

## UROMYCLADIUM NARACOORTENSIS, A NEW SPECIES OF RUST FUNGI (UREDINALES) FROM AUSTRALIA, WITH NEW OBSERVATIONS ON DESCRIBED UROMYCLADIUM SPECIES\*

REINHARD BERNDT

**Abstract.** *Uromycladium naracoortensis* R. Berndt is described as a new species on *Acacia irrorata* Sieber ex Spreng., *A. cf. iteaphylla* Benth. and *A. mearnsii* De Wild. from Australia. The species is microcyclic and comprises spermogonia and telia. It differs from similar rusts in teliospore morphology and life cycle. The spermogonia developed under the host cuticle and lacked sterile cells bounding the hymenium. New observations are reported concerning the spore morphology and ontogeny, life cycle and haustorial morphology of *U. notabile* McAlpine, *U. robinsonii* McAlpine and *U. fusisporum* (Cooke & Masee) Savile. Teliospore ontogeny was studied in *U. notabile* and *U. tepperianum* (Sacc.) McAlpine. Fertile teliospore cells were formed in sympodial succession by proliferation of the pedicels. In *U. maritimum* McAlpine it was observed that spore pedicels could transform into cyst-like cells. The life cycle of *U. robinsonii* was found to be variable; spore states occurred in different combinations, indicating that the rust can present itself as micro-, demi- or macrocyclic. *Uromycladium naracoortensis* and *U. notabile* revealed M-haustoria with an inflated proximal and a filiform distal part. In *U. robinsonii*, worm-like D-haustoria occurred connected with haustorial mother cells which contained the nuclei.

**Key words:** *Acacia*, host specificity, life cycle, spermogonium, teliosporogenesis

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### INTRODUCTION

The rust genus *Uromycladium* was erected by McAlpine (1905) for a number of rust fungi characterized by septate teliospore pedicels bearing 1–3 one-celled fertile spore cells and sometimes a strongly swelling hygroscopic cyst. The species are distinguished mainly by teliospore morphology (number of fertile teliospore cells, presence or absence of hygroscopic cysts) and characters of the aecio- and/or urediniospores. At present eight species are recognized, *U. acaciae* (Cooke) P. Syd. & Syd. (= *U. bisporum* McAlpine), *U. alpinum* McAlpine, *U. fusisporum* (Cooke & Masee) Savile, *U. maritimum* McAlpine, *U. notabile* McAlpine, *U. robinsonii* McAlpine, *U. simplex* McAlpine, and *U. tepperianum* (Sacc.) McAlpine. *Uromycladium cubense* Arthur & J. R. Johnst. was

excluded from *Uromycladium* by Arthur (1922) and made the type species of the genus *Diabole* Arthur.

Apart from teliospore morphology, *Uromycladium* species share a number of characters that indicate that the genus is monophyletic. All known species are autoecious on *Acacia* Mill. or a few *Paraserianthes* I. C. Nielsen species (Mimosaceae), the aecio- and urediniospores are typically more or less fusiform and provided with equatorial germ pores, and the indigenous geographical distribution is centered in Australia with some additional locations in the southern Pacific region (Old *et al.* 2000). A DNA-taxonomic study by Wingfield *et al.* (2004) including *U. notabile*, *U. tepperianum* and an undetermined species indicated as well that the genus is monophyletic. The placement of *Uromycladium* in the system of Uredinales is uncertain, however. The presence of compound teliospores composed of separate one-celled fertile

\* I dedicate the present work to the eminent mycologist Professor Tomasz Majewski, an authority on rust fungi, on the occasion of his 70<sup>th</sup> birthday.

cells and sterile cysts led McAlpine (1905) to assume that it represented a link between *Uromyces* (Link) Unger and *Ravenelia* Berk. Dietel (1921) noted the morphological similarity between *Uromycladium* and *Pileolaria* Castagne and hypothesized a relationship between the two genera. Later he placed them together in the tribe Raveneliae (Dietel 1928). In the phylogram presented by Wingfield *et al.* (2004), *Uromycladium* (*U. notabile*, *U. tepperianum*, *U. sp.*) fell into the large and very heterogeneous 'Clade 2' next to *Gymnosporangium* R. Hedw. (*G. clavipes* Cooke & Peck, *G. juniperi-virginianae* Schwein.). In contrast, Aime (2006) found *Pileolaria* (*P. brevipes* Berk. & Ravenel) to be sister to *Uromycladium* (*U. fusisporum*) in a study based on nuclear 18S and 28S rDNA sequences. However, in both of these studies the type species of the respective genera were not included and thus their phylogenetic position is still unresolved.

The present work was initiated by the discovery of a new species of *Uromycladium* in Australia which is described here as *U. naracoortensis* R. Berndt. In the course of the determination process, similar species were investigated and compared. This study yielded a number of new observations on the morphology, ontogeny and life cycle of these species, which are presented to complement the existing descriptions.

## MATERIAL AND METHODS

The studied specimens are listed with the respective rust species, and for each one the spore states occurring are given. The spore states are designated according to their position in the rust life cycle. Aecia resembling the anamorph genus *Uredo* Pers. are called 'Uredo-like aecia', indicated by the Roman numeral I. Uredinia are indicated by II, telia by III and spermogonia by 0. Roman numerals are used here for brevity only and one should keep in mind that they were originally adopted to designate morphological types of sori.

Spores and hand sections obtained from herbarium material were mounted in lactophenol on microscope slides and gently heated to facilitate soaking of the fungal structures and host tissue. The preparations were examined with an Olympus BX51 compound microscope equipped with a ColorView IIIu camera. The

Cell<sup>^</sup>B software package (Software Imaging System GmbH) was used to capture and edit micrographs. Normally 40–50 but at least 30 spores were measured for each preparation. The arithmetic means are given in brackets.

Names of herbaria are cited by their acronyms according to *Index Herbariorum* (Holmgren *et al.* 1990).

## RESULTS

### *Uromycladium naracoortensis* R. Berndt, *sp. nov.*

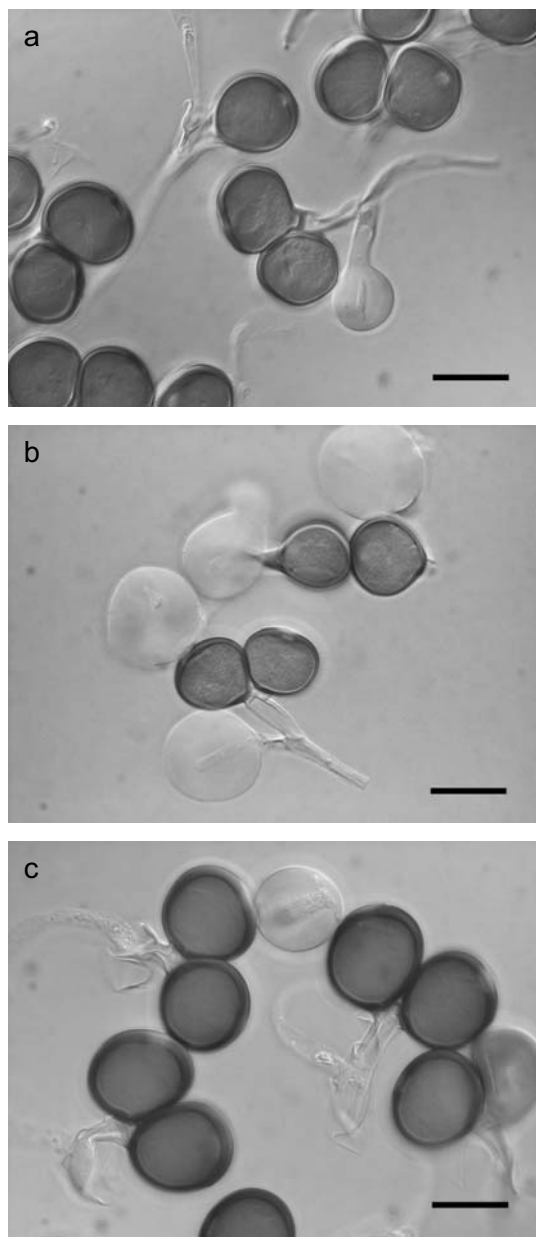
Figs 1 & 2

*Ab* *Uromycladio* maritimo *et* *U. alpino* *differt* *vita* *microcyclica* *et* *teliosporis* *minoribus* [*18–22* × *18–23* μm (*19.9* × *20.5* μm)] *tenu* *ca* *1.5* μm *crasso* *tunicatis*; *in* *U. bisporo*, *species* *microcyclica* *bisporata* *item*, *cystae* *absunt*. *In* *Acacia* *cf.* *iteaphylla* *et* *Acaciis* *speciebus* *crecens*.

TYPE: AUSTRALIA, VICTORIA: Naracoorte Caves, car park, *ca* 37°02'08"S/140°47'00"E, on *Acacia* *cf.* *iteaphylla* Benth., 2 Nov. 2009, *leg.* V. Faust-Berndt & R. Berndt (HOLOTYPE: MEL; ISOTYPE: ZT Myc 2091; 0, III).

ETYMOLOGY: Naracoorte Caves, Victoria, site of type collection.

Spermogonia densely crowded in small groups on dark green to olivaceous spots on pods, phyllodes and (more rarely) twigs, more or less dark brown, hemispherical, subcuticular with a ± flat hymenium lacking bounding structures ('group 1' / 'type 3'), often uplifted together with the epidermis ruptured by developing telia. Telia closely associated with spermogonia or not, bullate, round and discrete or often confluent and more or less ring-like around the spermogonia, subepidermal, early naked, rich dark brown to greyish brown, subpulverulent to fibrous, generally covered by a smooth, film-like amorphous and translucent pellicle hindering dispersal of spores; teliospores compound with two adjacent fertile one-celled spore cells and a single sterile proximal cyst, spore cells transversely broadly ellipsoid, obovoid or subpyriform, 19–25(–28) × 20–26 μm (21.7 × 22.7 μm) [on *A. cf. iteaphylla*], 18–22 × 18–23 μm (19.9 × 20.5 μm) [on *A. mearnsii*], spore wall smooth, light chestnut brown, *ca* 1.5 μm



**Fig. 1.** a – *Uromycladium naracoortensis* R. Berndt (ZT Myc 2091, type), teliospores. b – *U. naracoortensis* (BRIP 14256, paratype), teliospores. Note stalked cyst cells with differently swollen cell wall. Fertile teliospore cells are thin-walled, and caps over germ pores are lacking or at most inconspicuous. c – *U. maritimum* McAlpine (ZT Myc 2093), teliospores. Scale bars = 20  $\mu$ m.

thick, at apex to 3  $\mu$ m, single germ pore apical, lacking cap; pedicel colorless, thin-walled, col-

lapsing, with septum 10–15  $\mu$ m below fertile spore cells, bearing a stalked, swelling hygroscopic cyst directly proximal to the septum. With M-haustoria comprising a bulbous proximal part and a long, filiform, more or less twisted process.

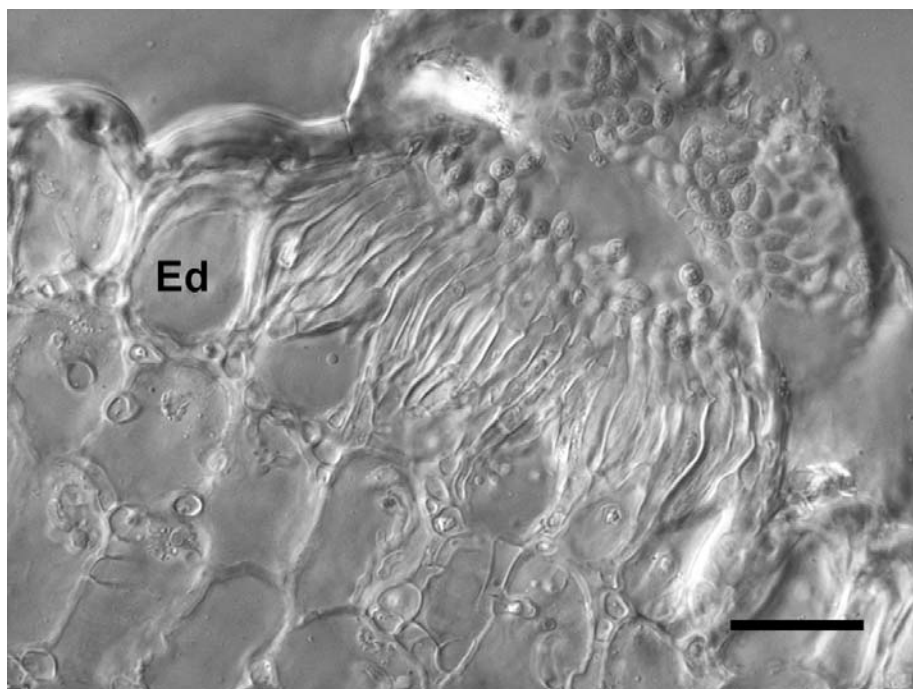
ADDITIONAL MATERIAL EXAMINED: AUSTRALIA, VICTORIA: Grampians Mts., picnic area near ‘Billimina’ aborigine shelter, 37°15'04.4"S/142°16'42.3"E, on *A. mearnsii* De Wild., 29 Oct. 2009, leg. V. Faust-Berndt & R. Berndt (ZT Myc 2092; 0, III). QUEENSLAND: Summit, on *A. irrorata* Sieber ex Spreng., 29 Dec. 1983, leg. K. C. Goulter (BRIP 14256; III).

*Uromycladium maritimum* – AUSTRALIA, VICTORIA: Cape Otway, coastal scrub near Cape Otway Lighthouse, on *A. longifolia* (Andrews) Willd. subsp. *sophorae* (Labill.) Court, 2 Nov. 2009, leg. V. Faust-Berndt & R. Berndt (ZT Myc 2093; 0, [I], III). Grampians District, Flat Top Rock area, 37°08'31"S/142°21'45"E, on *A. longifolia* subsp. *longifolia*, 30 Aug. 1962, leg. L. D. Williams 1488a (AD 33904; I, spermogonia not seen). TASMANIA, Mersey Bluff, on *A. longifolia*, 18 Jan. 1906, leg. G. H. Robinson (Sydow, Uredineen no. 2051, ZT Myc 2993; 0, I, III).

*Uromycladium naracoortensis* is similar to *U. maritimum* and *U. alpinum*, whose teliospores are composed of two fertile cells and a cyst as well. They differ in the presence of *Uredo*-like aecia and larger fertile teliospore cells (Fig. 1). *Uromycladium bisporum* and *U. notabile* agree with *U. naracoortensis* in their microcyclic life cycle but are readily distinguishable as their teliospores lack cysts. In addition, *U. notabile* has three verrucose fertile teliospore cells.

The spermogonia of *U. naracoortensis* are subcuticular with a more or less flat or slightly concave hymenium which is not bounded by sterile structures (Fig. 2). The epidermal cells are wedged apart by the subhymenial mycelium. Spermogonia occurred abundantly on *Acacia* cf. *iteaphylla*, while they were only sparingly present on *A. mearnsii* and lacking on *A. irrorata*. These differences could depend on the host species, though one should keep in mind that spermogonia may be evanescent and are sometimes shed with torn and flaking-off host tissue.

At present *U. naracoortensis* is known from *A. irrorata*, *A. cf. iteaphylla* and *A. mearnsii*. These



**Fig. 2.** *Uromycladium naracoortensis* R. Berndt (ZT Myc 2091, type). Spermogonium with flat, subcuticular hymenium. The epidermal cells (Ed) are wedged apart by hyphal bundles. Scale bar = 20  $\mu$ m.

hosts comprise species with phyllodes (*A. iteaphylla*) or composed-leaved adult foliage. The similar rust species *U. maritimum* is only known on *A. longifolia*, while *U. alpinum* appears to have a wider host spectrum with reports from *A. buxifolia* A. Cunn., *A. dallachiana* F. Müll., *A. dealbata* Link, *A. decora* Rchb., *A. implexa* Benth., *A. linifolia* (Vent.) Willd., *A. spectabilis* A. Cunn. ex Benth. and *A. terminalis* (Salisb.) J. F. Macbr. (McAlpine 1906; Morris *et al.* 1988; Old *et al.* 2002). It cannot be ruled out that single reports of these refer to *U. naracoortensis*.

### *Uromycladium robinsonii* McAlpine

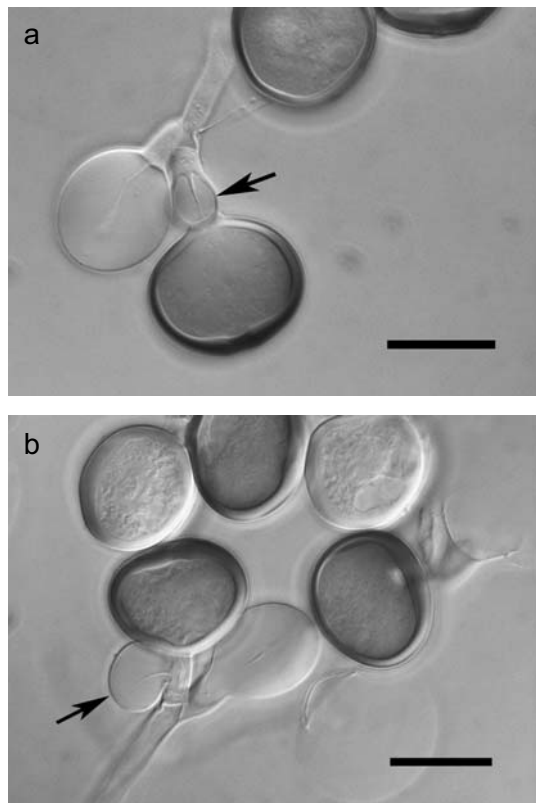
Annales Mycologici 3: 306. 1905.

MATERIAL EXAMINED: AUSTRALIA, VICTORIA: Great Otway National Park, at the car park of the Mait's Rest hiking trail, ca 38°45'S/143°33'E, on *Acacia melanoxylon* R. Br., 1 Nov. 2009, leg. V. Faust-Berndt & R. Berndt (ZT Myc 2108; 0, [I], III). Great Otway National Park, Beech Forest, hiking trail to Little Aire Falls, ca 38°40'S/143°30'E, on *A. melanoxylon*,

31 Oct. 2009, leg. V. Faust-Berndt & R. Berndt (ZT Myc 2126; 0, I, III). Otway Ranges, Skenes Creek Road (C 119), at entrance to Whispering Willow farm, 38°41'27.0"S/143°42'43.8"E, on *A. melanoxylon*, 31 Oct. 2009, leg. V. Faust-Berndt & R. Berndt (ZT Myc 2117; 0, [I], III). Otway Ranges, E of Beech Forest, Beech Road, 38°37'59.7"S/143°36'43.8"E, on *A. melanoxylon*, 31 Oct. 2009, leg. V. Faust-Berndt & R. Berndt (ZT Myc 2118; 0, I, III). Northwestern Grampians Mts, campground at Smith Road SW of Lake Wartook, at little creek E of camp ground, 37°06'29"S/142°25'29"E, on *A. melanoxylon*, 28 Oct. 2009, leg. V. Faust-Berndt & R. Berndt (ZT Myc 2125; [0, I, II], III).

Teliospores of *U. robinsonii* have a single fertile spore cell and a hygroscopic cyst cell. Many of the teliospores present in ZT Myc 2108 were peculiar by the partial or entire transformation of the stalks of the fertile spore cells into cysts (Fig. 3). This may be a morphological anomaly and was not observed in the other investigated specimens of the same species.

All but one of the specimens (ZT Myc 2125) revealed spermogonia, associated *Uredo*-like aecia



**Fig. 3.** a & b – *Uromycladium robinsonii* McAlpine (ZT Myc 2108). Teliospores with fertile spore cells and ordinary cysts; the stalk cells (arrows) show signs of transition to cyst cells. Scale bars = 20 µm.

and telia indicating a demicyclic life cycle. In ZT Myc 2125, a few uredinia were found associated with telia in addition to spermogonia accompanied by *Uredo*-like aecia. Occasionally telia developed from old aecia or (rarely) instead of aecia. These observations suggest that the life cycle of *U. robinsonii* is unstable and can be demi-, macro- or microcyclic.

Host cells located in the vicinity of telia revealed D-haustoria with a very slender, worm-like haustorial body. In all haustoria observed, two nuclei were present which remained in the haustorial mother cell and did not enter into the body.

*Uromycladium robinsonii* is apparently restricted to *A. melanoxylon* ('Black Wattle'), an important timber tree in moister parts of south-eastern and eastern Australia.

### *Uromycladium notabile* McAlpine

*Annales Mycologici* 3: 309. 1905.

**MATERIAL EXAMINED:** *Uromycladium notabile*. – AUSTRALIA, SOUTH AUSTRALIA: Yorke Peninsula, Warooka – Sturt Bay road, near Sturt Bay, on *A. ligulata* A. Cunn. ex Benth., 18 Oct. 1992, leg. T. W. May (MEL 270087; III). VICTORIA: Murrumbidgee Ranges, near Kergunyah, on *A. dealbata*, 5 Jan. 1905, leg. G. H. Robinson (ZT Myc 2219; 0, I). Grampians Mts, Victoria Valley, along road to Cavenish, 37°30'56.6"S/142°15'22.3"E, on *A. cf. mearnsii*, 29 Oct. 2009, leg. V. Faust-Berndt & R. Berndt (ZT Myc 2115; III).

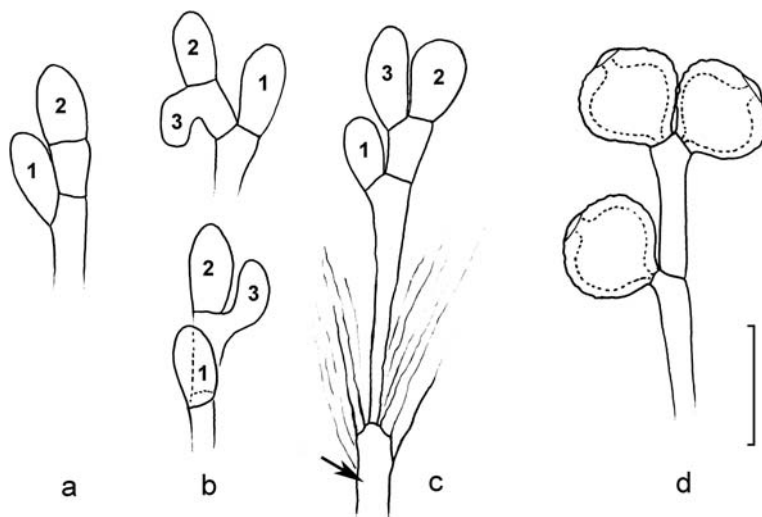
*Endoraecium digitatum* (G. Winter) M. Scholler & Aime. – AUSTRALIA, SOUTH AUSTRALIA: W of Gawler, along road to Mallala, 34°33'59.5"S/138°43'06.3"E, on *A. notabilis* F. Müll., 16 Oct. 2009, leg. V. Faust-Berndt & R. Berndt (AD – EPITYPE, ZT Myc 2100 – ISOEPITYPE; II, III). Eyre Peninsula, on roadside ca 1 km S of Cummins (ca 55 km NNW of Port Lincoln), 26 Aug. 1967, leg. D. J. E. Whibley 1931 (AD 96741090; [0, I], II, [III]).

*Uredo notabilis* F. Ludw. – AUSTRALIA, SOUTH AUSTRALIA: Southern Lofty Ranges, Roseworthy Scrub, 11 Sep. 1889, leg. J. G. O. Tepper (MEL 1054135 –TYPE?, sub *Uromycladium notabile* McAlp.; 0, I).

*Uromycladium tepperianum*. – AUSTRALIA, NEW SOUTH WALES, unknown provenance, on *A. pendula* A. Cunn. ex G. Don, 11 Jan. 1977, leg. L. D. Williams 8903 (AD 33457; III).

*Uromycladium notabile* was described as demicyclic with spermogonia, uredinia (actually *Uredo*-like aecia) and telia (McAlpine 1905). The aecial state (= *Uredo notabilis* F. Ludw.) was recently shown to belong to *Endoraecium digitatum* (G. Winter) M. Scholler & Aime (Berndt, in press). Hence, *U. notabile* is microcyclic, not demicyclic as assumed. The species apparently is closely related to *U. tepperianum*, which has very similar teliospores composed of three ornamented fertile cells, evokes large galls on the hosts, and shares the microcyclic habit.

*Uromycladium notabile* revealed M-haustoria with an inflated proximal part which tapered into a filiform twisted process. Very similar haustoria were illustrated for *U. tepperianum* by Burges (1934) and observed in *U. naracoortensis* as well.



**Fig. 4.** *Uromycladium notabile* McAlpine (ZT Myc 2115), development of teliospores. Fertile teliospore cells are numbered in the order of their formation. a – Teliospore with two young spore cells. b – Two teliospores, each with two spore cells. The third spore cell (3) is being formed by an outgrowth of the pedicel of the apical spore cell. c – Stage with three young spore cells. The teliospore was formed by an elongated meristematic cell (arrow). Collapsed and disintegrating pedicels of detached teliospores remain on the meristematic cell, giving it a brush-like appearance. d – Mature teliospore with three fertile spore cells. Scale bar = 25  $\mu$ m.

Teliospores of *U. notabile* comprise three spore cells but lack sterile cysts. Many such teliospores developed on elongated meristematic cells of the hymenium (Figs 4c & 5). The pedicels of detached teliospores remained on the meristematic cells, giving them a brush-like appearance. The spore cells were produced in a sympodial sequence (Fig. 4): a teliospore pedicel terminated its apical growth with the formation of the first teliospore cell. After that the pedicel budded out laterally and cut off a side branch which overtopped the first spore cell and formed a second one at its tip. The third spore cell sprouted from the pedicel of the second spore cell and developed adjacent to the latter. Teliospores of *U. tepperianum* were observed to develop in the same manner.

*Uromycladium notabile* is known with certainty from *A. dealbata*, *A. decurrens* Willd., *A. elata* A. Cunn. ex Benth. and *A. ligulata*. *Acacia mearnsii* is a probable host plant. Specimens that bear aecia and/or uredinia and stem from hosts shared with *Endoraecium digitatum* belong to the latter or represent double infections if teliospores of *U. notabile* are present as well.

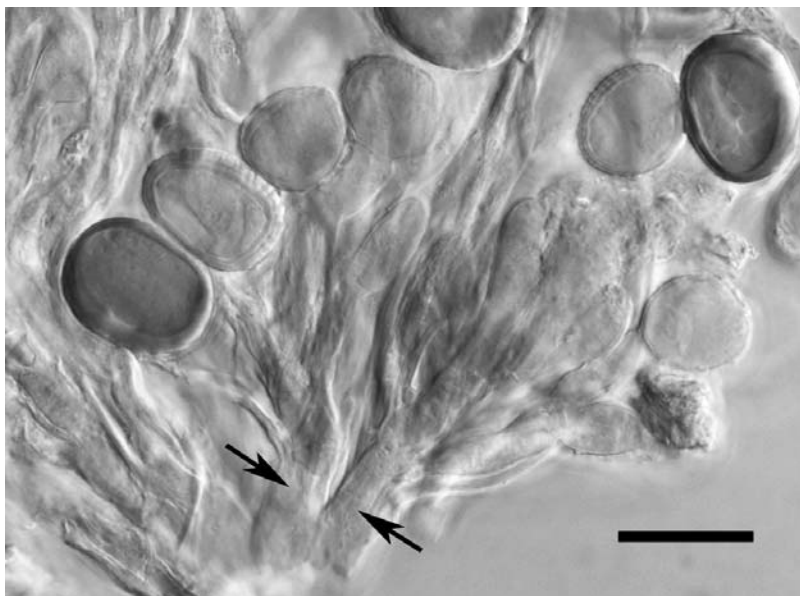
### *Uromycladium fusisporum* (Cooke & Masee) Savile

Mycologia **63**: 1091. 1971.

? *Uromyces fusisporus* Cooke & Masee, Grevillea **16**: 2. 1887.

MATERIAL EXAMINED: AUSTRALIA, VICTORIA: Lowan Mallee region, Dimboola, on *A. neriifolia* A. Cunn. ex Benth., 5 Dec. 1895, leg. F. M. Reader s.n. (MEL 1054067; II, III). Without locality, probably Australia: On cultivated *A. salicina* Lindl., collector and collection date unknown (MEL [labelled 'Type'] 1054154; II, III).

*Uromycladium fusisporum* is unique in the genus by having a septate teliospore pedicel bearing a single fertile teliospore cell at the apex (Fig. 6b). McAlpine (1906) retained this rust fungus in *Uromyces* though he emphasized that 'the nature of the teliospores and the presence of a septum in the stalk was so suggestive of *Uromycladium* that the material was specially examined to see if more than one spore was borne on a stalk ...'. Specimens kept in MEL, among them a type, revealed uredinia



**Fig. 5.** *Uromycladium notabile* McAlpine (ZT Myc 2115), bundles of teliospores in different stages of development on elongated meristematic cells (arrows). Scale bar = 20  $\mu$ m.

and telia. To the best of my knowledge, no other spore states are known in this species.

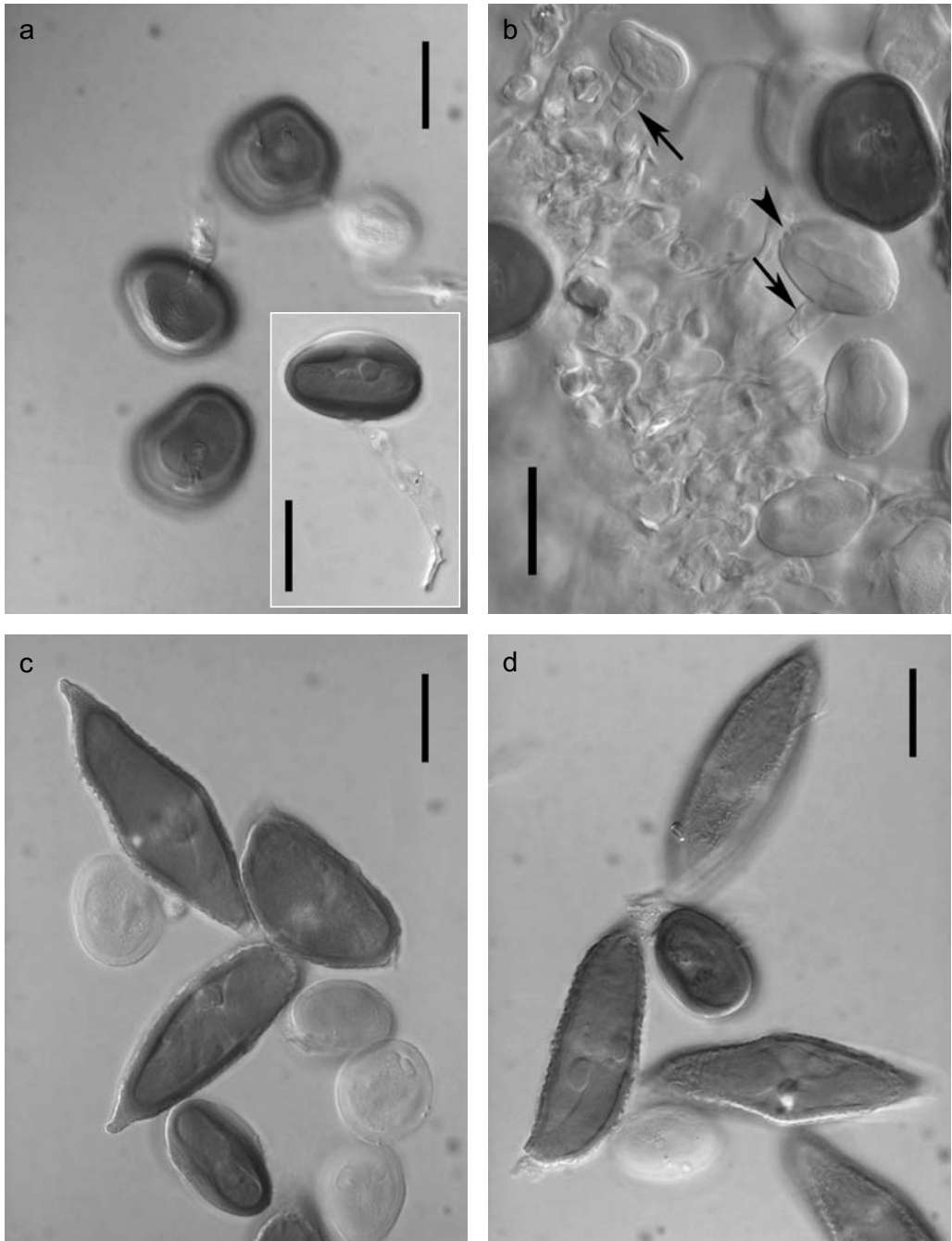
The teliospores were conspicuously transverse-ellipsoid and had an apical germ pore capped by a broad subhyaline papilla (Fig. 6a, inset). The spores were very finely rugulose on their proximal and distal sides but rather conspicuously rugose or rough around the equator (Fig. 6a, b). The urediniospores were rugose as well (Fig. 6c, d) rather than verrucose as is described in the literature (McAlpine 1906). Teliospores and urediniospores occurred intermixed and were produced on elongated basal meristematic cells similar to the ones observed in *U. notabile* and *U. tepperianum*.

## DISCUSSION

**SPECIES RICHNESS AND HOST SPECIFICITY.** Together with the newly described *U. naracoortensis* the genus *Uromycladium* comprises nine species which are biologically restricted to members of the genus *Acacia* and a few *Paraserianthes* spp. *Uromyces discoideus* Racib., described from Java on *Acacia* sp., might represent an additional *Uromycladium* sp. according to the description given

by Raciborski (1909). Geographically the genus is restricted to Australasia (Old *et al.* 2002). Records from outside this region most likely testify to accidental anthropogenic spread (Morris *et al.* 1988) or deliberate release as bio-control agents (Morris 1997).

In Australia these nine *Uromycladium* species contrast in number with the more than 1000 native species of *Acacia* (Maslin *et al.* 2003; Anonymous 2010), giving the low ratio of one *Uromycladium* sp. on about 110 potential *Acacia* hosts. Rust fungus-host-ratios can vary considerably depending on the host taxa involved and the region of the world considered (Berndt 2008), and the differences are very difficult to explain. One can speculate about the meaning of the low ratio in the case of *Uromycladium*. It could indicate, for example, that many species are still unknown and remain to be discovered in Australia. This is not very probable given the relatively good knowledge of the Australian mycobiota. It could also mean that the presently distinguished morpho-species represent a higher number of biologically specialized forms which differ little or not in morphology and which have not been recognized hitherto. As



**Fig. 6.** *Uromycladium fusisporum* (Cooke & Masee) Savile (a, c & d – MEL 1054154; b – MEL 1054067). a – Teliospores, showing finely rugulose- verruculose surface. Inset shows a spore in optical section, revealing the depressed-globose shape and the broad, conspicuous cap covering the apical germ pore. b – Telium with young teliospores. Arrows indicate short sterile cells intercalated between pedicel and fertile teliospore cell. The equator of the teliospores is more conspicuously rugose (arrowhead). c & d – Urediniospores in optical section and with focus on spore surface, showing the rugulose ornament.



far as is known, different *Uromycladium* species exhibit different host specificity. While species like *U. acaciae*, *U. maritimum* and *U. robinsonii* appear to be limited to a single or a few host species, others have a much wider host range, such as *U. tepperianum*, the champion with more than 100 recorded *Acacia* hosts. Burges (1934) suspected the presence of 'physiological strains' in *U. tepperianum* from field observations, and Morris (1987) found by inoculation experiments that acacias were more susceptible to isolates of *U. tepperianum* collected from the same *Acacia* species than to isolates from other species. This biological specialization went along with subtle morphological differences, and Morris (1987) concluded that *U. tepperianum* comprises a number of *formae speciales*. These results support the suggestion that more *Uromycladium* species exist in Australia and that it is worth collecting specimens from a broad geographic and host range for morphological and molecular investigation and infection experiments.

**MORPHOLOGY AND LIFE CYCLE.** All known *Uromycladium* species are autoecious and most of them pass through a shortened life cycle. *Uromycladium alpinum*, *U. maritimum* and *U. simplex* are demicyclic, while *U. acaciae*, *U. notabile* and *U. tepperianum* are microcyclic. Until recently *U. notabile* was considered demicyclic but the aecial state was shown to belong to the life cycle of *Endoraecium digitatum*. In *U. fusisporum*, spermogonia are unknown, to the best of my knowledge. Thus, the *Uredo*-like sori probably represent the uredinal state, and *U. fusisporum* may turn out to be macrocyclic. *Uromycladium robinsonii* was unusual as it revealed an unstable life cycle and showed itself to be either demi-, macro- or microcyclic. It is interesting to note that another essentially Australian/Pacific rust genus, *Endoraecium*, comprises a number of species as well that exhibit a variable life cycle (Berndt, in press). The plasticity of the life cycle is likely to reflect adaptation to an unstable environment, but field data are lacking to substantiate this suggestion.

**TELIOSPOROGENESIS.** Teliospores of *Uromycladium* are complex and composed of a slender stalk

bearing one-celled fertile spore cells and, in some species, sterile hygroscopic cyst cells. The cysts and spore cells are homologous and spores have sometimes been observed to replace cysts (Burges 1934). Here I report that pedicels also can have the potential to transform into cyst cells. This was observed in a specimen of *U. robinsonii*, where the pedicels of the fertile spores showed all kinds of transitions towards cysts.

Burges (1934, 1935) studied teliosporogenesis in *U. maritimum* and *U. tepperianum*. He did not describe the sequence of spore formation but his illustrations suggest that spore cells and/or cysts were formed in basipetal succession; that is, the most distal spore cells were the oldest ones. I investigated teliospore ontogeny in *U. notabile* and *U. tepperianum*, and found, contrary to Burges' observations, that the fertile spore cells were produced in a sympodial manner, rendering the most proximal spore cell the oldest one. In both cases the 'pedicels' proliferate and show sporogenous activity. 'Proliferating pedicels' also occur in Raveneliaceae, for example in *Ypsilospora* Cummins (unpublished results) and probably *Diabole*. I am unaware of 'proliferating pedicels' in other rust families.

**SPERMOGONIA.** In *Uromycladium naracoortensis*, spermogonia developed under the cuticle, formed small definite hymenia, and lacked sterile bounding cells. These features place the spermogonia in 'type 3' of 'group 1' according to the classification scheme established by Hiratsuka and Cummins (1963). This finding is in accordance with Sydow and Sydow (1915) and McAlpine (1906). The latter described subcuticular spermogonia in *U. maritimum* and pointed out that the spermogonia of *Uromycladium* lacked 'paraphyses at mouth'. Hiratsuka and Cummins (1963) stated that *U. fusisporum*, *U. robinsonii* and *U. simplex* had 'type 5' spermogonia. Such spermogonia are subepidermal and bounded by sterile cells which overarch the hymenium and normally reach the ostiolum. According to *Illustrated Genera of Rust Fungi* published by the same authors, spermogonia of *Uromycladium* are 'type 5 or perhaps sometimes type 7', that is, subcuticular in origin

(Cummins & Hiratsuka 2003). Burges (1934) observed subcortical spermogonia in *U. tepperianum* and remarked that a few of the elongated cells of the hymenium remained sterile and 'form a very poorly defined band of periphyses, which are never sufficiently developed to project as hairs.' The observed differences indicate that *Uromykladium* species form spermogonia at different positions in the host tissue and that these positions may be species-specific. Spermogonial morphology is thought to indicate the systematic position of a rust genus. The observations regarding the presence or absence of sterile bounding elements are not conclusive, however, and would allow *Uromykladium* to affiliate with a number of rust families.

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