. scirpifolia*	WA, Australia	KR994718	KR994764	KR994810	KR995018
U. simplex	BRIP 59214	*A. pycnantha*	Vic, Australia	KJ632990[d]	KJ633029[d]	KJ633010[d]	KJ639078[d]
U. tepperianum	BRIP 57307	*A. ligulata*	WA, Australia	KR994719	KR994765	KR994811	KR995019
	BRIP 57596	*A. ligulata*	WA, Australia	KR994720	KR994766	KR994812	KR995020
	BRIP 57707	*A. rostellifera*	WA, Australia	KR994721	KR994767	KR994813	KR995021
	BRIP 57714	*A. rostellifera*	WA, Australia	KR994722	KR994768	KR994814	KR995022
	BRIP 57742	*A. cupularis*	WA, Australia	KR994723	KR994769	KR994815	KR995023
	BRIP 57816	*A. cupularis*	WA, Australia	KR994724	KR994770	KR994816	KR995024
	BRIP 58146	*A. cupularis*	SA, Australia	KR994725	KR994771	KR994817	KR995025
	BRIP 58147	*A. cupularis*	SA, Australia	KR994726	KR994772	KR994818	KR995026
	BRIP 58160	*A. cupularis*	SA, Australia	KR994727	KR994773	KR994819	KR995027
	BRIP 59439	*A. xanthina*	WA, Australia	KR994728	KR994774	KR994820	KR995028
	BRIP 59895	*A. ligulata*	SA, Australia	KR994729	KR994775	KR994821	KR995029
	BRIP 59899	*A. ligulata*	SA, Australia	KR994730	KR994776	KR994822	KR995030
	BRIP 61265	*A. sclerosperma*	WA, Australia	KR994731	KR994777	KR994823	KR995031
U. tetragonophyllae	BRIP 57748	*A. tetragonophylla*	WA, Australia	KR994732	KR994778	KR994824	KR995032
U. woodii	BRIP 61600	*Paraserianthes lophantha*	WA, Australia	KR994733	KR994779	KR994825	KR995033
	BRIP 62249	*P. lophantha*	WA, Australia	KR994734	KR994780	KR994826	KR995034
	DAR[b] 52697	*P. lophantha*	WA, Australia	KR994735	N/A	N/A	KR995035

[a] Queensland Plant Pathology Herbarium, Department of Agriculture and Fisheries, Australia.
[b] Plant Pathology Herbarium, Department of Primary Industries, New South Wales, Australia.
[c] NSW = New South Wales, NT = Northern Territory, Qld = Queensland, SA = South Australia, Tas = Tasmania, Vic = Victoria, WA = Western Australia.
[d] Doungsa-ard et al. (2015).

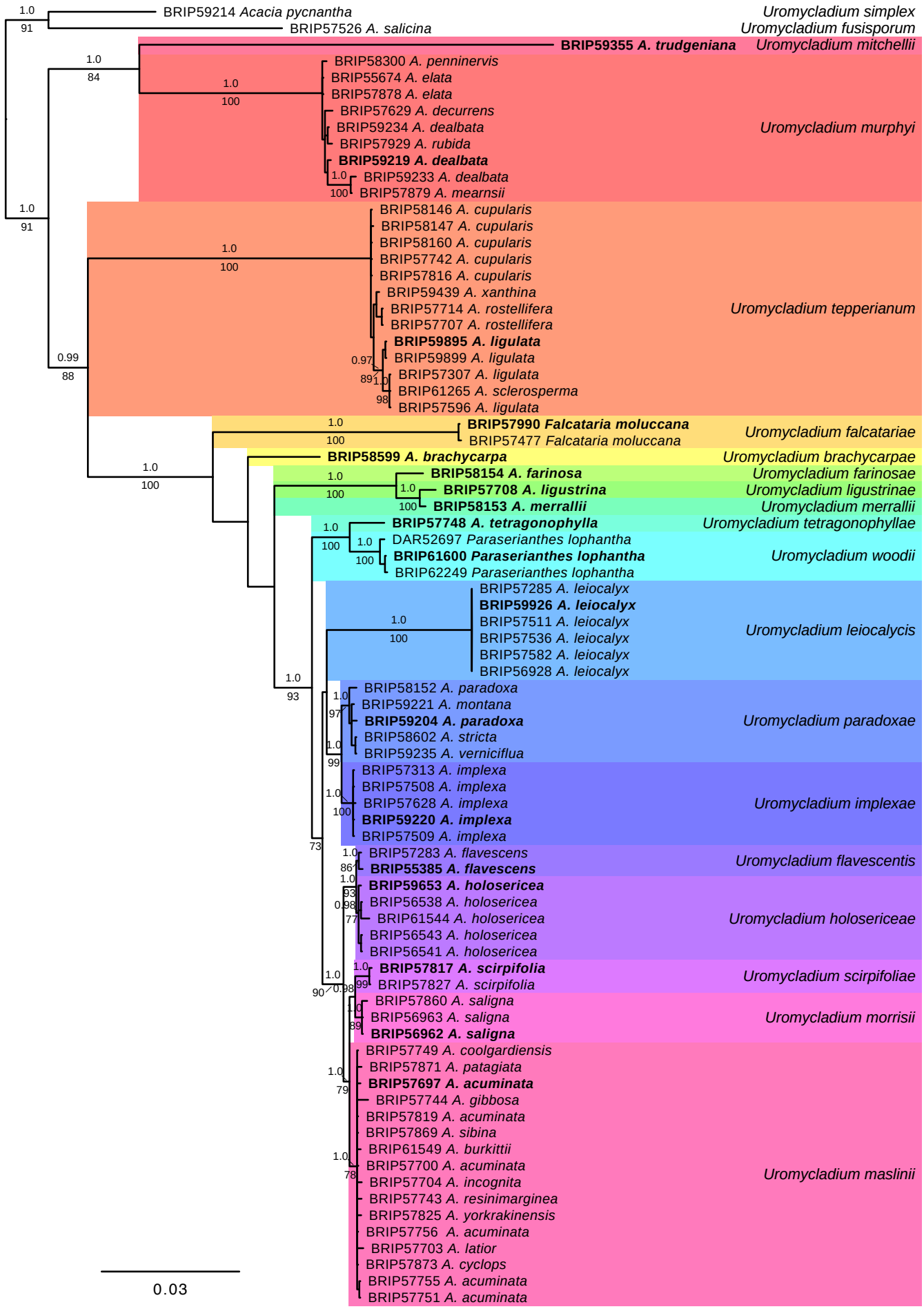

Fig. 1 Phylogram obtained in a maximum likelihood search in RAxML of concatenated SSU, ITS, LSU and *CO3* gene regions. Bootstrap support values (≥ 70 %) from 1000 replicates above nodes. Posterior probabilities (≥ 0.95) summarised from 30000 converged trees obtained in a Bayesian search are shown below 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 criteria. ML was implemented as a search criterion in RAxML v. 8.1.15 (Stamatakis 2014). The RAxML analyses were run with a rapid bootstrap analysis using a random starting tree and 1 000 maximum likelihood bootstrap replicates. A Markov Chain Monte Carlo (MCMC) search in a Bayesian analysis was conducted with MrBayes v. 3.2 (Ronquist & Huelsenbeck 2003). Four runs, each consisting of four chains, were implemented for 10 million generations. The cold chain was heated at a temperature of 0.25. Substitution model parameters were sampled every 1 000 generations and trees were saved every 1 000 generations. Convergence of the Bayesian analysis was confirmed using the cumulative and compare functions in AWTY (Nylander et al. 2008) (available at: ceb.csit.fsu.edu/awty/) and 30 000 trees were summarized to create a consensus tree. The ML and Bayesian analyses were run four times to test accuracy.

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 falcatariae 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. Sequences 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 58599), SSU, ITS, LSU and *CO3* sequences GenBank KR994781, KR994736, KR994685 and KR994986.

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

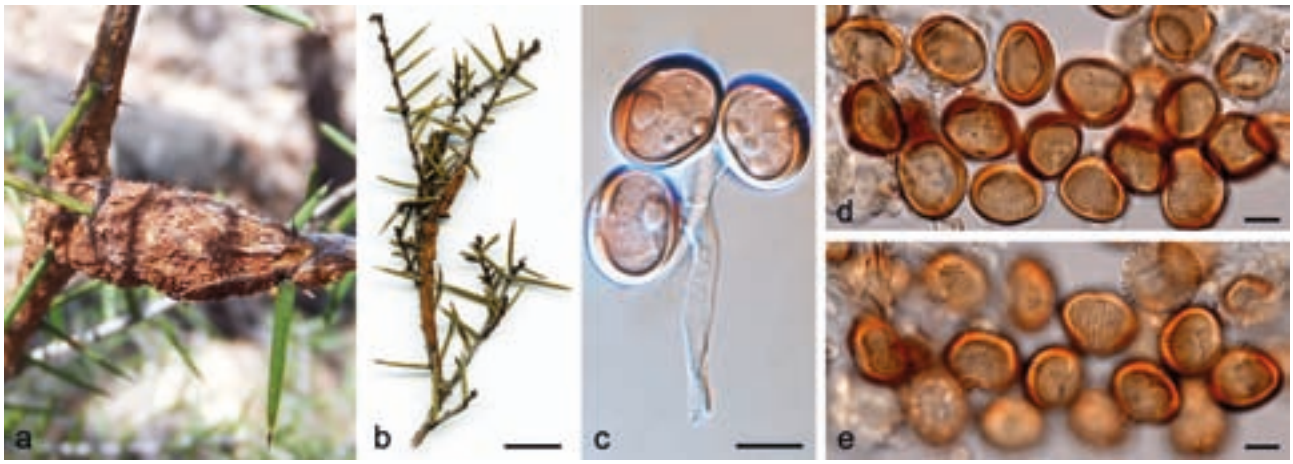

Fig. 2 *Uromycladium brachycarpae* on *Acacia brachycarpa* (BRIP 58599). a–b. Galls on branch; c. pedicellate teliospores; d. teliospores (equatorial view); e. teliospores (surface view). — Scale bars: b = 1 cm; c–e = 10 µm.

Fig. 3 *Uromycladium farinosae* on *Acacia farinosa* (BRIP 58154). a–b. Galls on branch; c. teliospores (equatorial view); d. teliospores (surface view). — Scale bars: b = 1 cm; c–d = 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–)39–57(–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. echinula*, *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. Shivas (as '*falcatarium*'), Australas. Pl. Pathol. 44: 28. 2015

Type. Philippines, Magsaysay, Siniloan Laguna, University of the Philippines Los Baños, Laguna-Quezon Land Grant, on *Falcataria moluccana*, 6 July 2012, *K.L. Lancetta*, *V.A. Felices*, *T.U. Dalisay*, *A.I. Llano*, *A.R. McTaggart*, *M.D.E. & R.G. Shivas* (holotype BRIP 57477), SSU, ITS, LSU and *CO3* sequences GenBank KJ633013, KJ632993, KJ632973 and KJ639059, MycoBank MB808468.

Galls on swollen distorted stems, up to 20 cm long and 2 cm wide, sometimes forming witches' brooms. *Spermogonia* subepidermal, scattered, associated with telia, 140 µm diam. *Spermatia* 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. Timor 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. falcatariae* speciated by a host jump from *Acacia* (tribe *Acacieae*) to *Falcataria* (as *Paraserianthes*) (tribe *Ingeae*), rather than by coevolution on related host species.

Uromycladium farinosae Doungsa-ard, McTaggart, Geering & R.G. Shivas, *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, KR994686 and KR994987.

Galls on stems and phyllodes, up to 3 cm diam or confluent to 7 cm long. *Spermogonia* 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(–20) × (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 flavescentis Doungsa-ard, McTaggart, Geering & R.G. Shivas, *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, KR994738, KR994687 and KR994988.

Galls on stems and trunks, up to 10 cm long and 2 cm wide. *Spermogonia* 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.

Fig. 4 *Uromycladium flavescentis* on *Acacia flavescens*. a–b. Galls on trunk and branch (BRIP 57283); c. gall on branch (BRIP 55385); d. teliospores (equatorial view) (BRIP 55385); e. teliospores (surface view) (BRIP 55385). — Scale bars: c = 1 cm; d–e = 10 µm.

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 56541, 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, KR994691 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

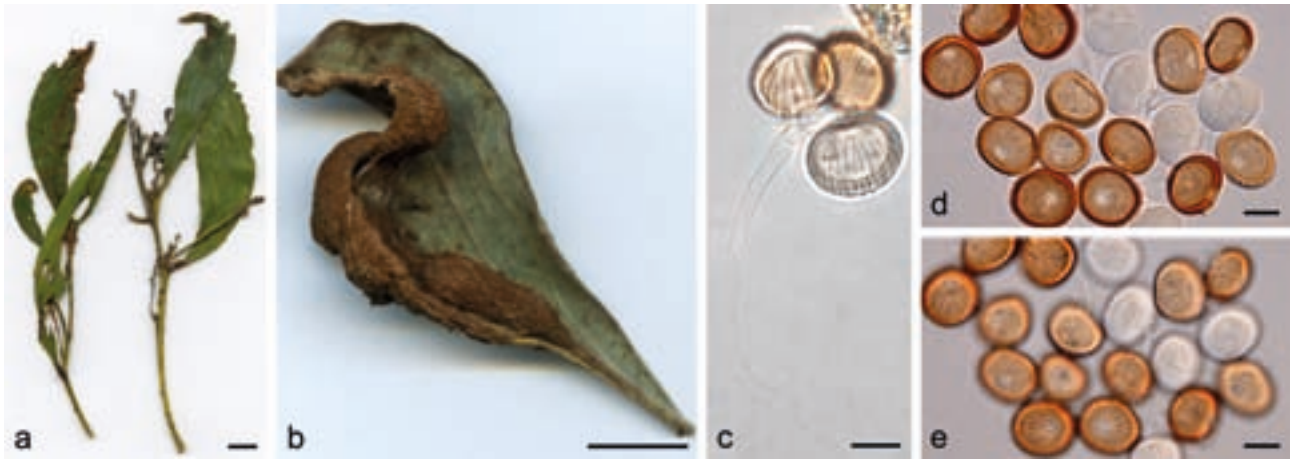

Fig. 5 *Uromycladium holosericeae* on *Acacia holosericea*. a. Galls on branches and phyllodes (BRIP 56538); b. gall on phyllodes (BRIP 59653); c. pedicellate teliospores (BRIP 59653); d. teliospores (equatorial view) (BRIP 59653); e. teliospores (surface view) (BRIP 59653). — Scale bars: a–b = 1 cm; c–e = 10 µm.

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. *Teliospores* 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 3–4.5 µm diam, deciduous; wall 1.5–2.5(–3) µm, thickened at the apex 2–3.5 µm; pedicel branched, with a long axis (42–)51–70 × 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 (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, Bucketts 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 57628, 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.

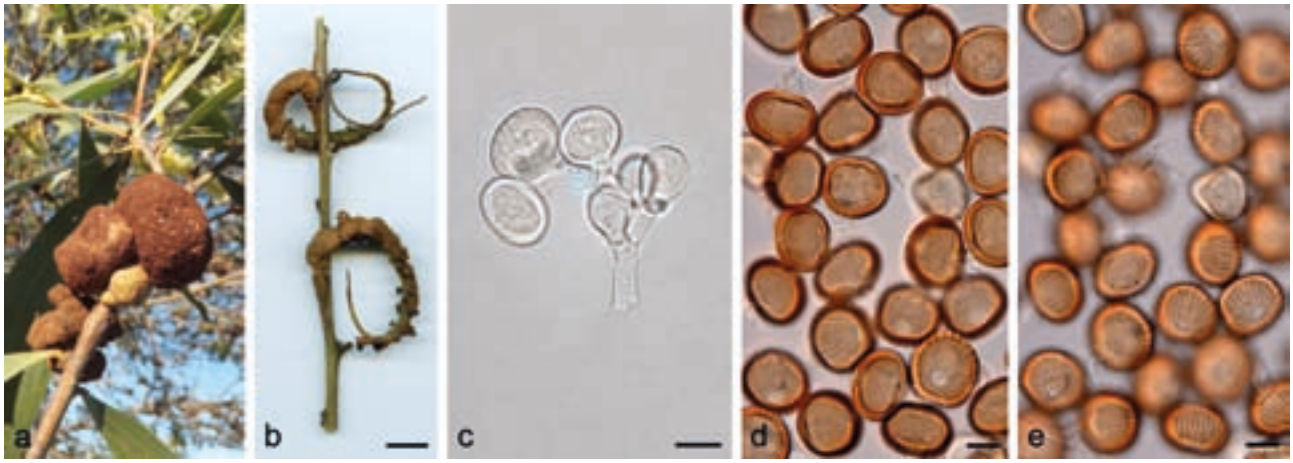

Fig. 7 *Uromycladium leiocalycis* on *Acacia leiocalyx*. a. Galls on branch (BRIP 57536); b. galls on inflorescences (BRIP 59926); c. young pedicellate teliospores (BRIP 59926); d. teliospores (equatorial view) (BRIP 59926); e. teliospores (surface view) (BRIP 59926). — Scale bars: b = 1 cm; c–e = 10 µm.

Galls on branches, stems, phyllodes and inflorescences, globose to irregular, up to 5 cm diam. *Spermogonia* subepidermal, associated with telia, scattered, reddish brown, depressed globose, 200–240 µm wide and 80–110 µm high. *Spermatia* hyaline, ellipsoid, 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 31–38 equatorial striae and 22–27 striae convergent at the apex, margin crenulate in equatorial view, 14–20(–27) × (19–)20–22(–23) µm, apical germ pore 4–4.5 µm diam, deciduous or with a fragment of the pedicel attached; wall 2–3 µm 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*, 17 May 2012, *C. Doungsa-ard & R.G. Shivas*, BRIP 56928, SSU, ITS, LSU and *CO3* sequences GenBank KJ633017, KJ633005, KJ632981 and KJ639073; Queensland, Noosa Heads (-26.3778, 153.1150), on *A. leiocalyx*, 9 June 2012, *C. Doungsa-ard*, *M.D.E. & R.G. Shivas*, BRIP 57285, SSU, ITS, LSU and *CO3* sequences GenBank KR994791, KR994746, KR994695 and KR994996; Queensland, Mount Coolum (-26.5622, 153.0942), on *A. leiocalyx*, 28 July 2012, *C. Doungsa-ard & A.R. McTaggart*, BRIP 57511, SSU, ITS, LSU and *CO3* sequences GenBank KJ633018, KJ633006, KJ632982 and KJ639074; Queensland, Mount Alford, Mount Alford 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, 153.2111), 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, Kokeby, 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 confluent 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).

Uromycladium maslinii Doungsa-ard, McTaggart, Geering & R.G. Shivas, *sp. nov*. — MycoBank MB818539; Fig. 9

Etymology. Named after the Australian botanist, Bruce R. Maslin, who generously identified many species of *Acacia* used in this study.

Type. Australia, Western Australia, Mocardy, Koorda-Wongan Hills Road (-30.8508, 116.8075), on *A. acuminata*, 6 Mar. 2012, *C. Doungsa-ard*, *A.R. McTaggart*, *A.D.W. Geering*, *Y.M. Li*, *M.D.E. & R.G. Shivas* (holotype BRIP 57819), SSU, ITS, LSU and *CO3* sequences GenBank KJ633026, KJ633001, KJ632978 and KJ639068.

Galls on branches, confluent along the margin of phyllodes, subglobose to irregular, up to 3 cm diam. *Spermogonia* subepidermal, associated with telia, scattered, reddish brown to black, depressed globose, 220–240 µm wide and 100–120 µm high. *Spermatia* hyaline, ellipsoid, (3.5–)4–6(–8) × (2.5–)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 33–44 equatorial striae and 22–34 striae convergent at the apex, margin crenulate in equatorial view, (12–)15–18(–20) × (17–)19–23(–26) µm, apical germ pore 4–5 µm diam, deciduous or with a fragment of the pedicel attached; 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 (32–)37–64(–65) × 4.5–5.5 µm and two shorter lateral branches, pedicel wall 1–2 µm thick at sides, septum situated near and above the basal branch and about (15–)16–20(–21) µm below the top fertile cell, hyaline.

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.

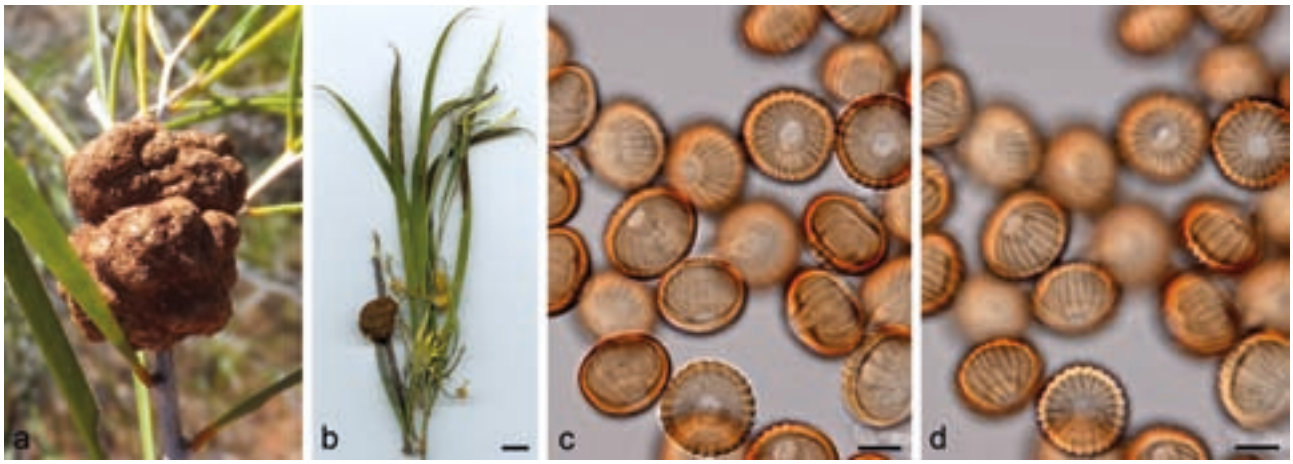

Fig. 9 *Uromycladium maslinii* on *Acacia acuminata* (BRIP 57819). a–b. Galls on branches and phyllodes; c. teliospores (equatorial view); d. teliospores (surface view). — Scale bars: b = 1 cm; c–d = 10 µm.

On branches and phyllodes of *A. acuminata*, *A. burkittii*, *A. coolgardiensis*, *A. cyclops*, *A. gibbosa*, *A. incognita*, *A. latior*, *A. patagiata*, *A. resinimarginea*, *A. sibina* and *A. yorkrakinensis*.

Additional materials examined. Australia, Western Australia, Yalgoo, 160 km west of Mount Magnet, off Geraldton-Mount Magnet Road (-28.3811, 116.3182), on *A. acuminata*, 29 Sept. 2012, *A.D.W. Geering*, *Y.M. Li*, *M.D.E. & R.G. Shivas*, BRIP 57697, SSU, ITS, LSU and *CO3* sequences GenBank KR994796, KR994751, KR994700 and KR995001; Western Australia, Mullewa, off Geraldton-Mount Magnet Road (-28.5783, 115.4503), on *A. acuminata*, 29 Sept. 2012, *C. Doungsa-ard & A.R. McTaggart*, BRIP 57700, SSU, ITS, LSU and *CO3* sequences GenBank KR994797, KR994752, KR994701 and KR995002; Western Australia, Yalgoo, Mount Magnet, off Geraldton-Mount Magnet Road (-28.3811, 116.3182), on *A. acuminata*, 29 Sept. 2012, *A.D.W. Geering*, *Y.M. Li*, *M.D.E. & R.G. Shivas*, BRIP 57703, SSU, ITS, LSU and *CO3* sequences GenBank KJ633023, KJ632999, KJ632975 and KJ639065; Western Australia, Pindar, Geraldton-Mount Magnet Road, Fegan Road (-28.5201, 115.8678), on *A. incognita*, 29 Sept. 2012, *A.D.W. Geering*, *Y.M. Li*, *M.D.E. & R.G. Shivas*, BRIP 57704, LSU sequence GenBank KR994702; Western Australia, Burakin, Dowerin-Kalannie Road, north west of railway track (-30.5214, 117.1744), on *A. resinimarginea*, 30 Sept. 2012, *C. Doungsa-ard*, *A.R. McTaggart*, *A.D.W. Geering*, *Y.M. Li*, *M.D.E. & R.G. Shivas*, BRIP 57743, LSU and *CO3* sequences GenBank KR994703 and KR995003; Western Australia, Cadoux, Hospital Road (-30.6433, 117.0100), on *A. gibbosa*, 30 Sept. 2012, *C. Doungsa-ard*, *A.R. McTaggart*, *A.D.W. Geering*, *Y.M. Li*, *M.D.E. & R.G. Shivas*, BRIP 57744, LSU and *CO3* sequences GenBank KR994704 and KR995004; Western Australia, Pindar, Geraldton-Mount Magnet Road, Fegan Road (-28.5070, 115.82699), on *A. coolgardiensis*, 29 Sept. 2012, *A.D.W. Geering*, *Y.M. Li*, *M.D.E. & R.G. Shivas*, BRIP 57749, SSU, ITS, LSU and *CO3* sequences GenBank KJ633024, KJ633003, KJ632976 and KJ639066; Western Australia, York, end of Thorn Street, in the park along Avon River (-31.8908, 116.7714), on *A. acuminata*, 1 Oct. 2012, *C. Doungsa-ard*, *A.R. McTaggart*, *A.D.W. Geering*, *Y.M. Li*, *M.D.E. & R.G. Shivas*, BRIP 57751, SSU, ITS, LSU and *CO3* sequences GenBank KR994798, KR994753, KR994705 and KR995005; Western Australia, Pingelly, 2 km north of Review Street, off Great Southern Highway, next to railway track (-32.5133, 117.0764), on *A. acuminata*, 1 Oct. 2012, *C. Doungsa-ard*, *A.R. McTaggart*, *A.D.W. Geering*, *Y.M. Li*, *M.D.E. & R.G. Shivas*, BRIP 57755, SSU, ITS, LSU and *CO3* sequences GenBank KR994799, KR994754, KR994706 and KR995006; Western Australia, Broomehill West, 13.1 km north of Tambellup, Great Southern Highway (-33.9331, 117.6456), on *A. acuminata*, 1 Oct. 2012, *C. Doungsa-ard*, *A.R. McTaggart*, *A.D.W. Geering*, *Y.M. Li*, *M.D.E. & R.G. Shivas*, BRIP 57756, SSU, ITS, LSU and *CO3* sequences GenBank KJ633025, KJ633000, KJ632977 and KJ639067; Western Australia, Paynes Find, Goodlands Road, 6.3 km from intersection with Great Northern Highway (-29.7711, 117.1017), on *A. yorkrakinensis*, 30 Sept. 2012, *C. Doungsa-ard*, *A.R. McTaggart*, *A.D.W. Geering*, *Y.M. Li*, *M.D.E. & R.G. Shivas*, BRIP 57825, SSU, LSU and *CO3* sequences GenBank KR994800, KR994707 and KR995007; Western Australia, Carnamah, off Midlands Road, 600 m south-east of Carnamah railway station (-29.6944, 115.8889), on *A. sibina*, 28 Sept. 2012, *C. Doungsa-ard & A.R. McTaggart*, BRIP 57869, SSU, ITS, LSU and *CO3* sequences GenBank KJ633019, KJ633002, KJ632979 and KJ639070; Western Australia, Katanning, Great Southern Highway (-33.7175, 117.5717), on *A. patagiata*, 1 Oct. 2012, *C. Doungsa-ard*, *A.R. McTaggart*, *A.D.W. Geering*, *Y.M. Li*, *M.D.E. & R.G. Shivas*, BRIP 57871, LSU and *CO3* sequences GenBank KR994708 and KR995008; Western Australia, Amelup, off Chester Pass Road near Ongarup Creek (-34.2553, 118.2081), on *A. cyclops*, 2 Oct. 2012, *C. Doungsa-ard*, *A.R. McTaggart*, *A.D.W. Geering*, *Y.M. Li*, *M.D.E. & R.G. Shivas*, BRIP 57873, SSU, ITS, LSU and *CO3* sequences GenBank KR994801, KR994755, KR994709 and KR995009; 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 on endemic species of *Acacia*. *Uromycladium maslinii* was found on *A. acuminata*, *A. burkittii*, *A. coolgardiensis*, *A. cyclops*, *A. gibbosa*, *A. incognita*, *A. latior*, *A. patagiata*, *A. resinimarginea*, *A. sibina* and *A. yorkrakinensis.* There was intraspecific 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*. — MycoBank MB818545; Fig. 10

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

Type. Australia, South Australia, Warramboo, Nantuma Road, next to railway line, 110 m from intersection with Tod Highway (-33.2964, 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, depressed globose, associated with telia, scattered. *Telia* erumpent, cinnamon brown, powdery. *Teliospores* in clusters of three, vesicle absent, depressed globose or subglobose, at first hyaline, later cinnamon brown, with 33–43 equatorial striae and 24–30 striae convergent at the apex, margin crenulate in equatorial view, (13.5–)15–17.5(–18) × (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) × (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).

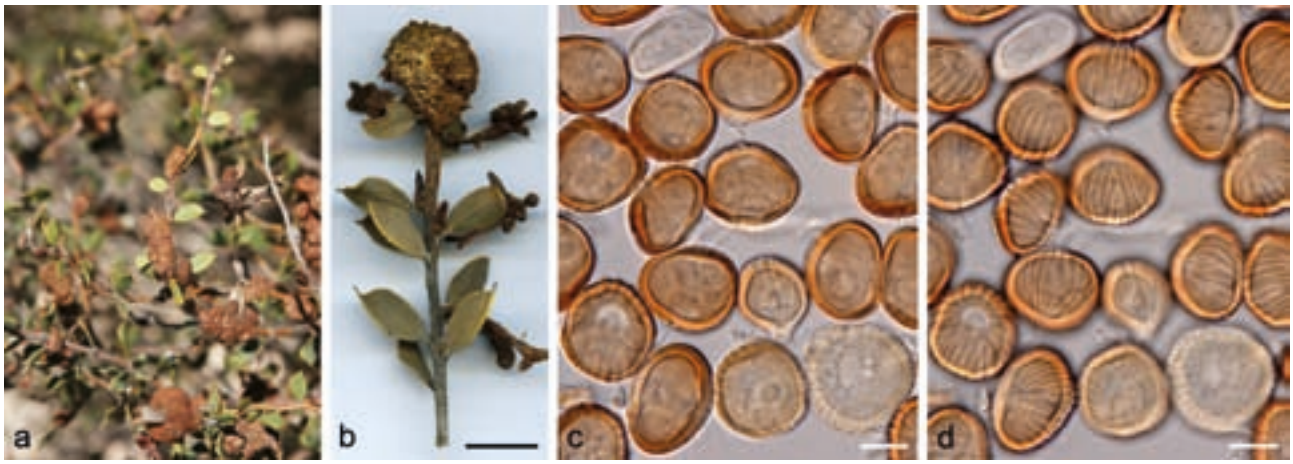

Fig. 10 *Uromycladium merrallii* on *Acacia merrallii* (BRIP 58153). a–b. Galls on branches; c. teliospores (equatorial view); d. teliospores (surface view). — Scale bars: b = 1 cm; c–d = 10 µm.

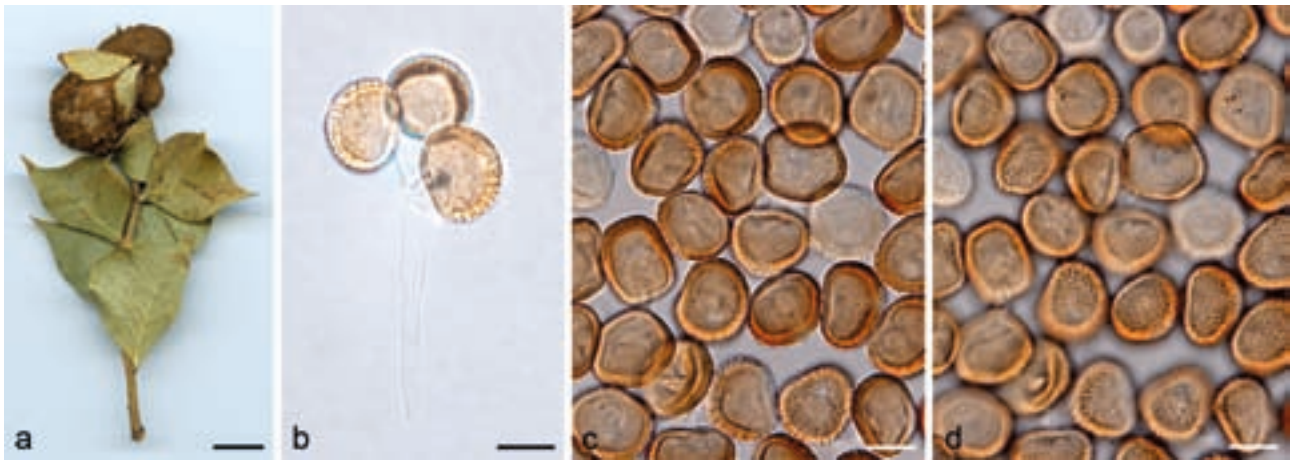

Fig. 11 *Uromycladium mitchellii* on *Acacia trudgeniana* (BRIP 59355). a. Gall on branch; b. pedicellate teliospores; c. teliospores (equatorial view); d. teliospores (surface view). — Scale bars: a = 1 cm; b–d = 10 µm.

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. murphyi* sp. nov.) and together formed a monophyletic group with a shared derived character of three warted 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. *Phyllodineae*, 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 morrisii 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

Fig. 12 *Uromycladium morrisii* on *Acacia saligna*. a. Galls on branches and phyllodes (BRIP 57860); b. gall on branch (BRIP 56962); c. teliospores (equatorial view) (BRIP 61661); d. teliospores (surface view) (BRIP 61661). — Scale bars: c–d = 10 µm.

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, deciduous 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 KJ633022, 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 murphyi 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* &

Fig. 13 *Uromycladium murphyi* on *Acacia dealbata* (BRIP 59219). a–b. Galls on branch; c. pedicellate teliospores; d. teliospores (equatorial view); e. teliospores (surface view). — Scale bars: b = 1 cm; c–e = 10 µm.

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*, 11 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, SSU, 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 5830; 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. decurrens*, *A. elata* (McAlpine 1905, 1906, 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, Tarrawingee (-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.

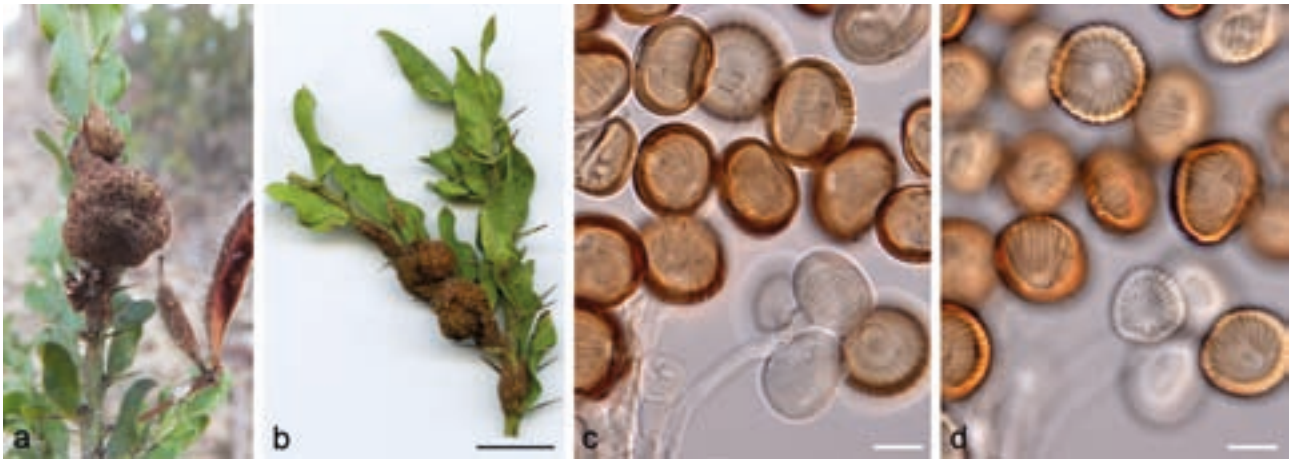

Fig. 15 *Uromycladium paradoxae* on *Acacia paradoxa* (BRIP 59204). a–b. Galls on branches; c. teliospores (equatorial view); d. teliospores (surface view). — Scale bars: b = 1 cm; c–d = 10 µm.

Galls globose on stems and branches, up to 3 cm diam, confluent along stems. *Spermogonia* subepidermal, associated with telia, scattered, reddish brown to dark brown, 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 30–44 equatorial striae and 26–32 striae convergent at the apex, margin crenulate in equatorial view, (15–)16–18.5(–20) × (18–)20–23(–26) µm, apical germ pore 3.5–5.5 µm diam, deciduous or with a fragment of the pedicel attached; wall (1.5–)2–2.5 µm, thickened at the apex 2.5–3.5 µm; pedicel branched, with a long axis (32–)33–57(–65) × 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–)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, Pyramids Road (-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, Ingliston, Werribee Gorge State Park, 138 Myers Road (-37.6556, 144.3650), on *A. montana*, 11 May 2013, *C. Doungsa-ard*, *W. Khemmuk & A.D.W. Geering*, BRIP 59221, SSU, ITS, LSU and *CO3* sequences GenBank KR994807, KR994761, KR994715 and KR995015; Tasmania, St Marys, Elephant Pass Road (-41.5989, 148.2042), on *A. verniciflua*, 7 Mar. 2013, *M. Glenn*, BRIP 59235, SSU, ITS, LSU and *CO3* sequences GenBank KR994808, KR994762, KR994716 and KR995016.

Notes — There was intraspecific variation from SNPs and indels in the ITS and LSU regions of *U. paradoxae* from five specimens on four host species, namely *A. montana*, *A. paradoxa*, *A. stricta* and *A. verniciflua*. This intraspecific variation in *U. paradoxae* 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 scripifolia*, 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 26–30 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, Angus 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

Fig. 16 *Uromycladium scirpifoliae* on *Acacia scirpifoliae* (BRIP 57817). a–b. Galls on branches; c. teliospores (equatorial view); d. teliospores (surface view). — Scale bars: b = 1 cm; c–d = 10 µm.

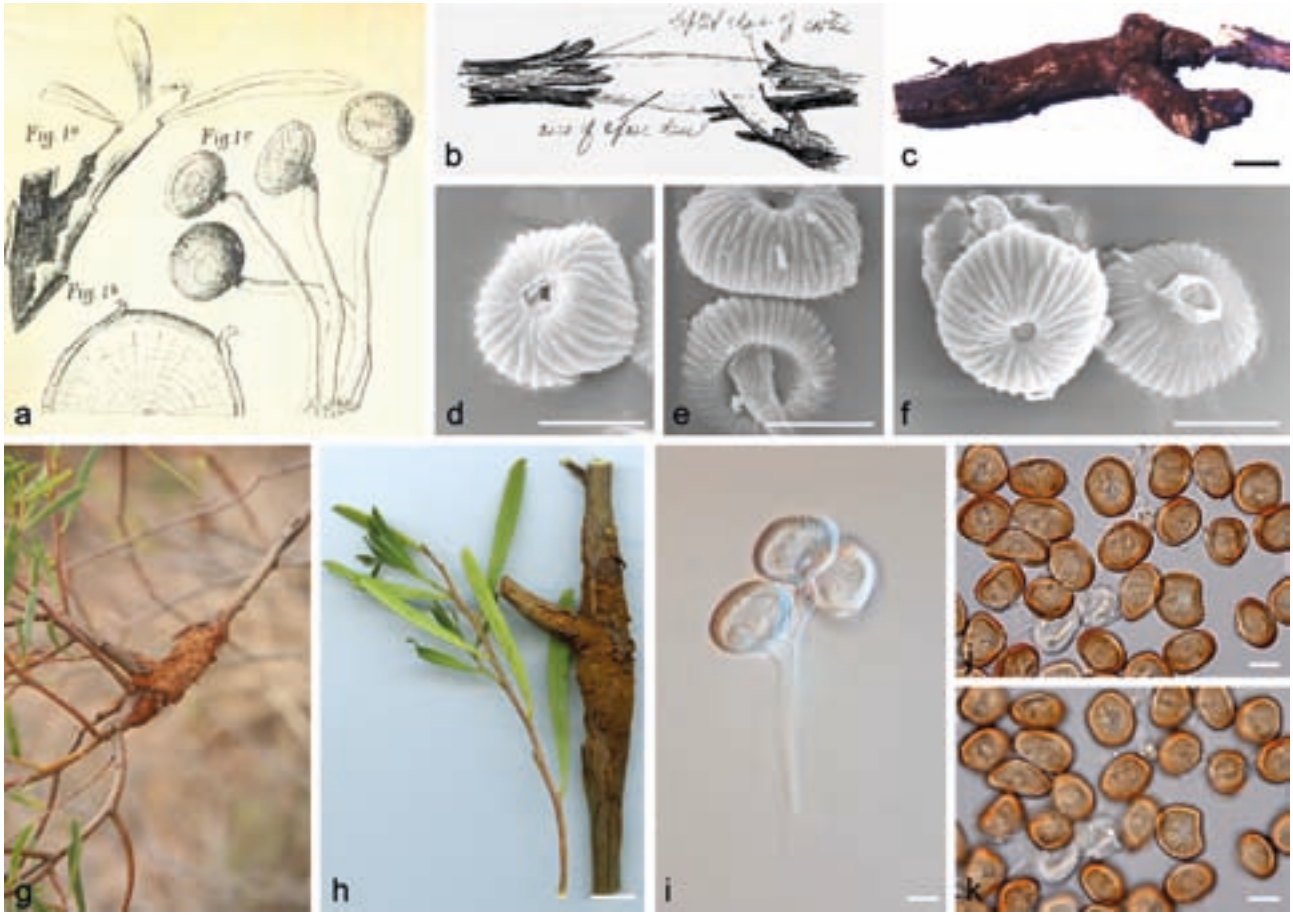

Fig. 17 *Uromycladium tepperianum* s.str. a. Illustration of holotype showing host symptoms on *A. salicina* and teliospores with convergent striae (Saccardo 1889); b. drawing of holotype preserved in PAD (sketched by John Walker in 1971); c. elongated gall symptom on *A. salicina* (holotype in PAD); d–f. teliospores from holotype specimen showing the longitudinal striae (micrographs were taken at the National Herbarium of New South Wales in 2001 by Carolyn Porter using a Cambridge Stereoscan 360 electron microscope, after having gold sputter-coated the teliospores in a Dynavac minicoater SC110M for 1.5–2 min; g–h. elongated gall on *A. ligulata* branches (BRIP 59895); i. cluster of three teliospores on a branched pedicel; j–k. teliospores (equatorial and surface view) on *A. ligulata* (BRIP 59895). — Scale bars: c, h = 1 cm; d–f, i–k = 10 µm.

the apex, margin crenulate in equatorial view, 14–16(–17) × (18–)19–23(–25) 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, KR994720 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. Shivas*, BRIP 57707, SSU, ITS, LSU and *CO3* sequences GenBank KR994813, KR994767, KR994721 and KR995021; Western Australia, Mullewa, Geraldton-Mount Magnet Road (-28.5783, 115.4503), on *A. rostellifera*, 29 Sept. 2012, *C. Doungsa-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. Doungsa-ard*, *A.R. McTaggart*, *A.D.W. Geering*, *Y.M. Li*, *M.D.E.* & *R.G. Shivas*, 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. Doungsa-ard*, *A.R. McTaggart*, *A.D.W. Geering*, *Y.M. Li*, *M.D.E.* & *R.G. Shivas*, 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, 135.8681), 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, Murdinga (-33.6900, 135.6881), on *A. cupularis*, 23 Dec. 2012, *A.D.W. Geering*, BRIP 58147, SSU, ITS, LSU and *CO3* sequences GenBank KR994818, KR994772, KR994726 and KR995026; South Australia, Murdinga (-33.7408, 135.7067), on *A. cupularis*, 24 Dec. 2012, *A.D.W. Geering*, BRIP 58160, SSU, ITS, LSU and *CO3* sequences GenBank KR994819, KR994773, KR994727 and KR995027; South Australia, Hallett Cove, Hallett Cove Conservation Park (-35.0764, 138.4975), on *A. ligulata*, 24 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. sclerosperma*, *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 only 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. sclerosperma* 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 59895) 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 phyllode of the host of *Uromyces tepperianus* (Fig. 17a). The phyllode 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 *Uromyces tepperianus* on an elongated stem gall (Fig. 17a), which is similar to the gall seen on *A. ligulata* in the type locality. The teliospores of *Uromyces tepperianus* 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 *Uromyces tepperianus* 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.

Uromycladium tetragonophyllae Doungsa-ard, McTaggart, Geering & R.G. Shivas, *sp. nov.* — MycoBank MB818554; Fig. 18

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

Type. Australia, Western Australia, East Yuna, Yuna-Tenindewa Road (-28.4289, 115.0833), on *A. tetragonophylla*, 29 Sept. 2012, *C. Doungsa-ard & A.R. McTaggart* (holotype BRIP 57748), SSU, ITS, LSU and *CO3* sequences GenBank KR994824, KR994778, KR994732 and KR995032.

Galls on branches, up to 3 cm long and 1 cm wide. *Spermogonia* subepidermal associated with telia, scattered, reddish brown to dark brown, depressed globose, 180–220 µm wide and 80–100 µm high. *Spermatia* hyaline, ellipsoid, (3–)3.5–5(–5.5) × (3.5–)4–8(–10) µm. *Telia* erumpent, cinnamon brown, powdery. *Teliospores* in clusters of three, vesicle absent, depressed globose or subglobose, at first hyaline, later cinnamon brown, with 34–45 equatorial striae and 24–30 striae convergent at the apex, margin crenulate in equatorial view, (12.5–)14–20(–22) × (17.5–)18–22.5(–25) µm, apical germ pore 3.5–5.5 µm diam., deciduous or sometimes with a fragment of the pedicel attached; 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 (25–)28–60(–65) × 4–5.5 µm and two shorter lateral branches, pedicel wall 1–2 µm thick at sides, septum situated near and above the basal branch and about (10–)12–20(–21) µm below the top fertile cell, hyaline.

On branches of *A. tetragonophylla.*

Notes — *Uromycladium tetragonophyllae* is only known from the type specimen on *A. tetragonophylla* in Western Australia.

Uromycladium woodii Doungsa-ard, McTaggart, Geering & R.G. Shivas, *sp. nov.* — MycoBank MB818556; Fig. 19

Etymology. Named after the South African plant pathologist, Dr Alan R. Wood, who has discovered and collected many rusts in Australia and South Africa.

Type. Australia, Western Australia, Porongurup, on *Paraserianthes lophantha*, July 2010, *L. Braun* (spores harvested by A.R. Wood on 24 Feb. 2011 from inoculated plants maintained at the Agricultural Research Council – Plant Protection Research Institute; ARC-PPRI) (holotype BRIP 61600), SSU, ITS, LSU and *CO3* sequences GenBank KR994825, KR994779, KR994733 and KR995033.

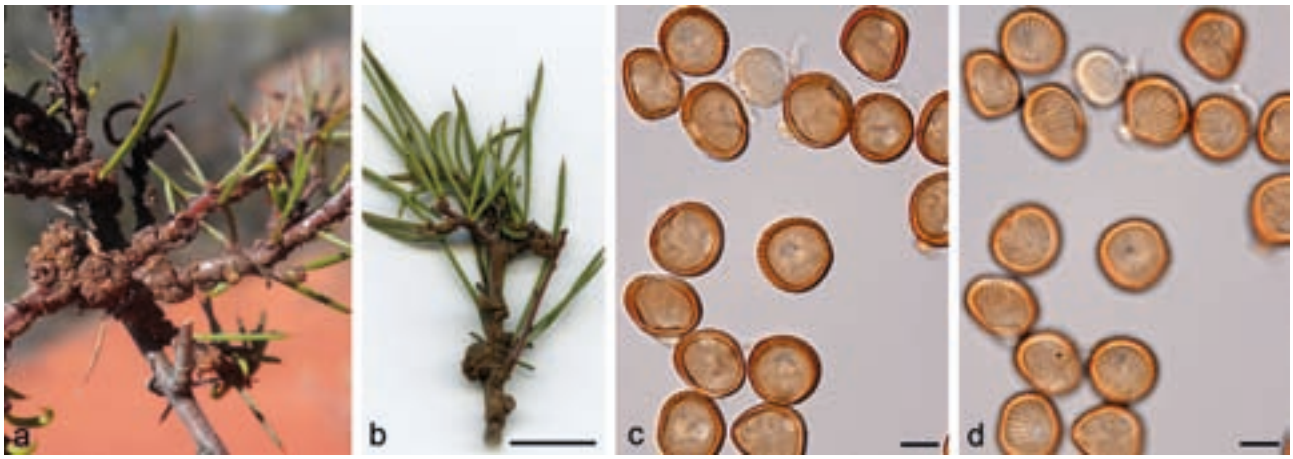

Fig. 18 *Uromycladium tetragonophyllae* on *Acacia tetragonophylla* (BRIP 57748). a–b. Galls on branches; c. teliospores (equatorial view); d. teliospores (surface view). — Scale bars: b = 1 cm; c–d = 10 µm.

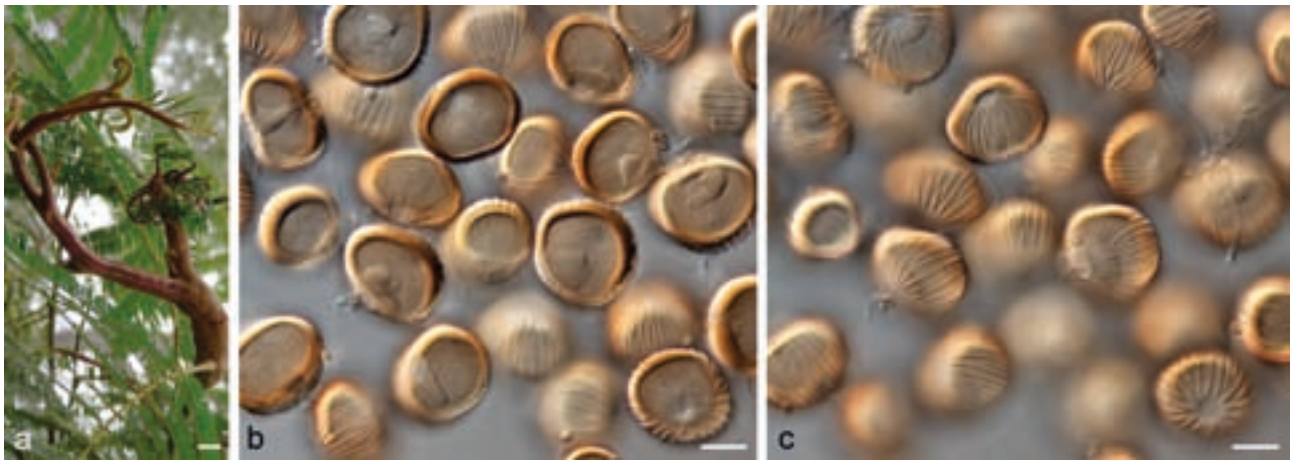

Fig. 19 *Uromycladium woodii* on *Paraserianthes lophantha*. a. Galls on stems (image provided by A.R. Wood, taken at Boranup Road, Leeuwin Naturaliste National Park, Western Australia); b. teliospores (surface view) (BRIP 61600); c. teliospores (equatorial view) (BRIP 61600). — Scale bars: a = 1 cm; b–c = 10 µm.

Galls on stems and branches, round to elongated, up to 3 cm diam. *Spermogonia* 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 for *P. lophantha* (Impson et al. 2011), and efforts to establish it are underway (A.R. Wood pers. comm.). *Uromycladium tepperianum* s.lat. was recorded on *P. lophantha* ssp. *montana* from Java, Indonesia (Magnus 1892, Boedijn 1959), although it has not been recorded there or on this plant recently. The relationship of this rust on *P. lophantha* ssp. *montana* in Indonesia to *U. woodii* should be determined, i.e., do they represent one widely distributed species or two distinct species. These rusts on *P. lophantha* represent a host jump from *Acacia* to *P. lophantha*, a sister species to *Acacia* (Brown et al. 2011).

DISCUSSION

The present study defined *U. tepperianum* s.str. by host range and a phylogenetic species concept. An epitype specimen of *U. tepperanium* was designated to provide future nomenclatural stability for this taxon. The phylogenetic hypothesis in this study has confirmed the observations by Samuel (1924), 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 teliospore 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. morrisii*, *U. murphyi* and *U. paradoxae*. This may reflect the intraspecific diversity of their host species, such as in *A. saligna* for *U. morrisii* (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*, *Lycopodifoliae* 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. falcatariae* 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 *Endoraecium*, 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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