

Taxonomic revision of *Endoraecium digitatum* (rust fungi, Uredinales) with description of four new species from Australia and Hawaii

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Abstract *Endoraecium digitatum* was described on *Acacia notabilis* from South Australia but has been reported on more than 20 *Acacia* spp. throughout the Australian and the Pacific regions. Results are presented on the micro-morphology and taxonomy of *E. digitatum* from different *Acacia* species and geographic provenience. *E. digitatum* revealed a highly non-uniform morphology and is considered a species complex comprising at least six morphologically distinct rust fungi. The name *E. digitatum* could not be applied to any of the distinguished species by a comparison with available type specimens or the original description as types were depleted and the diagnosis not detailed enough. An epitype is therefore proposed to supplement the lectotype of *E. digitatum* selected here and to allow delimitation of the new species *E. parvum*, *E. violae-faustae* and *E. walkerianum* from Australia, and *E. kauaianum* from Hawaii. *Endoraecium phyllodiorum* is shown to be different from *E. digitatum* and is proposed as a new combination for *Uromyces phyllodiorum*. Specimens from Hawaii formerly considered to be *E. digitatum* represent two species, *E. kauaianum* and another one preliminarily assigned to *E. phyllodiorum*. The investigated species show differences between and plasticity within their life cycles. *E. parvum*, *E. violae-faustae* and *E. kauaianum* are macrocyclic. In *E. walkerianum*, only demicyclic specimens were found, while demi- and macrocyclic specimens occurred in *E. digitatum*. *E. phyllodiorum* revealed variable combinations of spore states as well and comprised macro-, demi- and microcyclic life cycle variants. Life cycle variants were considered to express specific variability and were not

used to create new taxa. The present results indicate that members of the *E. digitatum* complex in Australia are not narrowly host specific. Keys are presented for the Australian and Hawaiian species. Taxonomical novelties: *Endoraecium kauaianum* R. Berndt, *Endoraecium parvum* R. Berndt, *Endoraecium phyllodiorum* (McAlp.) R. Berndt, *Endoraecium violae-faustae* R. Berndt and *Endoraecium walkerianum* R. Berndt.

Keywords *Acacia* · *Racospermyces* · Life cycle · Epitype · Species complex

Introduction

The rust fungus *Uromyces digitatus* G. Winter was described on *Acacia notabilis* F. Müll. from South Australia (Winter 1886). It was later regarded as a member of the genus *Pileolaria* Castagne (Dietel 1921; sub *P. phyllodiorum*) or *Atelocauda* Arth. & Cummins (Cummins and Hiratsuka 1983). Walker (2001) erected the new genus *Racospermyces* J. Walker to accommodate *U. digitatus* and five other species, four of which had been assigned to *Atelocauda*.

In 1984, Hodges and Gardner (1984) reported two endocyclic rust fungi with *Uredo*-like teliospores on *Acacia* spp. from Hawaii, *Endoraecium acaciae* Hodges & D. Gardner and *E. hawaiiense* Hodges & D. Gardner. They hypothesized them to be derivatives of the morphologically similar *U. digitatus* but placed them in a new genus, *Endoraecium* Hodges & D. Gardner. Scholler and Aime (2006) presented further evidence for a close relationship between *U. digitatus* and *Endoraecium* based on combined sequence data of the LSU and SSU region of nuclear DNA. Regarding *Racospermyces* and *Endoraecium* as congeners, Scholler and Aime (2006) stated that the name *Endoraecium* had priority over *Racospermyces* and recombined all

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known *Racospermyces* species into *Endoraecium*: *E. bicinctum* (McAlp.) M. Scholler & Aime and *E. tierneyi* (J. Walker & R.G. Shivas) M. Scholler & Aime, only known from Australia, *E. angustiphylloidium* (D. Gardner) M. Scholler & Aime and *E. koeae* (Arth.) M. Scholler & Aime, only known from Hawaii, *E. digitatum* (G. Winter) M. Scholler & Aime reported from Australia, New Caledonia, Hawaii and East Asia, and *E. hyalosporum* (Sawada) M. Scholler & Aime that is distributed in China, Japan and Taiwan. All known *Endoraecium* species are autoecious and restricted to *Acacia* subgen. *Phyllodineae* (DC.) Seringe (= *Racosperma* C. Martius; comp. Pedley 1986) of Leguminosae (Walker 2001).

Endoraecium digitatum is a variable rust fungus. Hodges and Gardner (1984) described some morphological differences between aeciospores of *E. digitatum* from Kauai and other Hawaiian islands and noticed that the fungus induced either witches' brooms or hypertrophy of shoots, flowers and pods or large bullate swellings on phyllodes, according to geographic location and host. Similarly, Walker (2001) pointed out to a considerable morphological variability of *E. digitatum* in Australia and hypothesized that this rust fungus could represent a complex of closely related taxa that may not only differ morphologically but also in life cycle, host range and geographical distribution. Specimens of *E. digitatum* recently collected in Queensland by the author revealed characteristic differences as well, especially in the morphology of the aecio- and urediniospores, and were considered to belong to several distinct species.

The finding that rust fungi assigned to *E. digitatum* belong to different albeit very similar species, the reportedly broad host range of *E. digitatum* and its wide distribution including a disjunct area in the Hawaiian Islands, raises a number of questions. (1) What does authentic *E. digitatum* look like in detail? (2) Which of the different species discovered in Australia complies with *E. digitatum*? (3) Is *E. digitatum* indeed the same as *U. phyllodiorum* and *U. phyllodii* as McAlpine (1906) affirmed? And (4) do specimens from Hawaii assigned to *E. digitatum* really belong to this species?

It is the aim of the present paper to answer these questions, to clarify the identity of *E. digitatum* and to delimit and describe similar species. The work is based on numerous vouchers from different host plants and geographic provenience and resulted in the recognition of *E. digitatum* as a species complex comprising at least six species, among them four new ones.

Materials and methods

Spores and hand sections of herbarium material were mounted in lactophenol on a slide glass and gently heated to accelerate

soaking of the fungal structures. Preparations were examined with an Olympus BX51 light microscope and micrographs taken with a ColorView IIIu camera. The "Cell^B" software package (Software Imaging System GmbH) was used to capture micrographs and to measure details of spore walls and their ornamentation. Such measurements are given to 0.1 µm while measurements made by the use of an ocular micrometer scale are given to the nearest 0.5 µm. Forty to fifty spores, but at least 30, were measured routinely for each specimen and spore state; occasional lower numbers are mentioned in the descriptions. Arithmetic means are presented in brackets after the measurement ranges.

Teliospores were very variable. Their size and shape, the apical thickening and the shape, number and length of the apical processes were considered to describe them. Measurements of the teliospore length include the apical thickening but not the processes. In aecio- and urediniospores, spore size and shape, number and location of germ pores, features of the surface reticulum, shape and thickness of the spore apex, the morphology of the spore base and the thickness of the spore wall were analyzed. Measurements of spore size and wall thickness include the reticulate ornamentation.

Infected host leaves were scanned with a HP Scanjet 4890 flatbed scanner.

Investigated specimens are listed under the rust species. For each specimen the occurring spore states are noted. The sori are designated according to their position in the life cycle. Aecia looking like the anamorph genus *Uredo* 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 were used for brevity only and one should keep in mind that they had been established originally to designate morphological types of sori (comp. Hennen and Hennen 2000). The names of herbaria are abbreviated by their acronyms according to 'Index Herbariorum' (Holmgren et al. 1990); 'HeRB' stands for the author's herbarium. The Australian States or Territories are abbreviated ACT (Australian Capital Territory), NSW (New South Wales), NT (Northern Territory), QLD (Queensland), SA (South Australia), WA (Western Australia), and VIC (Victoria).

Taxonomy

Endoraecium digitatum (G. Winter) M. Scholler & Aime. Mycoscience 47:163 (2006) (Figs. 1, 2, 3 and 4).

≡ *Uromyces digitatus* G. Winter. Rev. Mycol. (Toulouse) 8:209 (1886). Basionym.

≡ *Atelocauda digitata* (G. Winter) Cummins & Hirats. f. Illustrated Genera of Rust Fungi, 2 ed.:81 (1983).

≡ *Racospermyces digitatus* (G. Winter) J. Walker. Australas. Mycol. 20:13 (2001).

= *Melampsora phyllodiorum* auct. McAlpine (1906). The rusts of Australia: p. 95, not Berk. & Broome. Trans. Linnean Soc. London, 2. ser., 2:67 (1882).

≡ *Uromyces phyllodiorum* McAlp. The rusts of Australia: p. 95 (1906) [as *U. phyllodiorum* (Berk. & Broome) McAlp.].

≡ *Pileolaria phyllodiorum* (McAlp.) Dietel. Ann. Mycol. 19:302 (1921) [as *P. phyllodiorum* (Berk. & Broome) Dietel].

= *Uromyces phyllodii* Cooke & Massee in Cooke. Grevillea 17:70 (1889) (as *U. "phyllodiae"*).

= *Uredo notabilis* Ludwig. Bot. Centralbl. 43:6 (1890).

= ?*Uredo gemmata* Pat. & Hariot. Bull. Soc. Mycol. France 20:84 (1905). Fide Sydow and Sydow 1915.

Endoraecium digitatum has been reported from Australia (McAlpine 1906), New Zealand (introduced; McKenzie 1998), Indonesia, Papua New Guinea, China (Walker 2001), New Caledonia (Huguenin 1966), and Hawaii (Gardner 1994) on at least 20 species of *Acacia* (e.g. McAlpine 1906, Old et al. 2000, Walker 2001). The type specimen was collected by JGO Tepper on *A. notabilis* near Gawler in South Australia.

The diagnosis given by Winter (1886) characterized the urediniospores as “ovatae vel ellipticae, aureo-fulvae, dense verrucosae, membrana apice interdum parum incrassata, 32–35 μm longae, 20–25 μm crassae” and the teliospores as “oblongo-cuneatae, in stipitem ... attenuatae, apice valde incrassatae et processus plures (3–6) digitiformes erectos vel divaricatos, saepe recurvatos, obtusos gerentes, primo aureae, demum expallentes, hyalinae, 50–56 μm longae, 14–18 μm crassae”. The sori were described as “Acervuli in centro maculae atrae, rotundatae vel orbicularium ...”. This description is not detailed enough to distinguish *E. digitatum* from similar species with certainty. The alleged wartiness of the urediniospores is a misinterpretation of the reticulate spore surface, and the figures given for the urediniospore length may not aptly characterize the real interval of spore length.

To assess the morphological characters in more detail available types of *E. digitatum*, *U. phyllodiorum*, and of *U. phyllodii* were investigated. The original material of *E. digitatum* kept in B and S either did not bear any rust (B 700014001) or was almost entirely depleted (SF35352) so that spore characters could not be assessed. Another specimen, B 700014002, may represent a fragment of the original collection but this could not be verified due to incomplete data on the label. Micrographs and a line drawing prepared from this specimen were kindly provided by J. Walker. They showed only old and compressed urediniospores and three teliospores (teliospores illustrated in Walker 2001, Fig. 22).

Because existing original material of *E. digitatum* is not useful any more for identification purposes, the question, what authentic *E. digitatum* looks like, cannot be answered satisfactorily. This means that none of the species distinguished in the *E. digitatum* complex can be identified as *E. digitatum* s. str. and that it is impossible to name the species which are different from it.

In this situation, the creation of an epitype is justified to settle the outlined problems. According to Article 9.7. of the “Vienna Code” (McNeill et al. 2006) “an epitype is a specimen or illustration selected to serve as an interpretative type when the holotype, lectotype, or previously designated neotype, or all original material associated with a validly published name, is demonstrably ambiguous and cannot be critically identified for purposes of the precise application of the name of a taxon ...”. In order to find an appropriate epitype of *E. digitatum* the type locality was visited and rust-infected *A. notabilis* collected. Furthermore, all specimens of *A. notabilis* kept in AD were scrutinized for the presence of *Endoraecium*. A specimen collected at the type locality is selected as epitype to supplement the lectotype of *E. digitatum* that is designated here as well:

Lectotypus hic designatus: Australia, SA: near Gawler, on *A. notabilis*, leg. JGO Tepper, 1 July 1885 (SF35352).

Epitypus hic designatus ad *E. digitatum* SF35352 (lectotypus): Australia, SA: W of Gawler, along road to Mallala, 34°33'59.5" S / 138°43'06.3" E, on *A. notabilis*, 16 Oct. 2009, leg. V. Faust-Berndt & R. Berndt (AD s. n., isoeotype ZT Myc 2100; II, III).

The following description is based on the epitype (for uredinia and telia) and other available specimens on *A. notabilis* listed below (for the remaining spore states).

Spermogonia on bullate, blister-like swellings or at least on hypertrophied areas of phyllodes together with aecia. Aecia *Uredo*-like, subepidermal, large and early naked, ochraceous, pulverulent; aeciospores pedicellate, ellipsoid to broadly ellipsoid, with rounded to conical apex and a short wedge-shaped rugose socket-like base or without socket-like base, 31–47.5 \times 20.5–29 μm (39.1 \times 24.3 μm ; in type of *U. notabilis* 40.7 \times 24.2 μm), spore wall golden-yellow, often slightly more deeply pigmented towards apex, 3–4 μm thick, at apex to 5 μm , asymmetrically thickened in equatorial region to 5–6 μm (asymmetric thickening is variable and not always easily visible depending on orientation of spores), germ pores 7–8 more or less equatorial, without caps, spore surface reticulate, meshes 1.6–2.9 μm (2.1 μm) diam. with rugulose bottom, separated by delicate, rather high irregular ridges which give spores an almost spinulose aspect in optical section. Uredinia on more or less unaltered parts of phyllodes, subepidermal, small, often partly overarched by the rigid epidermis, ferruginous and pulverulent; urediniospores very similar to aeciospores,

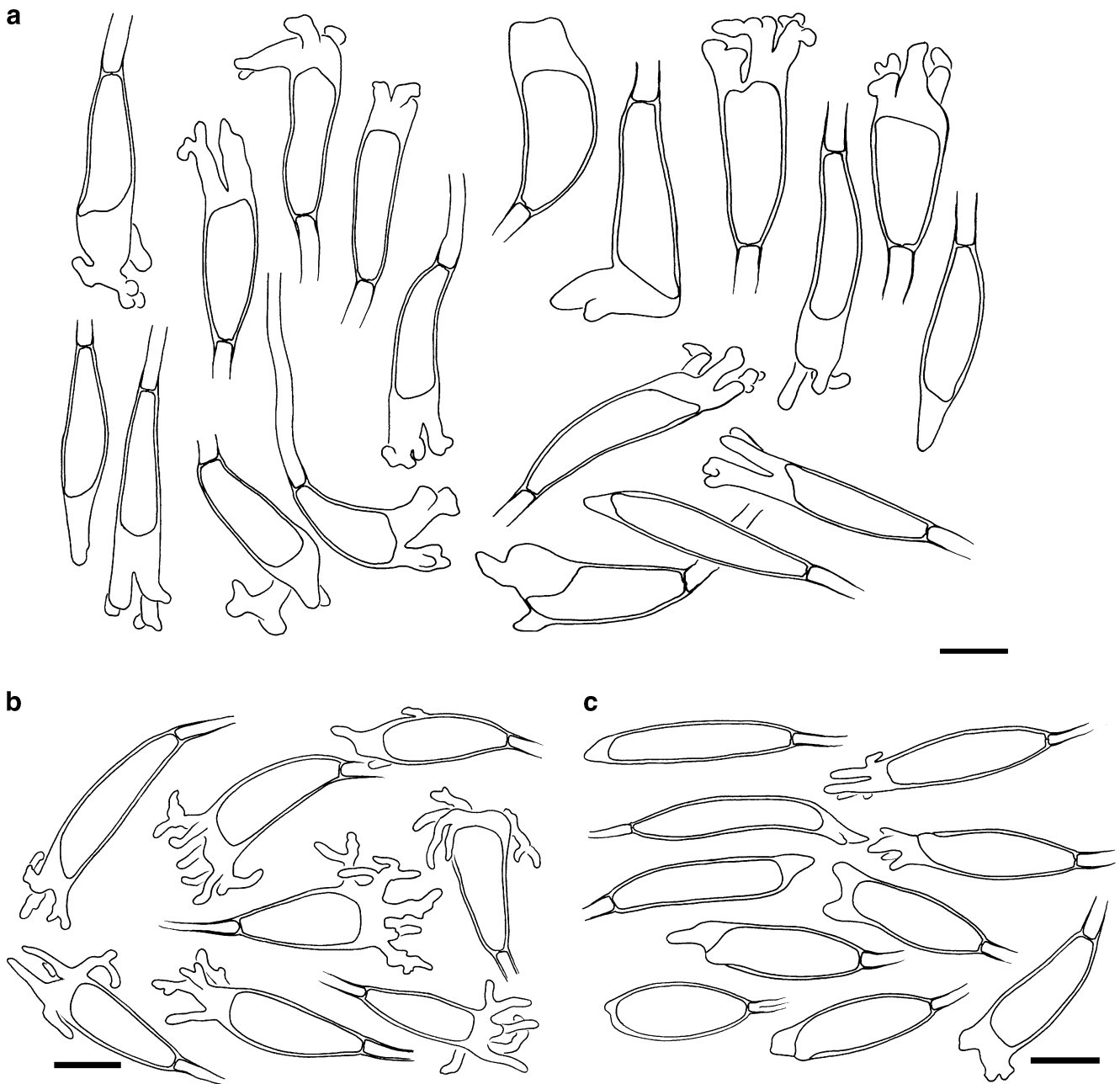
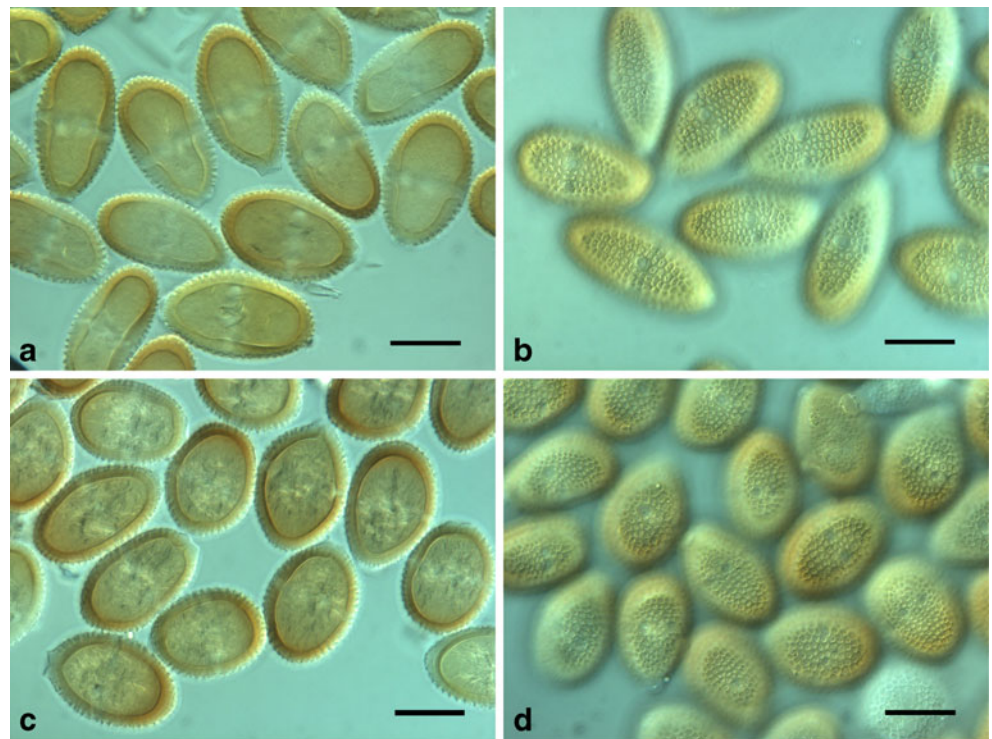


Fig. 1 *Endoraecium digitatum*. **a**. Teliospores from *Acacia notabilis* (isoeotype). **b**, **c**. Teliospores from *A. irrorata* (BRIP 14165). In **(b)**, teliospores with profusely digitate apices are shown, in **(c)**, spores with more simple apical digitations. Bar=20 μ m

ellipsoid, obovoid to broadly ellipsoid, often slightly compressed laterally, apex rounded or broadly conical, without or with a short rugose to almost smooth socket-like base, 31–49 \times 19–26(29) μ m (37.2 \times 21.3 μ m for epitype; range of averages: 37.2–42.8 \times 21.2–23.6 μ m), spore wall 2.5–3 μ m thick, asymmetrically thickened at equator to 4–5 μ m, at apex to 3–5 μ m, germ pores 5–8 (often 6) more or less equatorial, spore surface reticulate, meshes ca. 1.5–2.5 μ m wide, bounded by delicate ridges, with rugulose bottom. Telia scattered on more or less unaltered parts of phyllodes, pronouncedly pulvinate, semicompact with fibrous texture,

first ferruginous later assuming a sooty or dirty brownish tinge; teliospores fusiform, narrowly ellipsoid or obconical, sometimes slightly bent, apex generally much thickened, narrowly conical and simple or rather variably digitate, ranging between 2–3 simple and stout branches and rather long slender, sometimes distorted or weakly branching appendages, 35–80 \times 11–21 μ m (55.9 \times 15.5 μ m for epitype), spore wall smooth, pallid yellowish to golden yellow, apex generally more deeply pigmented (greenish-)golden, germ pore proximal to apical thickening, spores germinating upon maturity.

Fig. 2 *Endoraecium digitatum* from *Acacia notabilis*. **a, b.** Uredinospores, optical section and spore surface (AD 96045074). **c, d.** Aeciospores, optical section and spore surface (AD 966070527). Bars=20 μ m

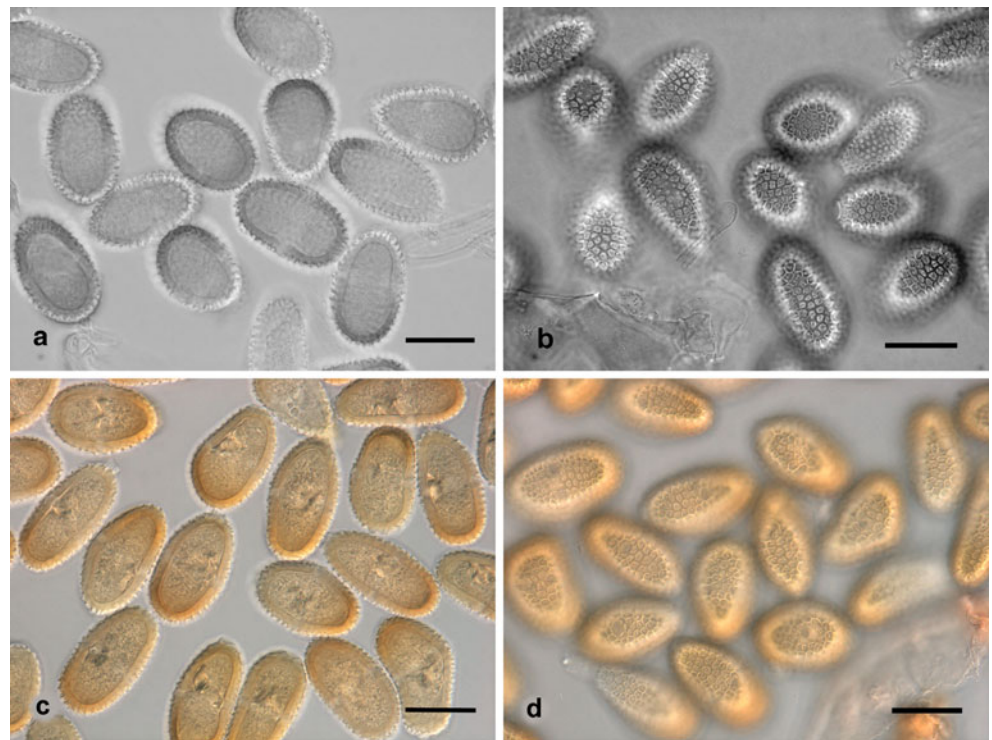


Additional material examined and used to complete the description of *E. digitatum*:

On phyllokinous Acacia spp. On *A. notabilis*. Australia, SA: Northern Lofty Region, South Hummocks, 34°02' S / 138°08' E, leg. JS Womersley no. 41, 24 Feb. 1963 (AD

966070527; 0, I). Head of Gulf of St. Vincent, Hummock Mt., ca. 20 km NNW of Port Wakefield, leg. HM Cooper, 11 Sept. 1963 (AD 96414049; [I, II], III). Eyre Peninsula, main highway between Kimba and Kyancutta, leg. F. Kutsche, 12 July 2001 (AD 123547; II, III). Eyre Peninsula, ca. 10 km E of Uno Station (“Mt. Helen”), 32°28' S / 136°

Fig. 3 *Endoraecium digitatum*. **a, b.** Uredinospores from *Acacia podalyriifolia* (ZT Myc 3015) in optical section and with focus on spore surface. **c, d.** Aeciospores from *A. irrorata* (BRIP 14165) in optical section and with focus on spore surface. Bars=20 μ m



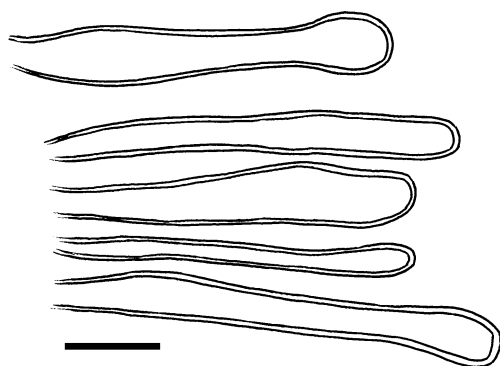


Fig. 4 *Endoraecium digitatum*. Paraphyses from urediniospore fascicles (ZT Myc 3015). Bar=20 μ m

44' E, leg. DJE Whibley no. 7979, 25 Sept. 1981 (AD 98150264; II). Eyre Peninsula, on roadside ca. 1 km S of Cummins (ca. 55 km NNW of Port Lincoln), leg. DJE Whibley no. 1931, 26 Aug. 1967 (AD 96741090; [0, I], II, [III]). Eyre Peninsula, Refuge Rocks area, track entrance to microwave tower, 33°11.5' S / 136°49.5' E, leg. JD Briggs no. 1053, 25 Aug. 1983 (AD 98527220; 0, I, III). Eyre Peninsula, County Buxton, Hundred Pinkawillinie, south corner of section 99–94, ca. 25 km W of Kimba, leg. KD Rohrlach no. 793, 27 Aug. 1960 (AD 96045074; II, III). Eyre Peninsula, Whyalla, Hummock Hill, 33°02'08" S / 137°35'15" E, leg. JD Sandham, D. Bosworth & D. New, 9 Dec. 1997 (AD 99845440; II). Roadside to Roseworthy, leg. FM Hilton, 3 Aug. 1954 (AD 98583644; II). Eyre Peninsula, Gawler Ranges, Paney Station (quadrate 3), woodland, 32°40'24" S / 135°30'20" E, collector unknown, 10 Oct. 1985 (AD 98715184; [I], II, III). Southern Lofty Ranges, Roseworthy Scrub, leg. JGO Tepper, 11 Sept. 1889 (MEL 1054135, sub *Uromycladium notabile* McAlp.; 0, I. Type of *Uredo notabilis*?). The following specimens of *A. notabilis* from AD bear *E. digitatum* as well but very scarcely or old: AD 123506 (0, I), AD 95921146 (I), AD 95708078 (II, III), AD 97803461 (II), AD 98583618 (II), AD 98548141 (0, I), AD 97940386 (II, III), AD 97135213 (II), AD 95928050 (I), AD 97806122 (I), AD 99616850 (I). On *A. podalyriifolia* A. Cunn. ex Don. Australia, QLD: Carnarvon Gorge, at main trail through gorge, leg. V. Faust-Berndt & R. Berndt no. Austr 9, 2 Aug. 2006 (ZT Myc 3015; II, III). Brisbane, leg. RF Langdon no. 32, 19 June 1930 (K(M) 146702, sub *At. digitata*; II, III). Redlands District, leg. K. Bodman, without date (BRIP 22895, sub *R. digitatus*; II, III). Brisbane, leg. RJ McAllister, 19 June 1930 (BRIP 6056 and 7546 ex BRIU 32, sub *R. digitatus*; II, III). Brisbane, leg. RFN Langdon, 23 June 1951 (BRIP 6057; probably II, 0 not seen). On *A. falciformis* DC. Australia, NSW: Brown Mountain 40 km W of Bega, leg. J. Walker, 11 Dec. 1975 (BRIP 14088 ex DAR 30202, sub *R. digitatus*; III).

On compound-leaved *Acacia* spp. On *A. dealbata* Link. Australia, VIC: Midlands, Murrumbidgee Ranges, leg. GH Robinson, 5 Jan. 1905 (MEL 1054763, sub *U. notabile*; I). Eastern Highlands, Cumberland Forest area, leg. GA Crichton, 20 Feb. 1966 (MEL 1054549, sub *U. notabile*; I). Midlands, Simpsons Place, Alexandra, leg. GA Crichton, 15 Nov. 1965 (MEL 2060932, sub *U. notabile*; 0, I). On *A. deanei* M.B. Welch, Coombs & McGlynn. Australia, QLD: Brisbane, Indooroopilly, DPI complex, leg. J. Barrett, 30 Aug. 1983 (BRIP 14106, sub *R. digitatus*; 0, I, III). Mt. Cotton, leg. L. Forsberg, 31 May 1990 (BRIP 17076, sub *R. digitatus*; I, II, III). On *A. irrorata* Sieber ex Spreng. Australia, QLD: Passchendaele, leg. J. Tierney, 7 March 1983 (BRIP 14165, sub *R. digitatus*; II [I?], III). The Summit, leg. KC Goulter, 29 Dec. 1983 (BRIP 14256, sub *R. digitatus*; 0, I, III). With telia of *Uromycladium* aff. *maritimum* McAlp.). On *A. oshanesii* F. Müll. & JH Maiden. Australia, QLD: Mt. Mee, leg. J. Tierney, 23 Nov. 1983 (BRIP 14170, sub *R. digitatus*; 0, I, III). On *Acacia* sp. ("Black Wattle"). Australia, VIC: Eastern Highlands, Mt. Margaret—Marysville Road, leg. GA Crichton, 11 April 1965 (MEL 2060933, sub *U. notabile*; 0, I).

Endoraecium digitatum differs from similar species by aecio- and urediniospores whose apex is not or hardly thickened and which have a delicate, wide-meshed, reticulate ornamentation with irregular narrow and rather high ridges and a conspicuously rugulose bottom (Figs. 2 and 3). The spore base is not or only inconspicuously socket-like. The teliospores have generally a thickened apex with one to several long, sometimes tortuous and ramifying processes (Fig. 1). As in other *Endoraecium* species, aecio-, uredinio- and teliospores are formed in conspicuous fascicles comprising slightly thick-walled and elongated basal cells bearing several pedicellate spores and many collapsed remnants of pedicels whose spores have already become detached. In the uredinia of ZT Myc 3015 and the aecia of AD 98527220, slenderly cylindrical and rather inconspicuous paraphyses were found (Fig. 4). Their walls were slightly thickened and pigmented yellowish.

Besides *A. notabilis* a number of other *Acacia* spp. bore rust infection assignable to *E. digitatum*. These are the phyllodinous *A. podalyriifolia* and *A. falciformis* and four species with bipinnate adult leaves, *A. dealbata*, *A. deanei*, *A. irrorata*, and *A. oshanesii*. The specimen on *A. falciformis* bore only telia and was assigned to the present species tentatively based on the strongly digitate teliospores. All investigated specimens on *A. dealbata* were only aecial (with or without spermogonia). Aeciospore morphology showed them to belong to *E. digitatum*. At present *E. digitatum* is the only known species distinguished in the *E. digitatum* complex occurring on both phyllodinous and compound-leaved members of *Phyllodineae*.

The specimens from *A. notabilis* tended to have longer teliospores and slightly larger aecio- and urediniospores than collections from the other *Acacia* spp. It was observed in addition that teliospores from specimens on compound-leaved acacias generally had longer and more profusely branching apical processes (Fig. 1b). As the digitate teliospores of *Endoraecium* species are often variable no taxonomic consequence was drawn upon this difference.

E. digitatum was originally described with uredinio- and teliospores (Winter 1886). McAlpine (1906) stated that it comprised spermogonia, uredinia and telia, while Hodges and Gardner (1984) established a macrocyclic life cycle by inoculation experiments using specimens from Hawaii. In the present study, all but one specimens on *A. notabilis* bore uredinia and telia separately from spermogonia and aecia that were produced together on blister-like swellings or galls. In one specimen, uredinia were lacking and telia were produced together with the aecia on galls. Demicyclic specimens were also encountered on *A. irrorata* and *A. oshanesii*. In BRIP 14256 on *A. irrorata*, the sori occurred in variable association, spermogonia with telia, spermogonia with aecia and telia, or telia unaccompanied by other sori. Because of the morphological similarity of the spores of the specimens, I consider all these variants to belong to *E. digitatum*. One can conclude that *E. digitatum* is a species with unfixed life cycle.

Uredo notabilis, hitherto considered the uredinial state of *Uromycladium notabile* (McAlpine 1906), is assigned to the present species as anamorph name of the aecial state. I compared a specimen collected by Tepper near Roseworthy on 11 Sept. 1889 (MEL 1054135), most probably a part of the type of *U. notabilis*, with the aecial state of *E. digitatum* and could not find any differences. Ludwig (1890) stated that the type was collected on 11 Feb. 1889 at Roseworthy and presented a detailed description and excellent drawings which strongly suggest as well that *U. notabilis* represents the aecial state of *E. digitatum*. In addition, the similarity between *U. notabilis* and the uredinial state of *E. digitatum* is striking. *Uredo gemmata* described from Melbourne on *Acacia* sp. is listed as a synonym of *U. notabilis* by Sydow and Sydow (1915) but was not investigated in this study.

Is *E. digitatum* the same as *Uromyces phyllodiorum* and *U. phyllodii*?—McAlpine (1906) gave a detailed description of *U. phyllodiorum* based on type material and of *U. phyllodii* which he considered synonymous. He reported the presence of spermogonia, uredinia (in fact *Uredo*-like aecia) and telia on “tubercles” of the phyllodes and described the aeciospores as 35–54 μm long. His micrographs show that the aeciospores are apically thickened. McAlpine’s observations were confirmed by a study of the syntypes of *U. phyllodiorum* (K(M) 146703, K(M) 146704) and an isotype of *U. phyllodii* (K(M) 146705). *E. digitatum* has shorter aecio- and urediniospores with more numerous germ pores and a different surface ornamentation. The

aeciospores are not or hardly thickened at the apex. In addition, most specimens of *E. digitatum* were found to be macrocyclic though spermogonia, aecia and telia associated together on swellings of the phyllodes were also encountered occasionally. It is concluded that *U. phyllodiorum* and *U. phyllodii* are names for the same fungus, as already stated by McAlpine (1906), but that both are different from *E. digitatum*. The new combination *Endoraecium phyllodiorum*, based on *Uromyces phyllodiorum*, is proposed for the separate species.

Endoraecium phyllodiorum (McAlp.) R. Berndt, comb. nov. (Figs. 5, 6, 7b, 9)

≡ *Melampsora phyllodiorum* Berk. & Broome. Trans. Linnean Soc. London, 2. ser., 2:67 (1882). On *Acacia* sp. A telial name applied to *Uredo*-like aecia (cf. Berkeley and Broome 1883, Plate 15, Figs. 6, 7 and 8). The telial stage is present, however, according to McAlpine (1906).

≡ *Uromyces phyllodiorum* McAlp. The rusts of Australia: p. 95 (1906) [as *U. phyllodiorum* (Berk. & Broome) McAlp.]. This is not a recombination but a new name for the holomorph based on teliospores encountered in the type specimen of *M. phyllodiorum* and described in McAlpine (1906). Basionym.

≡ *Pileolaria phyllodiorum* (McAlp.) Dietel. Ann. Mycol. 19:302 (1921) [as *P. phyllodiorum* (Berk. & Broome) Dietel]. A recombination of *U. phyllodiorum* McAlp., not of *M. phyllodiorum* Berk. & Broome.

= *Uromyces phyllodii* Cooke & Masee in Cooke. Grevillea 17:70 (1889) (as *U. “phyllodiae”*). On *Acacia* sp. A telial name applied to *Uredo*-like aecia (comp. protologue by Cooke (1889): “Maculis ... bullatis ... Teleutosporis ... episporio minute verruculoso.”). The telial stage is present, however.

Sori in combination 0/I, 0/I/III or 0/III on blister-like swellings of phyllodes which are up to 6×3 mm large, sometimes together with uredinia and/or telia on ± unaltered parts of phyllodes, or uredinia and/or telia on ± unaltered parts of phyllodes the only spore states present. Aecia small, *Uredo*-like, subepidermal, ferruginous, pulverulent, associated with spermogonia; aeciospores ellipsoid, subpyriform or more rarely subclavate, provided with a short socket-like base, (33)36–52(58)×17–26 μm (K(M) 146703: 44.3×20.2 μm , means ranging between 37.9–44.5×20.2–22.6 μm), rather coarsely reticulate, mesh width 1.5–2.6 μm , spore wall laterally about 2–3 μm thick, apically (5)6–9(10) μm , germ pores 4–5, more or less equatorial, without caps. Uredinia tiny, subepidermal, scattered or in loose groups on both sides of phyllodes, pulverulent, ferruginous, no paraphyses observed; urediniospores more or less like the aeciospores, (31)35–48(52)×18–23(25) μm (means ranging between 39.0–43.3×19.9–23.4 μm), with 3–5, mostly four germ pores, apex not or slightly to conspicuously thickened (4–

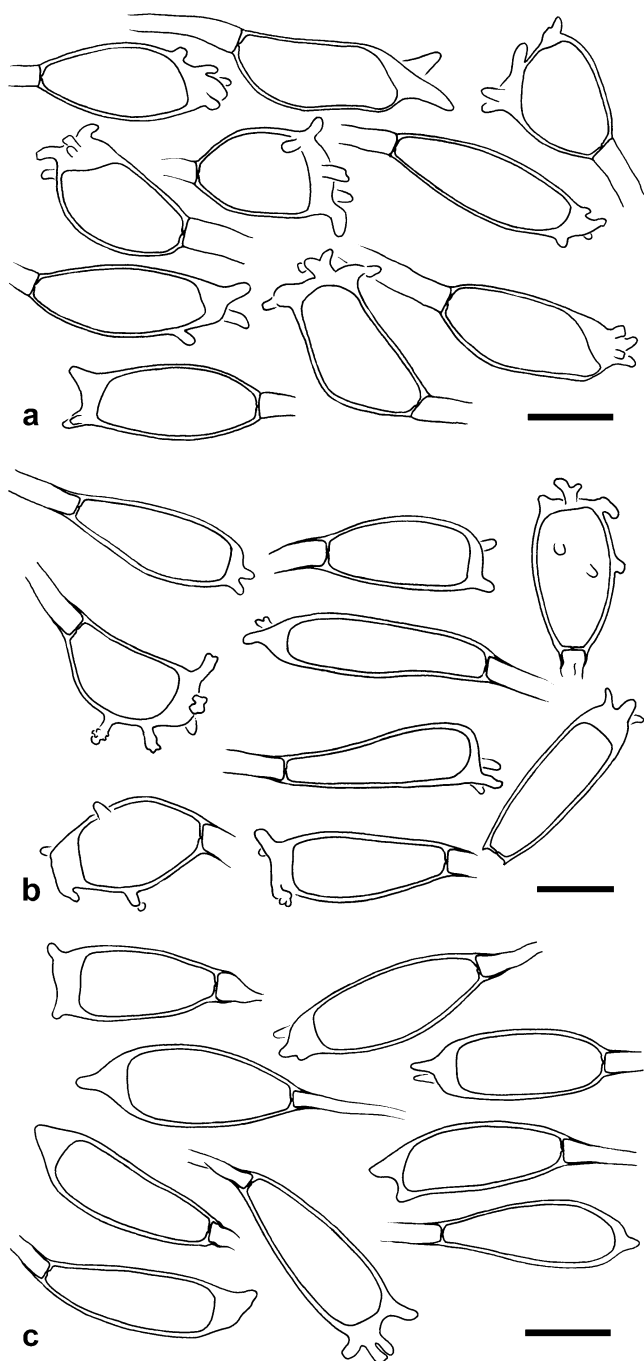


Fig. 5 *Endoraecium phyllodiorum*, teliospores. **a.** Spores from specimen bearing II and III on unaltered parts of phyllode and galls with spore states 0/I/III. Delineated spores are from telia not on galls (ZT Myc 3023). **b.** Teliospores from galls bearing spore states 0/I/III (BRIP 23281). **c.** Teliospores from microcyclic specimen with 0/III on galls (BRIP 39796). Bars=20 μm

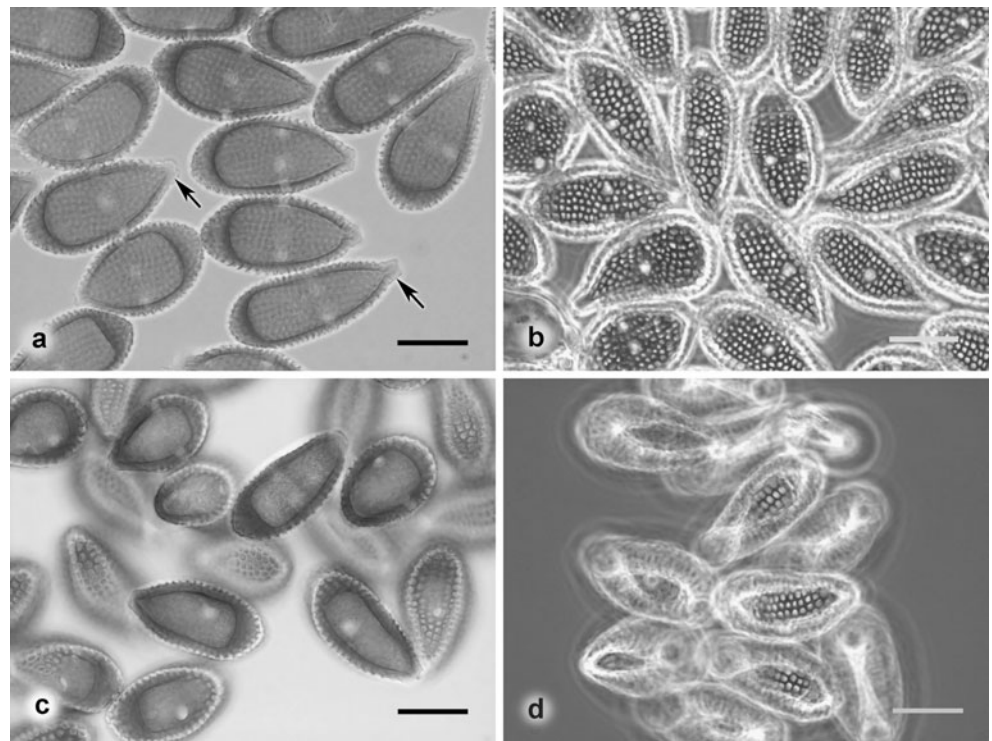
9 μm), with conspicuous smooth socket-like contraction of spore base. Gall-borne telia small, semi-immersed, compact, greyish, no paraphyses observed; non gall-borne telia tiny, scattered on both sides of phyllodes, pulvinate, yellowish brown to ferruginous, semi-compact and with fibrous

texture, no paraphyses observed; teliospores (gall-borne) broadly ellipsoid to ellipsoid or cuneate, $36\text{--}52 \times (18)20\text{--}27$ μm (means ranging between $43.4\text{--}48.3 \times 20.4\text{--}22.8$ μm), smooth and thin-walled, at apex slightly to moderately thickened (≤ 10 μm), greenish-yellow to golden-yellow, normally with 1–3 narrowly conical to cylindrical rather short outgrowths, more rarely more profusely digitate, pedicels subhyaline, stout and persistent, spores germinating upon maturity, non gall-borne teliospores ellipsoid, broadly ellipsoid or obconical, tapering towards the pedicel, apex rounded, conical or truncate, $(33)35\text{--}50(52) \times 16\text{--}25.5$ μm (means ranging between $40.5\text{--}54.6 \times 18.1\text{--}21.2$ μm), spore wall smooth, subhyaline, light yellowish or golden, ca. 1(2) μm thick, ca. (3)6–11 μm at apex, with 2–7, most often shortly cylindrical or knob-like or sometimes rather stout horn-like processes which are more rarely bifurcate or shifted to the subapical region, pedicels subhyaline to pale yellowish, delicate and thin-walled, up to 60 μm long.

Material examined:

Specimens with sori (0/I/III) on bullate swellings or galls of phyllodes (only the presence of additional spore stages or of swellings with other combinations of stages are mentioned with the particular specimens). Australia, QLD: On *Acacia* sp. Brisbane, leg. FM Bailey no. 643 [ex herb. Masee?] (K(M) 146705, isotype of *Uromyces phyllodii*; 0, I, [III]). Locality not given, from Bailey's herbarium, in Dept. of Agriculture Herbarium, VIC (PUR F 19689, type of *Uromyces phyllodii*; labelled 0, II, III. I saw only 0, I macroscopically on rather depleted specimen). Brisbane, leg. FM Bailey no. 269 [ex herb. Broome] (K(M) 146703 and 146704, syntypes of *Melampsora phyllodiorum*; 0, I). Paluma Range, hiking trails near Paluma village, at 'Witt's lookout', leg. V. Faust-Berndt & R. Berndt no. Austr 35, 9 Aug. 2006 (ZT Myc 3016; 0/I, 0/I/III or 0/III on galls, III not on galls). Cairns, Kuranda, Barron Gorge Natl. Park, 'Mc Donald's trail', open *Acacia* woodland, leg. V. Faust-Berndt & R. Berndt no. Austr 44 and 46, 18 Aug. 2006 (ZT Myc 3020 and ZT Myc 3021; 0/I, 0/III or 0/I/III on galls, some III not on galls). On *A. aulacocarpa* Cunn. ex Benth. Mossman, Mt. Molloy, leg. I. Hood, 8 April 1995 (BRIP 23281, sub *R. digitatus*; 0/III, 0/I and 0/I/III). Bellenden Ker Natl. Park, Behana Gorge, leg. RG Shivas, 29 July 1992 (BRIP 20500, sub *R. digitatus*). Cape Tribulation, Donovan Range, leg. RG Shivas, 7 Aug. 1992 (BRIP 20514, sub *R. digitatus*; II not on galls). Mission Beach, leg. I. Hood, 5 April 1995 (BRIP 23284, sub *R. digitatus*; 0/I and 0/III on galls, III not on galls). On *A. crassicarpa* Cunn. ex Benth. Cape York Peninsula, Coen, Peninsula Road, leg. RG Shivas & M. Gunther, 16 July 1999 (BRIP 26562, sub *R. digitatus*). On *Acacia* cf. *mangium* Willd. Cairns, Kuranda, Barron Gorge Natl. Park, 'Mc Donald's

Fig. 6 *Endoraecium phyllodiorum* (ZT Myc 3023). **a.** Aeciospores in optical section with thickened spore apex and equatorial germ pores. Note presence of more or less smooth stalk-like spore base (arrows). **b.** Aeciospores, focus on reticulate spore surface. **c, d.** Urediniospores in optical section and with focus on spore surface. Bars=20 μ m



trail', leg. V. Faust-Berndt & R. Berndt no. Austr 48, 18 Aug. 2006 (ZT Myc 3023; 0/I/III on galls, some II, III not on galls).

Specimens with sori not on bullate swellings or galls of phyllodes. Australia, QLD: On *Acacia* sp. 10 km S of

Townsville, leg. RG Shivas, 7 May 2005 (BRIP 44604, sub *R. digitatus*; II, III). Cairns, Mt. Whitfield conservation area, first (main) lookout, leg. V. Faust-Berndt & R. Berndt no. Austr 38, 24 Aug. 2006 (ZT Myc 3017; II). On *A. aulacocarpa*. Brisbane, leg. E. Jarvis, April 1911 (BRIP 6041 sub *R. digitatus*; II, III). Marcus Beach, leg. JL

Fig. 7 **a, b.** *Endoraecium* cf. *phyllodiorum* from Hawaii (K(M) 146700). Urediniospores in optical section and with focus on spore surface. Note the presence of a more or less smooth stalk-like spore base (**a**, arrow). **c, d.** *Endoraecium kauaianum* (holotype). Urediniospores in optical section and with focus on spore surface. Bars=20 μ m

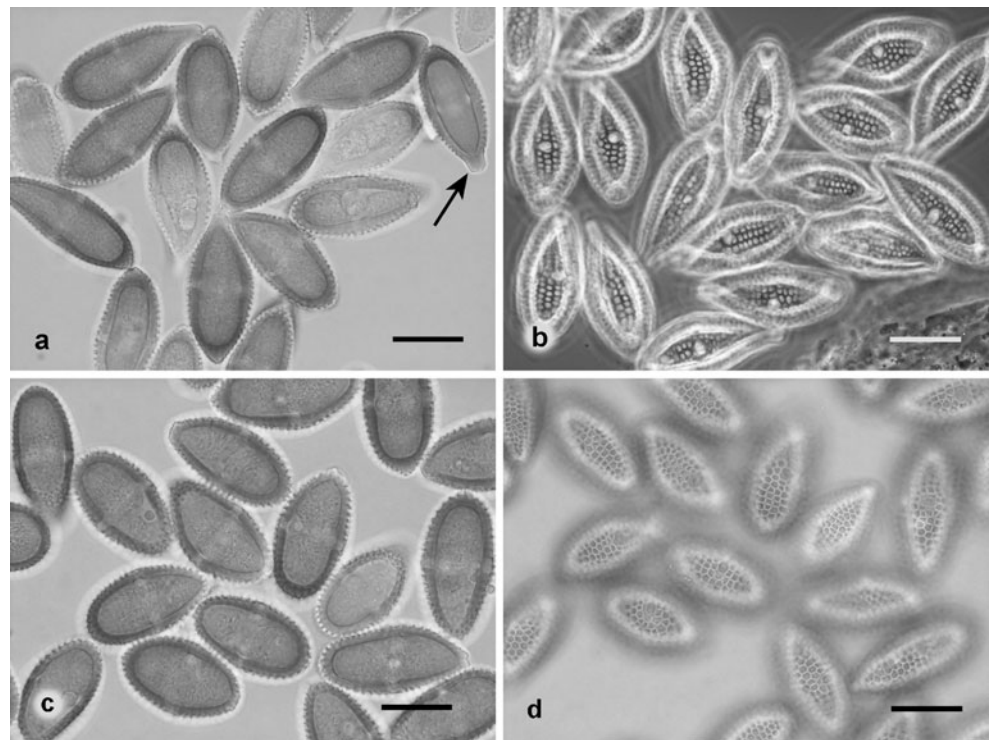
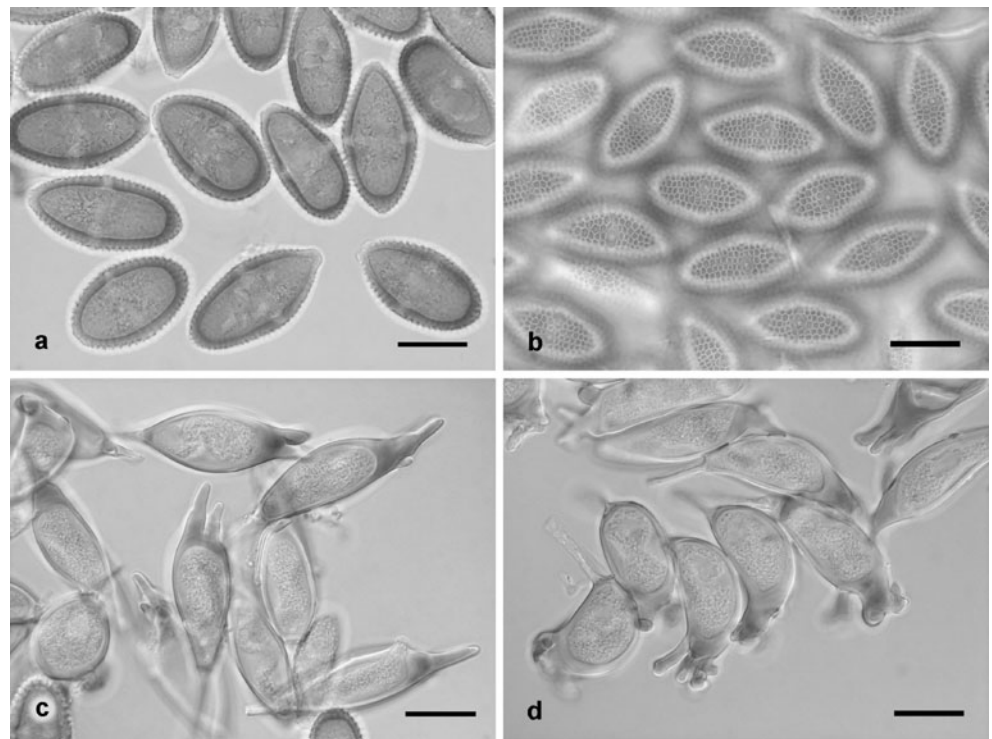


Fig. 8 *Endoraecium kauaianum* (holotype). **a, b.** Aeciospores in optical section and with focus on spore surface. **c, d.** Teliospores. Bars=20 μ m



Alcorn, 17 Aug. 1972 (BRIP 8769, sub *R. digitatus*; II, III). On *A. holosericea*. Elliott, leg. JH Simmonds, Aug. 1974 (BRIP 8934, sub *R. digitatus*; II). Gillies Range Natl. Park, leg. RG Shivas, 31 July 1992 (BRIP 20477, sub *R. digitatus*; II). Peach no. 1, Coen, leg. RG Shivas & M. Gunther, 18 July 1999 (BRIP 25819, sub *R. digitatus*; II). Coen Airport, leg. RG Shivas & M. Gunther, 16 July 1999 (BRIP 26550, sub *R. digitatus*; II). Australia, NT: Renner Springs, on *A. holosericea*, leg. RN Pitkethley no. 638, 25 Sept. 1975 (K(M) 146701, sub *A. digitata*; II). Australia, WA: Broome, Golf Course, on *A. holosericea*, leg. J. Ray no. JR 137, Oct. 2006 (BRIP 49108, sub *R. digitatus*; II, III).



Fig. 9 *Endoraecium phyllodiorum* (ZT Myc 3023). Infected phyllodes of *Acacia* sp. with blister-like swellings bearing spermogonia and *Uredo*-like aecia. Bar=20 mm

Microcyclic specimens with sori (0/III) on swellings or galls of phyllodes. Australia, QLD: On *Acacia* sp. Thursday Island, leg. FM Bailey, without date (BRIP 6064, sub *R. digitatus*). On *A. mangium*. Glenbora, leg. MH Ivory no. P9289, 23 Oct. 1997 (BRIP 39796, sub *R. digitatus*). Nursery Ingham, leg. B. Brown, 28 June 1990 (BRIP 30420a, sub *R. digitatus*). Tully, Mission Beach Rd., collector unknown, 27 June 1990 (BRIP 30422, sub *R. digitatus*). Garner's Beach, collector unknown, 27 June 1990 (BRIP 30423, sub *R. digitatus*). Wooloogin Creek near Japoonvale, collector unknown, 27 June 1990 (BRIP 30425, sub *R. digitatus*). Mena Creek Expt. 730, collector unknown, 27 June 1990 (BRIP 30426, sub *R. digitatus*). South Johnstone, collector unknown, 27 June 1990 (BRIP 30429, sub *R. digitatus*). Meunga, leg. MH Ivory, 23 Oct. 1997 (BRIP 39807, sub *R. digitatus*). Utchee Creek, leg. MH Ivory, 7 Dec. 1997, (BRIP 39804, sub *R. digitatus*). Ingham, Forestry Nursery, leg. M. Ivory, 3 July 2000 (BRIP 29567, sub *R. digitatus*). Mission Beach, leg. ex Forestry Dept., 10 Nov. 1983 (BRIP 14167, sub *R. digitatus*). Near Mission Beach, leg. I. Hood, 5 April 1995 (BRIP 23268, sub *R. digitatus*). Asherton, leg. M. Ivory, 3 March 1999 (BRIP 29732, sub *R. digitatus*). Innisfail, leg. A. Bragg, 7 Nov. 1988 (BRIP 31167, sub *R. digitatus*). Lannercost Expt. 734, leg. B. Brown, 28 June 1990 (BRIP 30418, sub *R. digitatus*). Lannercost, leg. M. Ivory, 9 Aug. 1999 (BRIP 29677, sub *R. digitatus*). Vanuatu, Prov. Tafea: Tanna, Middlebush, on *Acacia* sp., leg. JG Wright, 17 June 2003 (BRIP 44904, sub *R. digitatus*).

Specimens preliminarily assigned to R. phyllodiorum Australia, QLD: Mossman, Mossman Gorge, on *A. aulacocarpa*, leg. RG Shivas, 27 July 1993 (BRIP 21806, sub *R. digitatus*; 0, I, III on galls). Rifle Creek Bridge at Mt. Molloy, on *A. auriculiformis* Cunn. ex Benth., leg. I. Hood, 7 April 1995 (BRIP 23263, sub *R. digitatus*; 0, I on galls, III not on galls).

Endoraecium phyllodiorum revealed a remarkable plasticity with regard to the presence of spore states. In most specimens, sori were only produced on galls of which some bore the spore states 0/I, others 0/I/III, or 0/III. A considerable number of specimens produced exclusively galls with spermogonia and telia (microcyclic forms). In some specimens, galls occurred together with telia or with uredinia plus telia that were scattered over non-hypertrophied phyllodes or parts of the phyllodes. Sori on galls and scattered sori most likely belong to the same species as the aeciospores (from galls) and the urediniospores (from scattered sori) are closely similar (Fig. 6). In addition, both the galls and scattered uredinia and telia could be present on a single phyllode. It is concluded that *E. phyllodiorum*, like *E. digitatum*, has a variable life cycle with the potential to show itself macro-, demi- or microcyclic or even to produce different combinations of sori at the same time.

Teliospores were variable but similar regardless of their origin from gall-borne or scattered telia (Fig. 5). A considerable variability regarding spore length and thickness of the spore apex was also noted among urediniospores from different specimens.

Specimens of *E. phyllodiorum* were investigated from *A. aulacocarpa* A. Cunn. ex Benth., *A. holosericea* A. Cunn. ex G. Don., *A. mangium* Willd. and probably *A. auriculiformis* Benth. (determination of rust uncertain). McAlpine (1906) reported it on *A. dallachiana* F. Müll., *A. dealbata* Link, *A. microbotrya* Benth., *A. neriifolia* A. Cunn., *A. notabilis*, *A. penninervis* Sieber, and *A. pruinosa* A. Cunn. Most probably his reports do not only represent *E. phyllodiorum* but similar species as well. Outside of Australia the rust occurs in Vanuatu, and photographs presented in Old et al. (2000) indicate its presence in Kalimantan. Huguenin (1966) reported it from New Caledonia on *A. spirorbis* Labill.

What is 'Endoraecium digitatum' from Hawaii? The native phyllodinous acacias of Hawaii are *A. kauaiensis* Hbd., *A. koa* A. Gray with vars. *koa*, *latifolia* (Benth.) St. John and *waianaeensis* St. John and *A. koaia* Hbd. (St. John 1979). Pedley (1975) accepted only *A. kauaiensis* and *A. koa*, the latter comprising the varieties described at that time and *A. koaia*. Hodges and Gardner (1984) and Gardner (1994) reported the presence of *E. digitatum* on *A. koa* vars. *koa* and *latifolia*. Gardner (1991) supposed that the rust had been introduced to Hawaii, while in Gardner (1994) it is

regarded as indigenous. If, as hypothesized by Gardner (1994), the Hawaiian endemic *E. angustiphyllodium* is a derivative of *E. digitatum*, the latter assumption would be more probable.

A study of Hawaiian specimens determined as *E. digitatum* showed that aecio- and urediniospores were clearly distinct from *E. digitatum* s. str. but similar to *E. phyllodiorum*. A closer examination revealed that two different species were involved, one preliminarily left with *E. phyllodiorum*, the other one new for science.

Endoraecium kauaianum R. Berndt, sp. nov. (Figs. 7c, d and 8).

Etymology: After Kauai, island of the Hawaiian Archipelago, location of the type.

Spermogonia sparsim adsunt inter aecia. Aecia generi *Uredo* similia, cinnamomea ad ferruginea, pulverulenta, inflorescentias et fructua (scoparum hospiti?) omnino denseque tegentia; aeciosporae urediniosporis generaliter similes sed formae plus variabilis, ellipsoideae ad late ellipsoideae, subfusiformes, apice rotundato vel conico, contractionem basalem pedicelliformem generatim carentes vel cum contractione brevi rugoso-subreticulato, 28–44 × 19–23(25.5) μm (37.4 × 21.3 μm), pariete aureo ca. 3–4.5 μm crasso in parte aequatoriali, apicaliter non vel paulum incrassato usque ad 3.5–6 μm, reticulato, poris germinationis 7–10 aequatorialibus sine papillis. Uredinia in phyllodia vix mutata sparsa, teliis consociata, cinnamomea, pulverulenta; urediniosporae ellipsoideae ad late ellipsoideae, subfusiformes, apice rotundato vel conico, contractionem basalem pedicelliformem generatim carentes vel cum contractione brevi rugoso-subreticulato, (31)35–44 (46) × (17)19–22.5 μm (38.1 × 20.4 μm), pariete pallide aureo vel aureo, ca. 3–4.5 μm crasso in parte aequatoriali, paulum tenuiore basim versus, apicaliter non vel paulum incrassato usque ad 4–5(7) μm, reticulato maculis ca. 1.5–2.6 μm (2.0 μm) diam. et ca. 1 μm altis, poris germinationis 6–8 aequatorialibus sine papillis. Telia minuta, singularia, urediniis consociata in phyllodia vix mutata; teliosporae formae et processuum apicalium variabilissimae, plerumque ellipsoideae ad subfusiformes, rarius fusiformes vel late ellipsoideae, 29–48(50) × 14.5–19 μm (38.9 × 16.6 μm), pariete 1–1.5 μm crasso, subhyalino ad pallide aureo, apice valde incrassato, pallide aureo vel viridi-flavo, ornato processu singulo ad paucis brevibus vel longis, rectis vel incurvatis, plerumque integris; per maturitatem ex poro germinationis subapicali germinantes.

In phyllodiis, inflorescentiis fructibusque *Acaciae koae* (vel *A. kauaiensis*?).

Spermogonia scarcely present among aecia. Aecia *Uredo*-like, cinnamon to ferruginous, pulverulent, densely covering what may have been an inflorescence with young pods (on witches' brooms?); aeciospores essentially like urediniospores though more variable in shape, ellipsoid to

broadly ellipsoid, subfusiform, apex rounded to conical, generally without basal stalk-like contraction or with a short and rugose to subreticulate one, $28\text{--}44\times 19\text{--}23(25.5)\ \mu\text{m}$ ($37.4\times 21.3\ \mu\text{m}$), spore wall golden brown, ca. $3\text{--}4.5\ \mu\text{m}$ thick around equator, at apex not or slightly thickened to $3.5\text{--}6\ \mu\text{m}$, reticulate, germ pores $7\text{--}10$, equatorial, without caps. Uredinia scattered on unaltered(?) phyllodes and associated with telia, cinnamon, pulverulent; urediniospores ellipsoid to broadly ellipsoid, subfusiform, apex rounded to conical, generally without basal stalk-like contraction or with a short and rugose to subreticulate one, $(31)35\text{--}44(46)\times(17)19\text{--}22.5\ \mu\text{m}$ ($38.1\times 20.4\ \mu\text{m}$), spore wall pale golden or golden brown, about $3\text{--}4.5\ \mu\text{m}$ thick around equator, slightly thinner proximal, apex not or slightly thickened to $4\text{--}5(7)\ \mu\text{m}$, reticulate, meshes ca. $1.5\text{--}2.6\ \mu\text{m}$ ($2.0\ \mu\text{m}$) diam., with delicate up to $1\ \mu\text{m}$ high ridges, germ pores $6\text{--}8$, equatorial, without caps. Telia very small, singly and associated with uredinia on unaltered(?) phyllodes; teliospores very variable with regard to shape and apical processes, most often ellipsoid to subfusiform, more rarely fusiform or broadly ellipsoid, $29\text{--}48(50)\times 14.5\text{--}19\ \mu\text{m}$ ($38.9\times 16.6\ \mu\text{m}$), spore wall $1\text{--}1.5\ \mu\text{m}$ thick, subhyaline to pale golden brown, apex strongly thickened, pale golden with greenish tinge, bearing one to several, short to long, straight to bent, most often entire horn-like processes, germinating at maturity from a germ pore located proximal to the apical thickening.

Holotype (PUR 89860): USA, Hawaiian Islands: Kauai, Puu Ki-Waiialae trail, on *A. koa* A. Gray, leg. A. Kyono, Feb. 1991 (sub *At. digitata*, det. DE Gardner; I, II, III).

Additional material examined:

E. kauaianum. USA, Hawaiian Islands, Kauai: Collection site not indicated, on *A. koa* var. *koa*, leg. CS Hodges, May 1982 (PUR 66863, sub *A. digitata*, det. DE Gardner; 0, I). Collection site not indicated, on *A. koa*, leg. Swezey, without date (PUR F2890, sub *At. digitata*, det. DE Gardner, det. as *Uromyces koae* by JC Arthur; probably I, spermogonia not observed).

E. cf. phyllodiorum. USA, Hawaiian Islands, Oahu: Pacific Palisades, on *A. koa* var. *koa*, leg. CS Hodges, 9 Sept. 1982 (K(M) 146700, sub *At. digitata*; II). Waimea Falls Park, on *A. koa* var. *koa*, leg. CS Hodges, 23 Oct. 1981 (PUR 66873, sub *At. digitata*, det. DE Gardner; II). Wahiawa, Ahrens Ditch trail, on *A. koa* cf. var. *koa*, leg. FL Stevens no. 291, 8 June 1921 (PUR F2887, sub *At. digitata*; II). Hawaiian Islands, Kauai: Makaha Ridge, *Acacia* host not specified, from infection experiment with aeciospores, collector not indicated, 29 July 1982 (PUR 66861, sub *At. digitata*; II).

Endoraecium koae+*E. angustiphyllodium* USA, Hawaiian Islands, Hawaii: Hawaii Volcanoes Natl. Park,

on *A. koa* var. *latifolia*, leg. DE Gardner, Dec. 1986 (BISH 510514, sub *At. digitata*; III, III).

Endoraecium kauaianum differs from *E. phyllodiorum* mainly in aecio- and urediniospore characters. Spores of both states lack a smooth stalk-like base or have only a short, inconspicuous one that is subreticulate or rugose (Figs. 7c, d and 8a, b). The aeciospores have $7\text{--}10$, the urediniospores $6\text{--}8$ germ pores vs. $4\text{--}5$ and $3\text{--}5$ in *E. phyllodiorum*. *E. digitatum* differs in aecio- and urediniospores not thickened at apex and a differently reticulate spore surface.

PUR 66863 and PUR F2890 were only aecial (0, I and I, respectively) and had slightly larger aeciospores than the type of *E. kauaianum*. In PUR F2890, assigned to *E. digitatum* by Gardner and reported to have uredinia and telia (Gardner 1994), aeciospores measured $(33)37\text{--}50\times 20\text{--}25\ \mu\text{m}$ ($42.5\times 22.6\ \mu\text{m}$), in PUR 66863, $35\text{--}45(51)\times 19\text{--}25\ \mu\text{m}$ ($40.9\times 21.7\ \mu\text{m}$). I did not see in any investigated specimen the slender paraphyses observed by Gardner (1994) in the aecia and uredinia of '*E. digitatum*'. Hosts of *E. kauaianum* were given as *A. koa* or *A. koa* var. *koa*, but a comparison of the phyllodes present in the type specimen with illustrations provided by St. John (1979) suggests that the type host may be *A. kauaiensis*. Up to now, *E. kauaianum* is only known from Kauai Island.

Specimens K(M) 146700, PUR 66873 and PUR F2887, all from Oahu and most probably on *A. koa* var. *koa*, and PUR 66861 from Kauai on an undetermined *Acacia* showed only uredinia and were different from *E. kauaianum*. The urediniospores of these specimens (Fig. 7a, b) had a prominent, smooth stalk-like spore base. In this they resembled urediniospores of Australian *E. phyllodiorum* from which they slightly differed, however, by the presence of $5\text{--}7$, most often six germ pores. Urediniospores and aeciospores of Australian *E. phyllodiorum* have generally $3\text{--}5$, most often four pores. As there is overlap in this character the Hawaiian specimens are preliminarily assigned to *E. phyllodiorum*.

Hodges and Gardner (1984) described that spermogonia and *Uredo*-like aecia of '*E. digitatum*' were mostly formed on "compact witches' brooms" on *A. koa* var. *latifolia*, less commonly on "large, discrete, bullate swellings". In contrast, no witches' brooms were observed on *A. koa* var. *koa* where spermogonia and aecia were associated with a variety of other symptoms. It is difficult to interpret these observations given the possibility that *E. kauaianum* and *E. cf. phyllodiorum* were involved or even *E. koae*. The connection of uredinia and telia of '*E. digitatum*' with spermogonia and aecia formed on witches' brooms and other malformations of the hosts was proven by Hodges and Gardner (1984) with inoculation experiments. The authors reported that the aeciospores showed minor morphological differences (shape of the apex) between the

islands of Kauai and those of Hawaii and Maui but that inoculation experiments carried out with both forms led to “typical uredinia and telia”.

BISH 510514 on *A. koa* var. *latifolia* is listed in Gardner (1994) under ‘*E. digitatum*’ (spore stages 0, I). Its reinvestigation revealed spermogonia, associated *Uredo*-like aecia and very few telia. The fungus is different from *E. phyllodiorum* and *E. kauaianum* in aeciospores with 7–8 germ pores, a not thickened spore apex and the lack of a socket-like spore base. The aeciospores measured 31–39 × 18–23.5 μm (34.9 × 21.4 μm). In these characters they closely resemble aeciospores of *E. koae*. It is concluded that BISH 510514 bears both the spermogonial/aecial state of *E. koae* and teliospores that belong to another rust species, probably *E. angustiphyllodium*.

SEM micrographs of aecio- and urediniospores of *E. digitatum*-like rusts from Hawaii can be found in Gardner and Hodges (1985). A key to the rusts on endemic acacias in Hawaii was provided by Hodges and Gardner (1984). The following key is partly based on the latter.

Spore wall not reticulate, either with apical and lateral tubercles or laterally smooth and with one to several apical processes. Teliospores.

Spores apically and laterally with numerous short, blunt tubercles, generally associated with spermogonia and *Uredo*-like aecia *E. koae*
 Spores laterally smooth, apically with one to several ± long processes (‘digitate’)

Telia densely covering witches’ brooms, associated with spermogonia *E. angustiphyllodium*
 Telia scattered on ‘normal’ phyllodes, not on witches’ brooms, not associated with spermogonia but often with uredinia
 *E. cf. phyllodiorum* / *E. kauaianum*¹

Spore wall reticulate. Aecio- or urediniospores, or *Uredo*-like teliospores

Spores with conspicuous, smooth, stalk-like basal contraction, apically thickened to 4–8 μm, on average longer than 40 μm (urediniospores) *E. cf. phyllodiorum*
 Spores without smooth basal contraction; if stalk-like process present than short and usually subreticulate or rugose

Spores (aeciospores) not thickened apically, on average shorter than 40 μm, associated with spermogonia, often with teliospores *E. koae*

Spores slightly to strongly thickened apically, associated with spermogonia or not

Sori covering witches’ brooms, spermogonia often present

Spore apex thickened to 6–15 μm (*Uredo*-like teliospores) *E. acaciae*
 Spore apex thickened to 4–7 μm (*Uredo*-like teliospores or aeciospores)
 *E. hawaiiense* / *E. kauaianum*²

Sori not on witches’ brooms, not with spermogonia, spore apex thickened to 4–7 μm (urediniospores) *E. kauaianum*

A number of Australian specimens determined as *E. digitatum* tallied with the latter in essential morphological characters but were found to be sufficiently distinct to be described as separate species. For them the new species *E. walkerianum*, *E. parvum* and *E. violae-faustae* are proposed.

Endoraecium walkerianum R. Berndt, sp. nov. (Figs. 10, 11 and 12).

Etymology: Dedicated to John Walker, excellent mycologist and authority on rust fungi.

Spermogonia aeciis consociata in tumoribus phyllodiorum et fructuum usque ad 1 cm diam. Aecia generi *Uredo* similia primum spermogonia annuliforme circumdantia deinde tumores plus minusve omnino tegentia subepidermalia pulverulenta ochracea vel sordide luteo-aurantia; aeciosporae ellipsoideae rariter late ellipsoideae nonnunquam contractione basali breviter stipitifirmi delicate sulcato-rugosa praeditae, 35–48(50) × 19–25 μm (42.5 × 21.6 μm), pariete aureo ad aureo-brunneo magis saturate pigmentato apicem versus, inaequaliter crasso in parte aequatoriali, partibus crassioribus ca. 3–4.5 μm, partibus tenuioribus ca. 1.5–2 μm crasso, in apice (3)4–7(8) μm incrassato, reticulato maculis ca. 1.5–2.2 μm diam. margine ca. 1 μm alto limitatis, poris germinationis 5–7 praecipue 6 plus minusve aequatorialibus sine papillis. Uredinia et urediniosporae ignota. Telia in phyllodiis sparsa minuta rotunda pulvinata aurea semicompacta et fibrosa; teliosporae fusiformes ellipsoideae vel cuneatae hilum versus attenuatae, 44–60 × 15–21 μm (pro 20 sporis 51.2 × 17.4 μm), pariete levi ca. 1.5 μm crasso in apice 7–16 μm subhyalino ad aureo in apice, processus apicales absunt vel 1–4 conici.

In phyllodiis leguminibusque *Acaciae penninervis* Sieber ex DC. et *A. obliquinerviae* Tindale probabiliter.

Spermogonia together with aecia on large blister-like hypertrophies (up to 1 cm diam.) scattered on the phyllodes

¹ For a safe distinction of both species aecio- or urediniospores are necessary. Teliospores not reported hitherto from Hawaiian *E. cf. phyllodiorum*.

² Intermediate forms occur with regard to the thickness of the apex that are difficult to assign to either *E. acaciae* or *E. hawaiiense*. Aeciospores of *E. kauaianum* unaccompanied by uredinio- or teliospores are hardly distinguishable from aeciospore-like teliospores of *E. hawaiiense*.



Fig. 10 *Endoraecium walkerianum* (HeRB 5962). Infected phyllodes of *Acacia* cf. *obliquinervis* with blister-like hypertrophies bearing spermogonia and *Uredo*-like aecia. The sori are first ring-like (arrows) but cover the entire hypertrophies later. Bar=20 mm

and pods. Aecia *Uredo*-like, first surrounding the spermogonia like a ring, later more or less covering the entire hypertrophies, subepidermal, pulverulent, ochraceous or dull yellow-orange; aeciospores ellipsoid, rarely broadly ellipsoid, sometimes with a short, rugose or grooved stalk-like basal process, $35\text{--}48(50)\times 19\text{--}25\ \mu\text{m}$ ($42.5\times 21.6\ \mu\text{m}$), spore wall golden-yellow to golden-brown, more deeply pigmented towards spore apex, unevenly thickened around equator, thinner parts ca. $1.5\text{--}2\ \mu\text{m}$, thicker parts ca. $3\text{--}4.5\ \mu\text{m}$ thick, $(3)4\text{--}7(8)\ \mu\text{m}$ at the apex, reticulate with meshes ca. $1.5\text{--}2.2\ \mu\text{m}$ wide and ca. $1\ \mu\text{m}$ high, germ pores $5\text{--}7$, most often six, more or less equatorial, without caps. Uredinia and urediniospores unknown. Telia scattered on phyllodes, tiny, round, pulvinate, golden-yellow, semi-compact and with fibrous texture; teliospores fusiform, ellipsoid or wedge-shaped, tapering towards base, $44\text{--}60\times 15\text{--}21\ \mu\text{m}$ (mean for 20 measured spores $51.2\times 17.4\ \mu\text{m}$), spore wall smooth, ca. $1.5\ \mu\text{m}$ thick, apically $7\text{--}16\ \mu\text{m}$ thick, subhyaline to golden-yellow at thickened apex, apex without or with mostly $1\text{--}4$ stout, conical appendages.

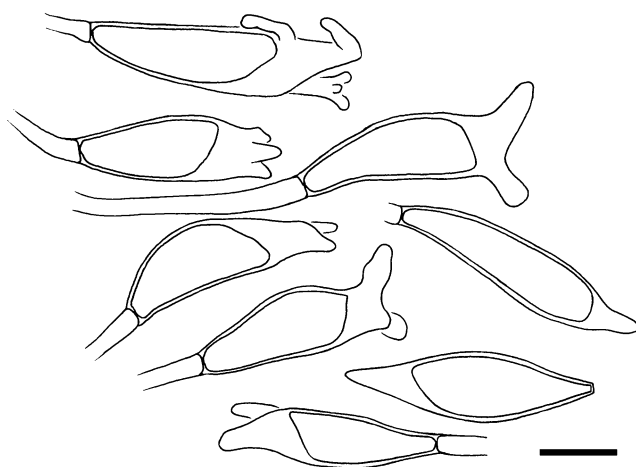


Fig. 11 *Endoraecium walkerianum* (holotype). Teliospores. Bar=20 μm

On phyllodes and pods of *A. penninervis* and *A. cf. obliquinervis*.

Holotype (SF35354, Reliq. Petrak. 1333, sub *U. phyllodiorum*): Australia, NSW: Cavan Gap, near Yass, on *A. penninervis*, leg. E. Gauba, 20 Nov. 1951. Isotypes distributed as Reliq. Petrak. 1333 (sub *U. phyllodiorum*; I [spermogonia not seen], III).

Additional material examined:

Australia, ACT: Mt. Corree near Canberra, alt. 4600 ft., on *A. penninervis*, leg. E. Gauba, 22 Dec. 1954 (SF35353, Reliq. Petrak. 1332, sub *U. phyllodiorum*; I [spermogonia not seen]). Australia, NSW/ACT: Brindabella Range, on *A. penninervis*, leg. E. Gauba, April 1959 (PUR F16457, sub *At. digitata*; 0, I). Australia, VIC: Ca. 35 km ENE of Melbourne, Mt. Donna Buang, alt. ca. 1220 m, on *A. cf. obliquinervis*, leg. C. & K. Vánky, 2 March 1996 (HeRB 5962; 0, I). Australia, NSW: Bald Rock, on *A. penninervis*, leg. J. Tierney, 26 Feb. 1984 (BRIP 14205, sub *R. digitatus*; 0, I).

Endoraecium walkerianum is very similar to *E. digitatum* which is basically different in the wider and higher meshes of the aeciospores provided with a more conspicuously rugulose bottom, a not or hardly thickened apex of the aeciospores and – generally – the presence of a uredinial state. Both species are probably closely related. *E. walkerianum* differs from *E. phyllodiorum* in several characters. The aeciospore wall is asymmetrically thickened in the equator region, the aeciospores lack a conspicuous smooth socket-like basal contraction and have a less thickened apex (Fig. 12). The aecial acervuli (Fig. 10) are large, conspicuous and have a saturated ochre colour. The teliospores of *E. walkerianum* appear to be larger than in *E. phyllodiorum*. Whether this is a constant character is uncertain given the generally high variability of the teliospores in *E. phyllodiorum* and the small number of teliospores measured in the present species. PUR F16457 was slightly different from the type in aeciospores with generally $7\text{--}8$ germ pores and a finer meshed reticulum (mesh diam. ca. $1.2\text{--}1.8\ \mu\text{m}$). As far as known, *E. walkerianum* lacks a uredinial state and has a demicyclic life cycle. The Hawaiian endemic *E. koeae* is demicyclic, too (Gardner 1994). It differs from the present species by smaller aeciospores with equally thickened walls and by different teliospores. The known host plants of *E. walkerianum*, *A. penninervis* and *A. cf. obliquinervis*, are morphologically rather similar and possibly closely related.

Endoraecium parvum R. Berndt, sp. nov. (Figs. 13 and 14).

Etymology: Denominating the comparatively small aecio- and urediniospores.

Spermogonia aeciis vel teliis consociata, amphigena, in maculis obscuris phyllodiorum non vel lenissime hypertrophicis vel in pedicellis. Aecia parva generi *Uredo* similia

Fig. 12 *Endoraecium walkeria-num*. **a, b.** Aeciospores in optical section (holotype) and with focus on spore surface (SF35353). **c.** Aeciospores showing apical thickening and unevenly thickened lateral wall of the spores (arrows) depending on their orientation (SF35353). **d.** Teliospores among aeciospores (holotype). Bars=20 μm

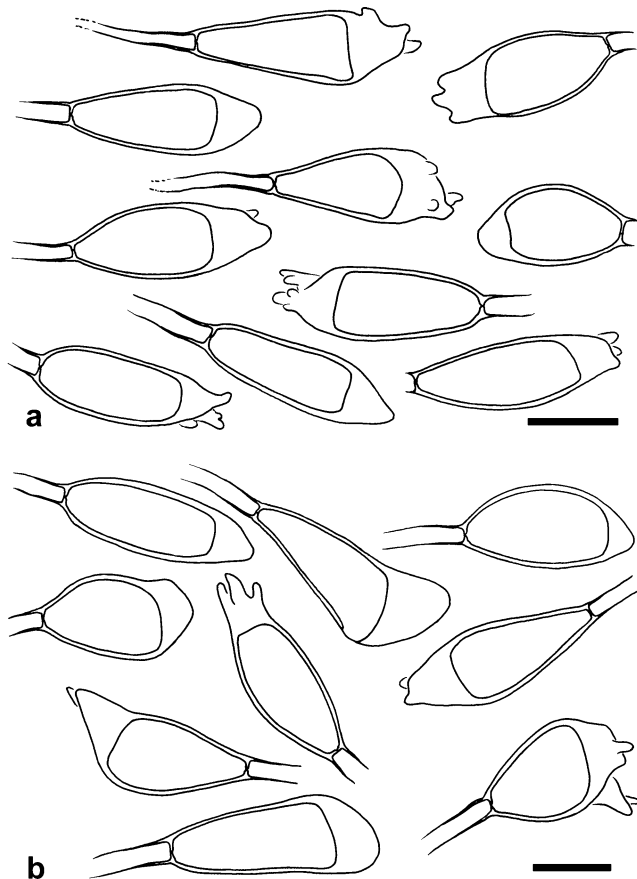
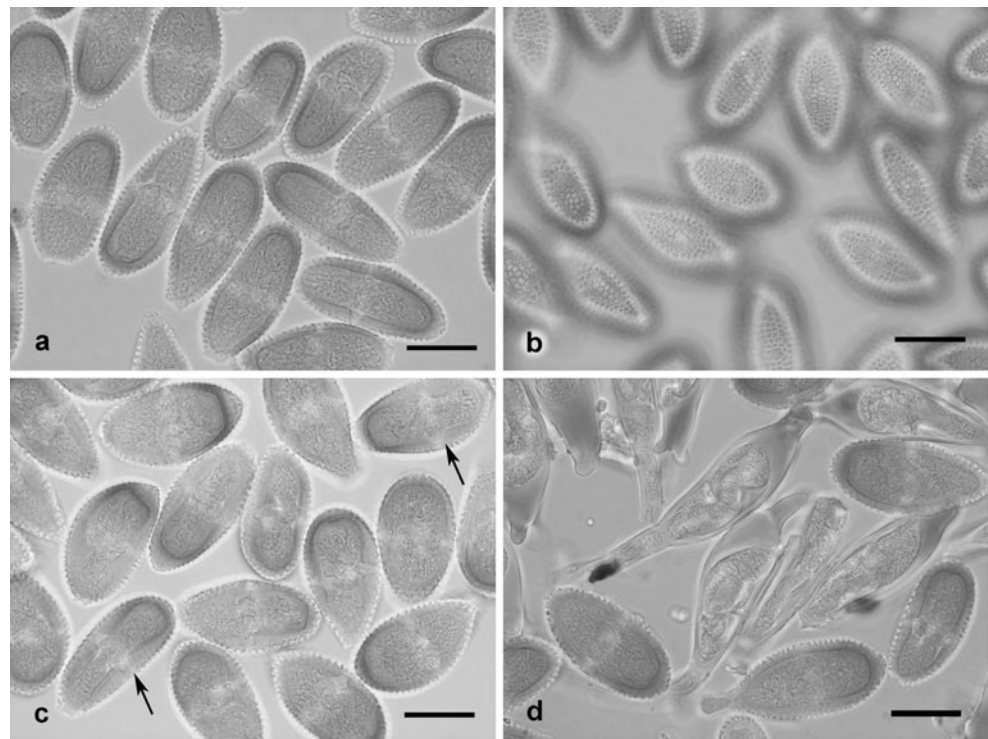
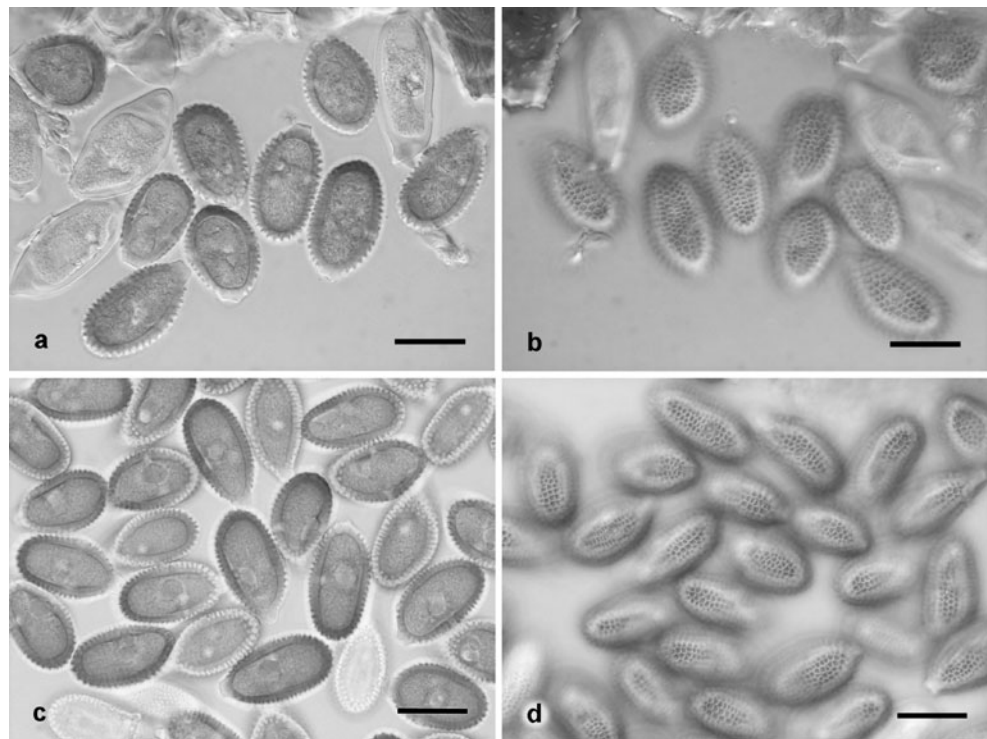


Fig. 13 *Endoraecium parvum*, teliospores. **a.** BRIP 7543 (holotype). **b.** BRIP 23071a. Bars=20 μm

crebre aggregata subepidermalia ferruginea; aeciosporae ellipsoideae vel late ellipsoideae apicaliter rotundatae, plerumque contractione basali breviter stipitifor mi levi, 27–38(42)×16–22 μm (33.0×18.5 μm), pariete pallide aurantio-brunneo, (2.5)3–4 μm crasso circa aequatorem, non vel leniter incrassato in apice, reticulato maculis ca. 1.2–2.3 μm diam. margine delicato limitatis, poris germinationis 3–5 praecipue 4 plus minusve aequatorialibus ad subaequatorialibus sine papillis. Uredinia sparsa vel laxe aggregata amphigena in maculis obscuris vel senescentibus phyllodiorum; urediniosporae ellipsoideae vel late ellipsoideae late obovoideae magis rariter oblongae vel subclavatae, apicaliter rotundatae ad late conicae, plerumque contractione basali breviter stipitifor mi subhyalina levi, 27–38(44)×16–22.5 (31.9×19.3 μm), pariete pallide aurantio-brunneo, ca. 3 μm crasso circa aequatorem, non vel leniter incrassato (ad 4–5 μm) in apice, reticulato maculis ca. 1.2–2.1 μm diam., poris germinationis 3–5 praecipue 4 plus minusve aequatorialibus sine papillis. Telia in phyllodiis spermogoniis consociata et aggregata vel sparsa et secum viventia nonnunquam ex aeciis nascentia, minuta pulvinata semi-compacta fibrosa, ferruginea albescentes post germinationem basidiorum; teliosporae formae varabili ellipsoideae vel late ellipsoideae magis rariter subfusiformes subrhomboidae vel subtriangulares, 32–52(56)×15–22 μm (42.0×18.7 μm), pariete levi ca. 1–2 μm crasso subhyalino ad pallide aureo, apice magis saturate pigmentato nonnunquam flavo-virescenti, 5–15 μm crasso formae variabili simpliciconico vel digitato processibus apicalibus 1–paucis conicis verruciformibusve, per maturitatem ex poro germinationis subapicali germinantes.

Fig. 14 *Endoraecium parvum*. **a, b.** Aeciospores in optical section, together with some teliospores, and with focus on surface reticulum (BRIP 6063). **c, d.** Urediniospores in optical section and with focus on surface reticulum (BRIP 23071a). Bars=20 μm



In phyllodiis *Acaciae cunninghamii* Hook. et *A. specierum* Spermogonia associated with aecia or telia, amphigenous on dark, not or hardly swollen spots of phyllodes or pedicels. Aecia small, *Uredo*-like, in dense groups, subepidermal, ferruginous; aeciospores ellipsoid to broadly ellipsoid, apically rounded, generally with a smooth, contracted stalk-like base, 27–38(42) \times 16–22 μm (33.0 \times 18.5 μm), spore wall pale orange-brown, (2.5)3–4 μm thick in equator region, not or hardly thickened at the apex, reticulate, meshes 1.2–2.3 μm wide, confined by delicate, smooth ridges, germ pores 3–5, often 4, equatorial to subequatorial, without caps. Uredinia single or in small groups, amphigenous on dark or senescent spots of phyllodes, subepidermal, pulverulent, ferruginous; urediniospores ellipsoid to broadly ellipsoid, broadly obovoid, more rarely oblong or subclavate, apically rounded or sometimes broadly conical, generally with a subhyaline, smooth, contracted stalk-like base, 27–38(44) \times 16–22.5 (31.9 \times 19.3 μm), spore wall pale orange-brown, ca. 3 μm thick in equator region, not or hardly thickened at the apex (to 4–5 μm), reticulate, meshes 1.2–2.1 μm wide, confined by smooth ridges, germ pores 3–5, often 4, more or less equatorial, without caps. Telia tiny, pulvinate, semi-compact and with fibrous texture, orange-brown or with whitish bloom after germination of basidia, either in groups and associated with spermogonia, some probably deriving from old aecia, or scattered and not closely associated with other sori; teliospores variable in shape, ellipsoid to broadly ellipsoid, more rarely subfusiform, subrhomboid or subtriangular, 32–52(56) \times 15–22 μm (42.0 \times 18.7 μm), spore

wall smooth, subhyaline to pale golden, sometimes with greenish tinge, at the apex slightly more deeply pigmented, ca. 1–2 μm thick, at the apex thickened to 5–15 μm , apex variable in shape, simple and conical or with one to few knob-like outgrowths or digitate with one to few, generally short and simple processes, germination upon maturity from a germ pore located proximal to the thickened spore apex.

On phyllodes of *A. cunninghamii* and *Acacia* spp.

Holotype (BRIP 7543): Australia, QLD: Caloundra, on *A. cunninghamii* (= *A. leiocalyx* (Domin) Pedley var. *leiocalyx*?), leg. ST Blake, 25 Aug. 1932 (sub *R. digitatus*; 0, I, III). The same collection is represented in BRIP 6045 (isotype).

Additional material examined:

Australia, QLD: Brisbane, Mt. Coot-tha, on *Acacia* sp. (narrow-leaved'), leg. RE Harrison, 5 May 1955 (BRIP 6063 and 7548, sub *R. digitatus*; 0, I, III). Cairns, Mt. Whitfield, on *Acacia* sp. (possibly *A. mangium*), leg. V. Faust-Berndt & R. Berndt no. Austr 41, 20 Aug. 2006 (ZT Myc 3019; II). On *A. concurrens* Pedley. Brisbane, Indooroopilly, Meiers Road, leg. DE Shaw, 30 Sept. 1996 (BRIP 23071a, sub *R. digitatus*; II, III). On *A. mangium*. Near Mission Beach, leg. I. Hood, 5 April 1995 (BRIP 23266, sub *R. digitatus*; II). Australia, NT: On *A. mangium*. Sylvatech Pine Forest, leg. PM Stephens, 16 June 2003 (BRIP 42379, sub *R. digitatus*; 0, I, III).

The short aecio- and urediniospores (Fig. 14) distinguish *E. parvum* from other species of the *E. digitatum* complex. In addition, the teliospores are relatively short and their

apices quite often not or only slightly digitate (Fig. 13). The life cycle appears to be variable. In BRIP 7543/6045 and BRIP 6063/7548, spermogonia were associated with aecia or with telia or with aecia and telia, of which some possibly developed from old aecia. The sori occurred on darkly decoloured but otherwise more or less unaltered phyllode spots, not on galls or blister-like swellings. In BRIP 23071a and BRIP 23266, no spermogonia and aecia were present but telia and/or uredinia on non-hypertrophied parts of phyllodes as well. These specimens could be linked to the forms with aecia by the virtually identical teliospores and the urediniospores which closely resembled the aeciospores. The known hosts, *A. concurrens*, *A. cunninghamii* and *A. mangium* belong to *Phyllodineae* section *Juliflorae*.

Endoraecium violae-faustae R. Berndt, sp. nov. (Figs. 15 and 16).

Etymology: Dedicated to Viola Faust-Berndt, indefatigable collector and companion on field stays, discoverer of the rust fungus.

Spermogonia aeciis consociata in maculis tumidis phyllodiorum usque ad 8×6 mm largis obscure olivaceis. Aecia generi *Uredo* similia, parva pulverulenta ferruginea; aeciosporae plus minusve ellipsoideae ad subfusiformes,

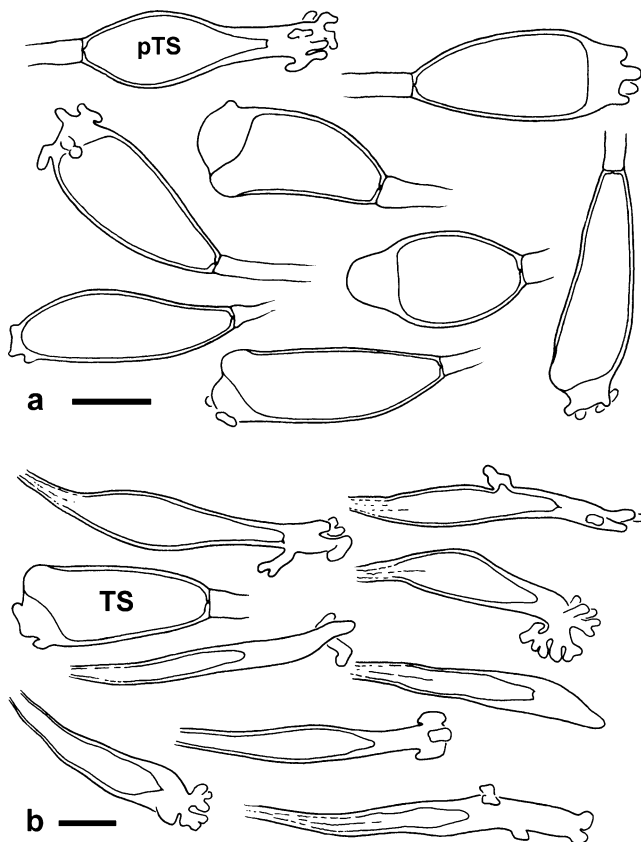


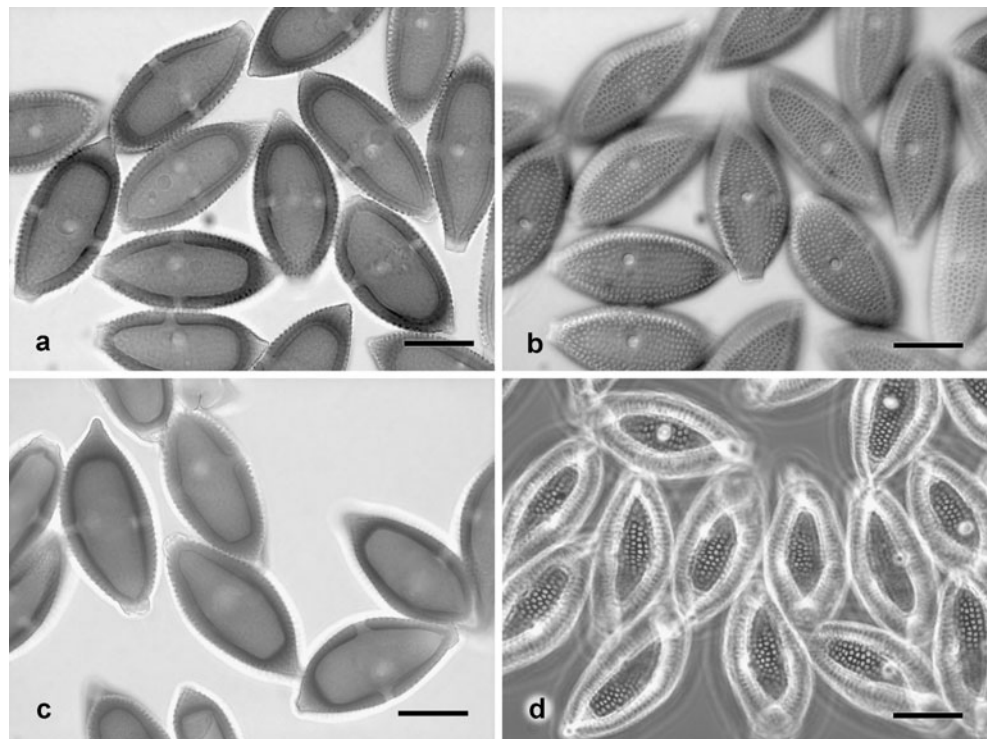
Fig. 15 *Endoraecium violae-faustae* (ZT Myc 3018). **a.** Teliospores. 'pTS' marks a teliospore resembling a paraphysis. **b.** Paraphyses from telia. 'TS' indicates a single teliospore. Bars=20 µm

saepe contractione basali pedicelliformi brevi levique praeditae, apice conico vel subapiculato, 45–60×18–25 µm (52.1×21.6 µm), pariete aurantiaco-brunneo foveolato-reticulato maculis ca. 1.1–1.8 µm diam. basim et apicem versus angustioribus, ca. 3 µm crasso in parte aequatoriali, incrassato usque ad (5)6–9(10) µm in apice, poris germinationis 4–5 plus minusve aequatorialibus sine papillis. Uredinia minuta subepidermalia, in phyllodiis utrinque sparsa vel laxe aggregata pulverulenta ferruginea, saepe paraphysibus flavescens vel stramineis, ut in teliis, circumdata; urediniosporae generaliter aeciosporis similes, ellipsoideae ad subfusiformes, plerumque contractione basali pedicelliformi brevi levique praeditae, apice conico vel subapiculato, 40–57(64)×20–25.5 µm (48.5×22.5 µm pro typo; magnitudo variationis 44.6–52.1×22.4–27.1 µm), pariete aurantiaco-brunneo interdum inconspicue laminato foveolato-reticulato maculis ca. 1.1–1.8(2.0) µm diam. basim et apicem versus angustioribus et tenuioribus, ca. 3–3.5(4) µm crasso in parte aequatoriali incrassato usque ad 5–12 µm in apice, poris germinationis 3–5, plerumque 4 plus minusve aequatorialibus sine papillis. Telia subepidermalia, in phyllodiis inter uredinios sparsa, minuta vix confluentia flavo-brunnea ad aurantiaco-brunnea deinde obscure ferruginea semcompacta et textura fibrosa; teliosporae ellipsoideae ad late ellipsoideae, interdum cuneatae ad obconicae, 32–66(76)×16–25 µm (57.4×19.5 µm), pariete dilute citrino ad aureo levi ca. 1–1.5 µm crasso, in apice incrassato 5–10(12) µm, processu singulo ad paucis conicis cylindricis vel gongylodibus integris praeditae, interdum cum processibus singulis inferioribus, per maturitatem ex poro germinationis subapicali germinantes; pedicellis hyalinis pariete leniter incrassato persistentibus; paraphysibus numerosis interpositis, filiformibus ad leniter clavatis, 80–136(150)×8–16 µm, levibus, parte apicali incrassato ca. 10–35 µm longo processibus uno ad paucis brevibus variabilissimis saepe cylindricis vel conicis praeditis.

In phyllodiis *Acaciae* spp.

Spermogonia together with aecia on blister-like, up to 8×6 mm large, dark or brownish green hypertrophied swellings of phyllodes. Aecia *Uredo*-like, small, subepidermal, pulverulent, ferruginous; aeciospores ellipsoid to subfusiform, often with a short smooth stalk-like base, apically conical to subapiculate, 45–60×18–25 µm (52.1×21.6 µm), spore wall dull orange-brown, reticulate-foveolate with ca. 1.1–1.8 µm wide meshes which become finer and shallower towards the spore apex and base, laterally ca. 3 µm thick, apically thickened to (5)6–9(10) µm, germ pores 4–5, more or less equatorial, without caps. Uredinia tiny, subepidermal, scattered over entire surface of phyllodes or in loose groups, pulverulent, ferruginous, often bordered by a fringe of yellowish or straw-coloured paraphyses which are similar to telial paraphyses; urediniospores essentially like the aeciospores, ellipsoid to fusiform, often with a subhyaline, short,

Fig. 16 *Endoraecium violae-faustae*. **a, b.** Aeciospores in optical section and with focus on spore surface (holotype). **c, d.** Urediniospores in optical section and with focus on spore surface (ZT Myc 3018). Bars=20 μ m



smooth stalk-like base, apically conical to subapiculate, 40–57(64)×20–25.5 μ m (48.5×22.5 μ m for type; range of means 44.6–52.1×22.4–27.1 μ m), spore wall dull orange-brown, sometimes indistinctly layered, reticulate-foveolate with ca. 1.1–1.8(2.0) μ m wide meshes which become finer and shallower towards the spore apex and base, laterally about 3–3.5(4) μ m thick, apically thickened to 5–12 μ m, germ pores 3–5, mostly 4, more or less equatorial, without caps. Telia subepidermal, scattered on phyllodes among the uredinia, tiny and hardly confluent, yellowish-brown to orange-brown, later dull orange-brown, semi-compact with fibrous texture; teliospores ellipsoid to broadly ellipsoid, sometimes wedge-shaped to obconical, 32–66(76)×16–25 μ m (57.4×19.5 μ m), spore wall faint lemon-yellow to golden-yellow, smooth, ca. 1–1.5 μ m thick, apically thickened to 5–10(12) μ m, at apex with one to several conical, cylindrical or knob-like entire projections, more rarely with single projections more proximal, germinating at maturity from below of the apical thickening, pedicels hyaline, slightly thick-walled and persistent though collapsing; paraphyses numerous, interspersed among teliospores, filiform or slenderly clavate, most often partially compressed, 80–136(150)×8–16 μ m, smooth, with a 10–35 μ m long apical thickening which bears one to few very irregular, short, often cylindrical or conical outgrowths.

On phyllodes of *Acacia* spp.

Holotype (BRIP 53388). Australia, QLD: Cairns, Kuranda, Barron Gorge Natl. Park, ‘Mc Donald’s trail’, on *Acacia* sp., leg. V. Faust-Berndt & R. Berndt no. Austr 47, 18 Aug. 2006 (ZT Myc 3022, isotype; 0, I, II, III).

Additional material examined:

Australia, QLD: On *Acacia* sp. Cairns, Mt. Whitfield conservation area, first (main) lookout, leg. V. Faust-Berndt & R. Berndt no. Austr 39, 24 Aug. 2006 (ZT Myc 3018; II, III). Cape York, leg. GS Pegg, Nov. 2001 (BRIP 28985 and 28987, sub *R. digitatus*; II). On *A. aulacocarpa*. Rockingham Bay, without collector and date (SF35351, sub *U. phyllodiorum*, ex herb. Sydow; II, III). Cape Tribulation, Emmagen Creek, leg. RG Shivas, 4 Aug. 1993 (BRIP 21805, sub *R. digitatus*; II). On *A. crassicarpa* A. Cunn. ex Benth. Cape York Peninsula, 9 km N of Bamaga, leg. JL Alcorn, 30 May 1981 (BRIP 13711, sub *R. digitatus*; II, III). Injinoo, leg. RI Davis, 15 Jan. 1998 (BRIP 26599, sub *R. digitatus*; II). On *A. flavescens* A. Cunn. ex Benth. Peach no. 7, Coen, leg. RG Shivas & M. Gunther, 18 July 1999 (BRIP 25816, sub *R. digitatus*; II). Australia, NT: Darwin, Fog Dam, on *Acacia* sp., leg. R. Berndt & V. Faust-Berndt, 23 Aug. 2003 (BRIP 44497; II, III).

Endoraecium violae-faustae differs from *E. phyllodiorum* by larger aecio- and urediniospores which are foveolate rather than reticulate, which have a more pronounced apical thickening and are apically more acute (Fig. 16). The most obvious difference is the presence of characteristic paraphyses in the uredinia and telia (Fig. 15b). Their abundance is variable. McAlpine (1906) described uredinial and telial paraphyses for *E. phyllodiorum*. One may assume that his observation was based on specimens of *E. violae-faustae* as I could not find paraphyses in *E. phyllodiorum*. His description suggests a

different morphology of the paraphyses, however, as they are said to be “variously shaped, but generally somewhat cylindrical, thickened and rounded at the apex”. The teliospores of *E. violae-faustae* (Fig. 15a) were very variable especially with regard to spore size. In the type collection, they measured 32–50×18–24 μm (40.5×21.4 μm), while they were much longer, (47)50–66(76)×16–23(25.5) μm (57.4×19.5 μm), in ZT Myc 3018. As all other characters tallied well I have no doubt that this specimen belongs to *E. violae-faustae* as well. BRIP 44497 was preliminarily assigned to the present species. Its urediniospores were considerably smaller than in the other specimens (mean 39.0×20.8 μm) and the meshes of the spore reticulum wider. The typical uredinial paraphyses were present, however.

E. violae-faustae is known up to now on *A. aulacocarpa*, *A. crassicarpa* (both *Phyllodineae* section *Juliflorae*), and *A. flavescens* (*Phyllodineae* section *Plurinerves*).

The following key covers the known Australian species of the *E. digitatum* complex and is based on aecial and/or uredinial characters. Telial characters were included only in as far as they aid identification.

Aecio- and urediniospores with foveolate spore surface, large (generally longer than 44 μm on average), often with subacute apex. Uredinia and telia with ± cylindrical or club-shaped, apically thick-walled and often shortly digitate paraphyses (Figs. 15 and 16) *E. violae-faustae*
 Aecio- and/or urediniospores with reticulate surface, generally shorter than 44 μm on average and apically rounded or conical, sori without paraphyses, if paraphyses are present with other characters than in *E. violae-faustae*

Aecio- and urediniospores generally with a smooth, stalk- or socket-like basal contraction

- Majority of aecio- and urediniospores between 35 and 48 μm long, apically slightly to conspicuously (5–10 μm) thickened (Figs. 6 and 7a, b) *E. phyllodiorum*
- Aecio- and urediniospores mostly between 27 and 38 μm long, apex not or only slightly thickened (Fig. 14) *E. parvum*
- Aecio- and urediniospores without a stalk-like spore base or with a short, subreticulate to rugose, not a smooth one

Aecio- and urediniospores apically not or hardly thickened, reticulate with wide meshes (to 3 μm) confined by delicate, somewhat uneven and high ridges, bottom of meshes conspicuously rugulose (Figs. 2 and 3); teliospores (Fig. 1) often profusely digitate with long, tortuous and branching processes *E. digitatum*

Uredinial state unknown. Aeciospores with thickened apex, more narrowly meshed reticulum and coarser, even ridges between meshes (Fig. 12) *E. walkerianum*

Conclusions and general discussion

Endoraecium digitatum, a species complex – For more than a century *E. digitatum* was regarded as a single species with a wide distribution in Australasia and a disjunct area in Hawaii. Only recently Walker (2001) pointed out to the high variability of this rust fungus and suggested that it may comprise several taxa. In the present paper, four new species and the known *E. phyllodiorum* are distinguished from *E. digitatum* based on characters observable with light microscope. Another species apparently related to this complex is the Hawaiian *E. angustiphyllodium*.

E. digitatum, as understood hitherto, has been reported on numerous *Acacia* species and from an extensive area of distribution. It could be shown in the present study that reports of *E. digitatum* from the Hawaiian Islands do not belong to this species whose proven records are restricted to Australia (SA, VIC, NSW, QLD). The Hawaiian records of ‘*E. digitatum*’ were demonstrated to represent two species, the new *E. kauaianum* and *E. cf. phyllodiorum*. The latter would be the only species shared between Australia and Hawaii. Only uredinia were present on specimens from Hawaii and their identity with Australian representatives of *E. phyllodiorum* is therefore only indicated by the overall similarity of the urediniospores. Yet, slight differences noticed between the urediniospores allow for the possibility that two species are involved. Another clue for this hypothesis would be that, according to Gardner (1994), ‘*E. digitatum*’ has never been observed in Hawaii on any of the introduced Australian acacias. A more definite decision will only be possible after the remaining spore states of the supposed *E. phyllodiorum* have been discovered in Hawaii and by DNA sequence comparisons.

The host range of *E. digitatum* s. str. was shown to be narrower than assumed but is still rather broad comprising presently three phyllodinous and four compound-leaved *Acacia* spp. from subgen. *Phyllodineae*. Specimens from compound-leaved acacias revealed minor morphological differences to specimens from phyllodinous acacias but did not seem to represent a distinct species. It should be remarked in this connection that the morphological difference between phyllodinous and compound-leaved adult foliage needs not reflect a wide phylogenetic distance of the respective acacias. This was demonstrated by Murphy et al. (2010) who found out that some phyllodinous and pinnately-leaved acacias, among them the hosts *A. falciformis* and *A. irrorata*

of *E. digitatum*, fell together in a common clade, the “*Botryocephalae* subclade”. *Acacia penninervis*, host of *E. walkerianum*, is also a member of the *Botryocephalae* subclade. This phylogenetic relatedness of the hosts together with the morphological similarity between *E. digitatum* and *E. walkerianum* indicates a close kinship of both species.

The remaining Australian *Endoraecium* spp. also occur on more than one host species, *E. phyllodiorum* and *E. violae-faustae* even on members of different sections of *Phyllodineae*. It can be misleading to deduce from this finding a low host specificity of *E. phyllodiorum* and *E. violae-faustae* as sections distinguished within *Phyllodineae* have been shown to be poly- or paraphyletic (Murphy et al. 2010). Other *Endoraecium* spp., as *E. bicinctum* and *E. tierneyi*, are only known from a single *Acacia* species each (Walker 2001) and may be host species-specific. It was observed that a single host species may be parasitized by more than one *Endoraecium* species, such as *A. mangium* which supports *E. parvum* and *E. phyllodiorum* or *A. aulacocarpa* hosting *E. phyllodiorum* and *E. violae-faustae*.

Life cycle and ‘correlated species’ – Some of the investigated species were found to exhibit variable spore combinations and to present themselves with different life cycles. *E. phyllodiorum* was especially variable with macro-, demi- and microcyclic specimens encountered. The taxonomic significance of such life cycle variants has been judged in different ways. In some cases, they were assigned to a single species, e. g. in *Puccinia helianthi* Schw. (Jackson 1931). In other cases, life cycle variants were regarded as separate ‘correlated species’, like in the species pair *P. punctata* Link / *P. celakovskyana* Bub. (Gäumann 1959) or in *P. tragopogonis* Corda and *P. brachycyclica* E. Fischer (Gäumann 1959). Referring to the correlated hetero-microcyclic *P. monoica* (Peck) Arth., the microcyclic *P. holboellii* (Hornem.) Rostr. and the demicyclic *P. consimilis* Ellis & Everh., Arthur (1962, p. 149) annotated that “the collective species is remarkable in possessing independent heteroecious, autoecious, and microcyclic conditions, which can be considered to be either separate species or else varieties of one polymorphic species”. The latter opinion was held by Roy et al. (1998) in a molecular study of the “*Puccinia monoica* complex”.

I regard macro-, demi- and microcyclic forms of *E. phyllodiorum* and of other *Endoraecium* spp. as life cycle variants of the parental species, not as separate species. Their belonging to a single species is shown by their morphological similarity and the existence of specimens bearing different combinations of spore states. Another case of related life cycle variants in *Endoraecium* appears to exist in Hawaii. Gardner (1991) described a microcyclic *Endoraecium* on *A. koa*. He considered it a derivative of the macrocyclic ‘*E. digitatum*’ as their teliospores were indistinguishable. In

contrast to my point of view, Gardner (1991) segregated the microcyclic form as *E. angustiphyllodium* from the parental species. Hawaiian ‘*E. digitatum*’ was shown to represent two species, *E. kauaianum* and *E. cf. phyllodiorum* – the latter only known with uredinia in Hawaii. Therefore, *E. angustiphyllodium* cannot be linked to either of them by teliospore morphology at present and it seems reasonable to keep it separate.

Endoraecium was originally erected for two endocyclic rust fungi, *E. acaciae* and *E. hawaiiense*, that are likely to have descended from parental species with more complex life cycle and classified in *Racospermyces* by Walker (2001). Scholler and Aime (2006) combined all described *Racospermyces* spp. into the older genus *Endoraecium*. This is justified if the following prerequisites are fulfilled: That *Endoraecium* is as a telial genus and that it belongs to the same genus as *Racospermyces*. The telial nature of *Endoraecium* could be questioned. Hodges and Gardner (1984) described that spores germinated with a germ tube into which the nuclei of the dikaryon migrated. After having moved to the tip of the tube they were cut off by formation of a septum. The subsequent nuclear behaviour was suggestive of karyogamy and meiosis but the authors conceded the absence of a typical phragmobasidium and basidiospore formation. As many microcyclic rust fungi are well known to exhibit an unusual basidium morphology and aberrant karyology (comp. review by Ono 2002), I prefer to accept the telial nature of *Endoraecium*.

A close relationship between *E. acaciae*, *E. hawaiiense* and *Racospermyces* seems to be undeniable. It is strongly indicated by similar spore morphology, host range and results obtained from comparison of DNA sequences. According to the latter *Endoraecium* and *Racospermyces* are congeners (Scholler and Aime 2006). The endocyclic *Endoraecium* spp. do not form a natural group and their affiliation with any of the potential parental *Endoraecium* spp. is uncertain. *E. hawaiiense* may be derived from *E. kauaianum* as the teliospores of the former and aeciospores of the latter are hardly distinguishable. *E. acaciae* clustered with *E. koae* in the phylogram published by Scholler and Aime (2006). This result is not supported by spore morphology, the aeciospores of *E. koae* being apically not thickened while the *Uredo*-like teliospores of *E. acaciae* are strongly thickened. It should be noted that *E. acaciae* is connected with *E. hawaiiense* by morphologically intermediate forms (unpublished results).

In Australia, some 1000 species of *Acacia* occur among them only 11 native species that do not belong to subgenus *Phyllodineae* (Maslin et al. 2003, www.worldwidewattle.com). Though there does not seem to be a fixed ratio between the species numbers of a given plant taxon and its rust fungi (Berndt 2008) it is nonetheless astonishing that only very few *Endoraecium* species have been reported on

the extremely speciose *Phyllodineae*. The discovery that *E. digitatum* s. l. of Australia includes five distinct species suggests that more *Endoraecium* species may be discovered on Australian acacias if surveyed closely. It also shows that many overlooked species may still be hidden among allegedly well-known rust fungi. Last but not least this finding emphasizes the importance of thorough morphological studies to recognize meaningful taxonomic entities and to discern ecological or biogeographic patterns as a basis for ongoing research.

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