A REVISION OF THE GENUS *ATELOCAUDA* (UREDINALES) AND DESCRIPTION OF *RACOSPERMYCES GEN. NOV.* FOR SOME RUSTS OF *ACACIA*

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Abstract

The genus *Atelocauda* is redefined with two species, the type species *A. incrustans* on *Lonchocarpus* from Central America and *A. shivasii sp. nov.* on *Ormosia* from Queensland, Australia. Subcuticular type 7 pycnia, lobed echinulate aecial and/or uredinial urediniospores, unicellular pedicellate ornamented pigmented teliospores and hosts in Fabaceae *s. str.* characterize the genus. Five *Acacia* rusts more recently included in *Atelocauda* are redisposed in *Racospermyces gen. nov.*, and a sixth, *R. tierneyi sp. nov.* on *Acacia harpophylla* from Queensland, is described. Species of *Racospermyces* have subepidermal type 5 pycnia, unlobed reticulate aecial and/or uredinial urediniospores, unicellular pedicellate smooth or mainly ornamented lightly pigmented teliospores and hosts in Mimosaceae. The affinities of *Atelocauda* appear to lie with some Central and South American species of *Dicheirinia*. It is suggested that *Racospermyces* is Australasian in origin, associated with groups of Australasian and Pacific species of *Acacia* placed by some authors in the segregate genus *Racosperma*. Keys to the genera and species are given.

Introduction

Atelocauda incrustans Arthur & Cummins (1933), the type species of *Atelocauda*, was described from two collections made in Panama in 1920 on leaves of *Lonchocarpus* sp. (Fabaceae). Subcuticular, aparaphysate pycnia (type 7 of Hiratsuka & Hiratsuka 1980) and subepidermal telia producing unicellular, brown, pedicellate teliospores ornamented with block-like warts characterized the genus. No other spore stage was described. Arthur & Cummins (1933) commented that the genus resembled *Uromyces* in general appearance, except for the subcuticular pycnia, and that teliospore wall ornamentation was similar to that seen in *Dicheirinia* and *Diabole*. A relationship to *Pileolaria*, with both genera having teliospores borne singly on their pedicel, was also noted. In a discussion of species of *Ravenelia* and *Dicheirinia* on *Lonchocarpus*, Cummins (1937) stated that *A. incrustans* on the same host genus could '... be considered as directly derived from *Dicheirinia* by continued simplification'.

In their summary of rust genera, Thirumalachar & Mundkur (1949) accepted *Atelocauda* as a valid genus but Thirumalachar & Kern (1955) reduced *A. incrustans* to synonymy under *Pileolaria* as *P. incrustans* (Arthur & Cummins) Thirum. & F. Kern 1955. This decision was accepted by Cummins (1959, p. 76) in his first compilation of rust genera and in his treatment of North American leguminous rusts (Cummins 1978). Hiratsuka & Hiratsuka (1980) used the binomial *P. incrustans* in their list of pycnial types in the rusts.

Atelocauda remained monotypic until Cummins & Hiratsuka (1983) recognized it as distinct from *Pileolaria* and transferred to it three *Acacia* rusts described originally as species of *Uromyces*. These were *U. bicinctus* McAlpine 1906 on *Acacia fasciculifera* Benth. from Queensland, Australia, *U. digitatus* G. Winter 1886 on several *Acacia* spp. from Australasia and Hawaii and *U. koae* Arthur in F. Stevens 1925 on *A. koa* A. Gray in Hawaii. They expanded the original description to include characters derived from the *Acacia* rusts *i.e.* subepidermal type 5 (as well as subcuticular) pycnia, and aecial uredinia and uredinia, producing spores with a reticulate wall ornamentation. Subsequently, two other *Acacia* rusts have been placed in *Atelocauda*. Ono (1984) transferred *Uromyces hyalosporus* Sawada 1913, described from *Acacia confusa* Merrill in Taiwan, to this genus and *Atelocauda angustiphyllodia* D.E. Gardner 1991 (as '*angustiphylloda*') was described from phyllodes and witches' brooms on *Acacia koa* var. *latifolia* (Benth.) H. St.John in Hawaii.

There are thus now six rusts included in *Atelocauda* in the sense of Cummins & Hiratsuka (1983), the type species on *Lonchocarpus* (Fabaceae) and five species on *Acacia* (Mimosaceae). Hodges & Gardner (1984), Ono (1984) and Gardner (1991) have all expressed doubts about the suitability of placing the *Acacia* rusts in *Atelocauda* and the same question has interested the present author for many years. This paper presents results of investigations on the type species of *Atelocauda*, on a previously undescribed species of the genus on *Ormosia* (Fabaceae) in Australia, on the relationships of *Atelocauda* to the various genera suggested by Arthur & Cummins (1933) and Cummins (1937), and on the taxonomic position of the *Acacia* rusts.

Materials and methods

Specimens studied are listed under each species. Mounts for microscopic examination were made in clear lactophenol, warmed gently to expel air and to expand the dried material and examined immediately. After scanning slides to determine the range of spore sizes present, 10 spores of each type from each specimen were measured with notes on abnormally large or small spores. Spore appendages are included in spore measurements with additional notes on the size of appendages relative to the body of the spore. Spores for SEM studies were mounted on stubs on double-sided sticky tape, gold sputter-coated in a Dynavac Minicoater SC100M and examined with a Cambridge Stereoscan 360 microscope. Herbarium abbreviations are taken from Holmgren, Keuken & Schofield (1981) and author abbreviations for fungus and plant names from Brummitt & Powell (1992). The terms and Roman numeral symbols used for rust spore states are those based primarily on morphology and used by Laundon (1967, 1973) and Savile (1968, 1988), with a qualifying term to denote function, where necessary. Thus sori that are morphologically uredinia but accompany pycnia are referred to as aecial uredinia (II^I), with the symbol II for uredinia, and the superscript ^{I} for aecia, to denote function. A more complete discussion is given by Laundon (1967). The detailed reasons for choosing this terminology rather than the 'ontogenic' system preferred by Cummins (1959), Hiratsuka (1973), Cummins & Hiratsuka (1983) and other workers will be given elsewhere. The two terminologies are summarized by Hawksworth *et al.* (1995, pp. 473–474). For fungal binomials, the year of publication is given after the author citation; where this is a reference listed in the reference list, the year is enclosed in brackets, otherwise no brackets are used.

The position of lesions and sori on host organs is described using terms defined by Pascoe & Sutton (1986). For leguminous hosts, family concepts used in the *Flora of Australia* series are adopted here, with Fabaceae *s. str.*, Mimosaceae and Caesalpiniaceae as separate families. The identity of hosts given is that on the herbarium labels but checking of many of these is necessary, especially those in the *Acacia aulacocarpa* group, in the light of the recent revision by McDonald & Maslin (2000). Accurate host identification is essential in determining the precise host ranges and geographic distributions of these rusts, especially as some *Acacia* rust species appear to be complexes of closely related but distinct taxa, each perhaps confined to one or a small group of hosts.

Taxonomy

The type species of *Atelocauda*

Two collections made in the Department Bocas del Toro, Chinguinola, Panama were listed in the original description of *Atelocauda incrustans*. The type collection, PUR 44631, was made in August 1920 by J.R. Johnston and the details given on the specimen label are the same as those in the original description. The other collection, PUR 44632, made by M.A. Carleton (No. 12) on 15 August 1920 has the additional locality 'United Fruit Co., Farm Six' given on the specimen label. There is no evidence that the two collections are portions of the one gathering. A duplicate of PUR 44631 is also present in K. The three specimens have been examined. All show dark brown leaf lesions which penetrate the leaf thickness and occur often on either the leaf midrib or a main lateral vein. Pycnia, telia and teliospores as described originally were found on all specimens and agreed with the brief original description. Pycnia and telia were present also on a few larger lesions with whitish centers and dark borders. On PUR 44632, aecial uredinia were found surrounding pycnia on one lesion. They contained a very few teliospores characteristic of the species and many brown lobed aecial urediniospores. The lesion bearing them was on the leaf midrib and in macroscopic appearance was not different from lesions bearing pycnia and telia. Aecial urediniospores have not been found previously in this species and are described fully below.

Atelocauda incrustans Arthur & Cummins, *Annales Mycologici* **31,** 41 (1933)
Pileolaria incrustans (Arthur & Cummins) Thirum. & F. Kern, *Bulletin of the Torrey Botanical Club* **82,** 105 (1955)

Leaf lesions dark brown, both amphigenous and hologenous, 1–2 (–3) mm diam., often on the midrib or a main side vein and then elongated along the vein, to 4 mm long, thickened, bearing a mass of erumpent sori surrounding a central depressed area with minute pycnia. *Pycnia* (Fig. 4) subcuticular, 60–90 µm diam., 30–50 (–55) µm high, basal layer of hyaline, cylindrical sporogenous cells to 20 µm long, 2 µm wide, with a hyaline *peridium* (Fig. 5) of elongated to hexagonal cells 6–7 × 3–5 µm. *Pycniospores* hyaline, subglobose to somewhat angular, 2–2.5 µm diam. *Aecial uredinia* surrounding pycnia on one leaf midrib spot, to 150 µm diam., subepidermal. *Aecial urediniospores* (Figs 1, 9) reddish brown in a powdery mass, pedicellate, individually triangular or rarely quadrangular, 20–24 × 20–24 µm, with 3, rarely 4, obtuse, apically rounded lobes making up

the body of the spore, each lobe 10–12 µm wide at a distance of 4 µm below its apex, with a germ pore 2 (–3) µm diam. present in the apex of each lobe, wall to 1 µm thick and covered with short hyaline spines to 1 µm high and spaced 1.5–2 µm apart; hilum 4 µm wide, often with a hyaline pedicel remnant to 25 µm long remaining attached. *Telia* surrounding pycnia, to 150 µm diam., seated in the cortex of the hypertrophied leaf spot and erumpent through the epidermis and cuticle, which remain as a marginal flap surrounding the sori, sparse marginal incurved *paraphyses* (Fig. 8) present, hyaline, narrowly clavate to cylindrical, 40–50 µm long, 4 (–7) µm wide, with a uniformly thin wall or slightly thickened to 1.5–2 µm at the apex, reducing the size of the lumen near the apex. *Teliospores* (Figs 2, 3, 6, 7,) golden brown, ellipsoidal to obovate, 22–30 × 18–22 µm, wall thin (1 µm) with large, raised block-like, square, rectangular to irregular warts, often elongated along the spore, up to 2–2.5 µm high, 1.5–2 µm wide and, in surface view, 2–3 µm across, concentrated at the spore apex but also running in lines down the spore, at their apex warts often extended into 2–4 (–6) short finger-like projections up to 1 µm long (Figs 3, 7), wall uniformly 1–1.5 µm thick, germ pore apical amongst apical warts, hilum 2–4 µm wide, unthickened, fragment of pedicel to 30–40 µm long often remaining attached.

Specimens examined: **Panama**: Department Bocas del Toro, Chinguinola, on leaves of *Lonchocarpus* sp., Aug. 1920, 0, III, *J.R. Johnston*, PUR 44631, Holotype (microscope slides as DAR 69637); 0, III, duplicate of PUR 44631 in K, ex IMI 65342 (microscope slide as DAR 69548); Department Bocas del Toro, United Fruit Co., Farm Six, on leaves of *Lonchocarpus* sp., 15 Aug. 1920, 0, II[I], III, *M.A. Carlton No. 12*, PUR 44632 (microscope slide as DAR 72144).

Atelocauda incrustans is known only from the collections made in Panama. Leaf lesions are thickened, with host cells hypertrophied and an abundant firm reddish brown substance in tissues beneath the sori. This is not present in healthy, unthickened leaf tissue. Whilst pycnia are subcuticular, other sori arise beneath the epidermis in the hypertrophied tissue. Neither aecial uredinia nor telial paraphyses have been described previously for *A. incrustans*. A few teliospores were present in the aecial uredinia and all spore stages appear to belong to the one species. Further collecting in Central America is needed to confirm this observation. Similar aecial urediniospores have been found in a second species of *Atelocauda* on *Ormosia* in Australia, described below.

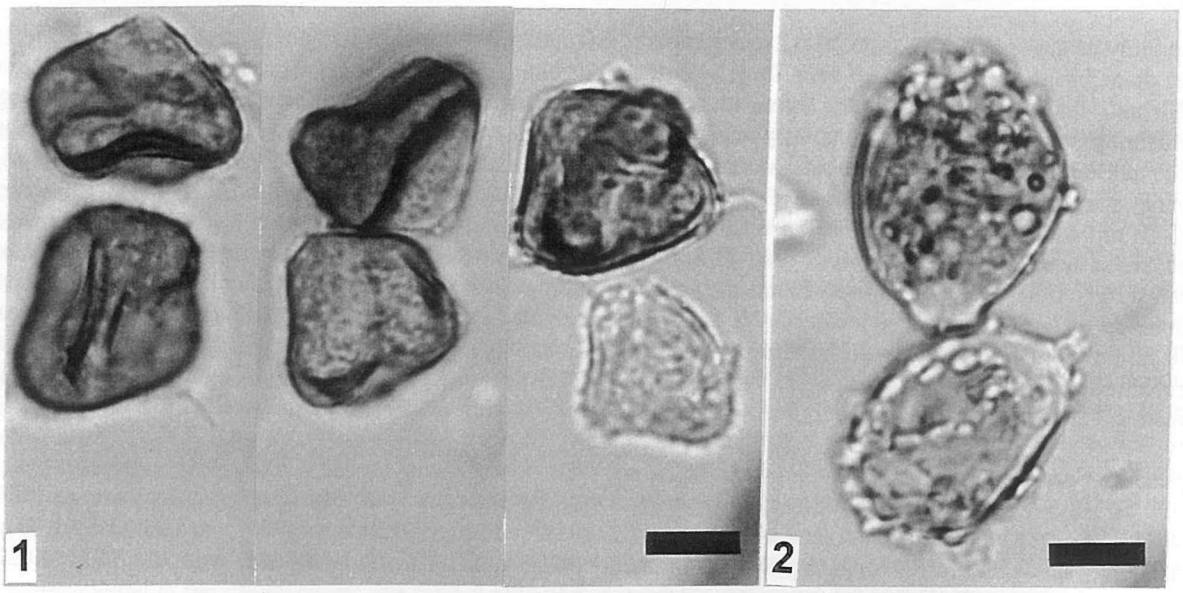
Germ pores were often difficult to detect. In aecial urediniospores, the pore at the apex of each of the two lateral lobes was usually readily seen but the third pore in the lobe seen from above was more difficult to detect. In teliospores, the apical germ pore was most easily seen between the apical tubercles in spores viewed obliquely from above. A teliospore germ pore was not mentioned in the original description by Arthur & Cummins (1933) or by Cummins (1978, as *Pileolaria incrustans*), although the two spores drawn in 1978 each show an apical pore. The shortly digitate apex of the teliospore warts can be observed with the light microscope but is clearly shown in SEM photographs. Paraphyses in telia were sparse and not observed in all sections. In contrast to immature teliospore pedicels, they did not stain readily in 0.1% acid fuchsin in lactophenol.

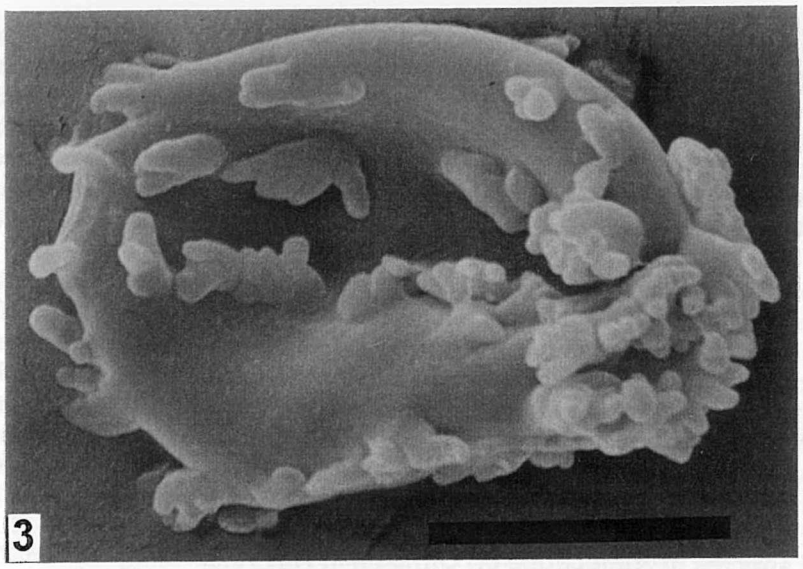
An undescribed species of *Atelocauda* on *Ormosia* in Australia

In August, 1992, Dr R.G. Shivas collected a leaf rust on *Ormosia ormondii* (F. Muell.) Merrill in North Queensland. In sending a duplicate of this rust to me for study, he commented 'The digitate teliospores resemble *A. digitata* but the urediniospores are not those of *A. digitata*' (*in litt.* Oct. 1992). Both aecial uredinia, in association with pycnia, and solitary, unaccompanied uredinia are present. Spores present in both types of sori are brown, lobed and similar to, but distinct from, the aecial urediniospores described above for *A. incrustans*. The *Ormosia* rust is considered congeneric with *A. incrustans* and is described as a new species of *Atelocauda*.

Atelocauda shivasii J. Walker *sp. nov.*
Etymology. Roger Graham Shivas, collector, conlega, amicus.

Pycnia epigena, subcuticulares, 100–130 µm diam., 70–120 µm alta, in gregibus 10–12 mm diam. aggregata. *Sori* hypogeni, subepidermales, erumpentes, ad marginem paraphysibus sparsis, (120–) 150–200 µm diam., urediniosporas (aeciales vel urediniales) solum vel etiam teliosporas continentes. *Urediniosporae aeciales* pedicellatae, unicellulares, aureo-brunneae vel rubri-brunneae, rotundatae vel rhombicae lobis tribus obtusis distinctis, 28–37 × 24–28 µm, echinulatae, praeter rasuram 11–16 µm diam. super porum germinationem, basi poro germinatione uno. *Urediniosporae* urediniosporis aecialibus similes. *Teliosporae* pedicellatae, unicellulares, pallidae brunneae vel aureo-brunneae, infra pallidiores, late fusiformes vel late ovales, 4–6 appendices apicales digitatae porum germinationem cingentes, 33–45 × 16–20 (–22) µm, appendices 2–10 (–13) µm longae, basim 3 µm latae, rectae, curvatae vel flexae.

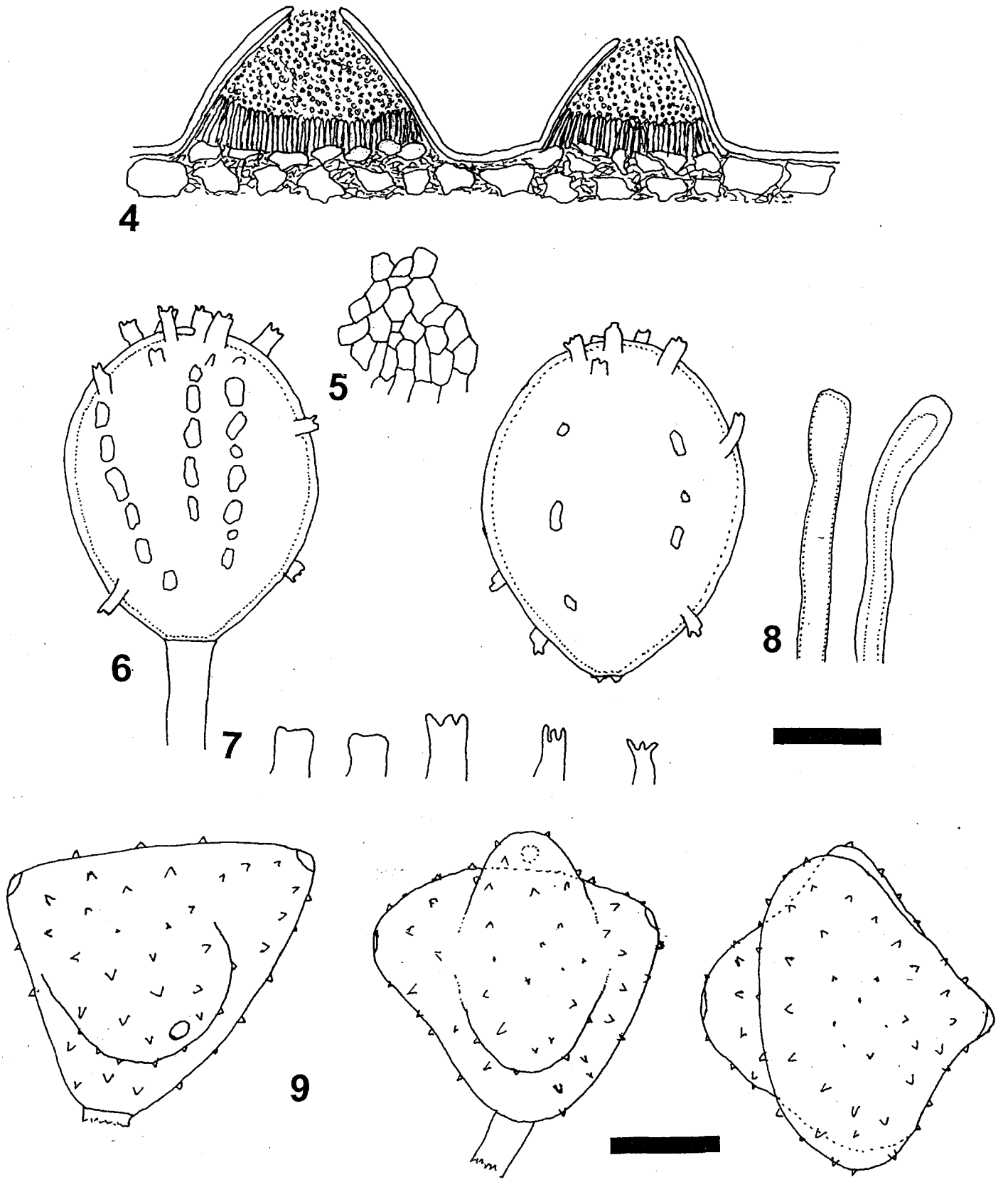




Figs 1 & 2. *Atelocauda incrustans*. **Fig. 1.** Six lobed aecial urediniospores, ex PUR 44632. **Fig. 2.** Two teliospores in surface view showing warts at apex and in lines on side, ex PUR 44631 (holotype). Bars: 10 µm.
Fig. 3. *Atelocauda incrustans*. SEM of teliospore (partly collapsed) showing digitate warts clustered at apex and in lines on side (hilum at left of spore), ex PUR 44631 (holotype). Bar: 10 µm.

Holotypus hic designatus: **Australia**: *Queensland*, Horto Civiles Cape Tribulation, sectio Noah Beach, in foliis *Ormosiae ormondii*, 10 Aug. 1992, 0, II[I], II, III, *R.G. Shivas*, DAR 68494 (isotypi hic designati BRIP 20529, PERTH 2595206).

Leaf lesions hologenous, pale greyish brown with a darker reddish brown margin and surrounded by a yellow halo 2–3 mm wide, becoming necrotic, to 10–12 mm across or fused into larger irregular patches up to 3.5 cm long and 1.5 cm wide, or lesions absent except for pale yellow blotches. *Pycnia* (Fig. 14) epigenous, subcuticular but with some disruption of the underlying epidermis, grouped in the centre of the sori, 100–130 µm diam., 70–120 µm high and protruding 40–50 µm above the leaf surface, with a basal layer of sporogenous cells 20–25 µm long, 2–3 µm wide, *pycniospores* hyaline, broadly oval, 3–4 × 2–2.5 µm, marginal *peridium* (Fig. 15) of hyaline, septate hyphae 3–4 µm wide, arranged radially around the apical pore. *Sori* hypogenous, arising deep in the leaf mesophyll (to a depth of 110 µm below the leaf surface), erumpent, surrounded by remnants of torn epidermis and cuticle but often opening by splitting across the middle, (120–) 150–200 µm diam., consisting of a basal 4–6 layers of interwoven hyphae, 18–22 µm thick, which extends about half-way up



Figs 4–8. *Atelocauda incrustans* ex PUR 44631 (holotype). **Fig. 4.** Two subcuticular pycnia. **Fig. 5.** Fragment of pycnial peridium in surface view. **Fig. 6.** Two teliospores with apical and lateral warts. **Fig. 7.** Branched apex of warts. **Fig. 8.** Two paraphyses. Bar: **Fig. 4** = 40 µm. **Fig. 5** = 20 µm. **Fig. 6** = 8 µm. **Fig. 7** = 4 µm. **Fig. 8** = 16 µm.
Fig. 9. *Atelocauda incrustans*. Three lobed aecial urediniospores with an apical pore in each lobe, ex PUR 44632. Bar: 8 µm.

the sides of the sori, becoming thinner and giving rise at the margin of the sorus to a few hyaline, clavate, thin-walled *paraphyses*, 35–45 (–50) µm long, 10–12 µm thick at the rounded apex, slightly thinner below; sori either *aecial uredinia* (on the underside of lesions with pycnia) or *uredinia* (on the underside of the yellow blotches) and containing either only urediniospores or a mixture of urediniospores and teliospores. *Aecial urediniospores* (Figs 12, 13, 16) pedicellate, unicellular, deep golden brown to reddish brown, rounded to rhomboidal in outline, with three distinct lobes, 28–37 × 24–28 µm, wall 1.5 µm thick, sometimes to 2 µm at the base near the hilum, closely echinulate with spines 1–1.5 µm high and (1.5–) 2 (–2.5) µm apart, except for one or two smooth patches (tonsures) 11–16 µm diam. between the lobes above the germ pore, germ pore 1, located near the base of the spore 4–8 µm above the hilum and in the basal curve of the spore wall, hilum protruding 2–4 µm beyond the contour of the spore wall, sometimes a hyaline fragment of pedicel to 20 µm long and 5–6 µm wide remaining attached. *Urediniospores* similar to aecial urediniospores. *Teliospores* (Figs 10, 17, 19) unicellular, pedicellate, pale brown to golden brown at the apex and top third, becoming paler towards the base, broadly fusiform to broadly oval (particularly in smaller spores), with 4–6 apical digitate appendages surrounding an apical pore 4–6 µm wide, spores (with appendages) measuring 33–45 × 16–20 (–22) µm, wall very thin (1 µm) except towards the apex where it is browner and 1.5–2 µm thick, appendages 2–10 (–13) µm long, 3 µm wide at the base and tapering to 1.5–2 µm above, with a rounded apex, straight or more commonly curved or bent, hilum 4–6 µm wide, often with fragment of non-septate pedicel to 15–20 µm long still attached, teliospores germinating in the sorus. *Basidia* (Figs 11, 18) arising from apical pore of teliospores, hyaline to pale golden yellow with granular contents, 40–45 × 8–9 µm, four-celled, each cell with a tapering sterigma 10–11 µm long, 3–4 µm wide at the base, tapering to a small rounded tip (before basidiospore formation). *Basidiospores* hyaline, unicellular, oval to unequally oval to globose, 11–13 × 9–13 µm.

Other specimen examined: **Australia**: *Queensland*, Cape Tribulation National Park, Noah Beach section, 30 July 1993, on leaves of *Ormosia ormondii*, 0, II^{I}, II, III, *R.G. Shivas*, BRIP 21803.

Atelocauda shivasii is known from only two collections on *O. ormosii* from tropical Queensland. It is a full-cycled rust but apart from this, nothing is known of its seasonal life cycle. Teliospores occur in the same sori as aecial urediniospores and urediniospores. The smooth patch free of spines on the wall of the aecial urediniospores is seen readily under the light microscope. Under SEM, some spores (Fig. 13) show smooth patches on either side of a central lobe. The proportion of each spore type present varies greatly between sori from very few teliospores to predominantly teliospores. The presence of asymmetrical lobed echinulate urediniospores (aecial and uredinial) and of appendaged unicellular pedicellate teliospores with an apical pore, together with a host in Fabaceae, relate this rust more closely to *Atelocauda* than to any other rust genus. The finding of aecial urediniospores in the type species of *Atelocauda* and in *A. shivasii*, and the presence of uredinia in *A. shivasii*, require an emendation to the generic circumscription of *Atelocauda* given by Arthur & Cummins (1933). Unlike the generic emendation made by Cummins & Hiratsuka (1983), the present concept of *Atelocauda* does not include characters drawn from the *Acacia* rusts. These species are discussed below.

***Atelocauda* Arthur & Cummins emend. J. Walker**
Pycnia subcuticular, aparaphysate, with a peridium consisting of a single layer of septate vertical hyphae. *Aecial uredinia* associated with pycnia, subepidermal. *Aecial urediniospores* pedicellate, asymmetrical, angular and lobed, echinulate, one or more germ pores present. *Uredinia* not associated with pycnia, subepidermal. *Urediniospores* similar to aecial urediniospores. *Telia* subepidermal. *Teliospores* unicellular, pedicellate, borne singly at the pedicel apex, epispore pigmented, germ pore apical, wall ornamented especially in the upper half with tuberculate or digitate processes, often germinating in sori without a rest period. *Paraphyses* present at margin of sori. Known hosts in Fabaceae *s. str.*

Relationships of *Atelocauda*

Cummins (1937) suggested that, on *Lonchocarpus* spp. in Central and South America, there is a series of related rusts, with decreasing complexity of teliospore heads, from *Ravenelia bakeriana* Dietel 1908, through *Dicheirinia guianensis* Cummins 1937 to *D. manaosensis* (P. Henn.) Cummins 1935 and then *D. archeri* Cummins 1937. *Ravenelia bakeriana* has complex teliospore heads with several spores and angular lobed aecial urediniospores and urediniospores. Baxter (1968) observed occasional small 3- or 4-spored teliospore heads in *R. bakeriana* with modified cysts resembling the apical cells of *D. guianensis*. *Dicheirinia guianensis* and *D. manaosensis* both have three teliospores per head and the former has lobed aecial urediniospores and urediniospores. *Dicheirinia archeri* is the simplest in this series, with two teliospores per head; aecial uredinia and uredinia are not known. Cummins (1937) suggested that further simplification from *D. archeri* could have given rise to *Atelocauda incrustans* with a single teliospore. The present finding of lobed aecial urediniospores in *A. incrustans* supports Cummins' (1937) hypothesis. The lobed spores of *R. bakeriana* and *D. guianensis* each have three germ pores, one located at the apex of each of the three lobes (Baxter 1968, Cummins 1937)

and they are thus similar to the aecial urediniospores of *A. incrustans*, described above. They are, however, much larger, those of *R. bakeriana* being 29–43 × 26–35 µm (Baxter 1968) and of *D. guianensis* 39–50 × 29–40 µm (Cummins 1937).

A similarity in urediniospore morphology to a species of *Dicheirinia* exists also with *A. shivasii* on *Ormosia*. *Dicheirinia ormosiae* (Arthur) Cummins 1935 occurs on *O. krugii* Urban in the West Indies (Dominican Republic and Puerto Rico) (Cummins 1935, Kern, Ciferri & Thurston 1933 as *Puccinia ormosiae* Arthur 1917, Petrak & Ciferri 1932 as *P. ormosiae*, Roure 1963). As noted by Cummins (1935) and observed here in two collections of *D. ormosiae*, urediniospores are irregularly triangular to oval, with one germ pore located just above the hilum. A smooth patch, 15 (–20) µm diam., free of echinulations, not previously reported, is present on one side of the urediniospores in their lower half (Fig. 20). This is very similar to the rhomboidal aecial urediniospores and urediniospores of *A. shivasii* which also have one basal germ pore associated with a smooth patch. The urediniospores of *D. ormosiae* measure 24–33 × 22–28 µm (Cummins 1935 gives 24–32 × 20–26 µm) and are thus slightly smaller than those of *A. shivasii*.

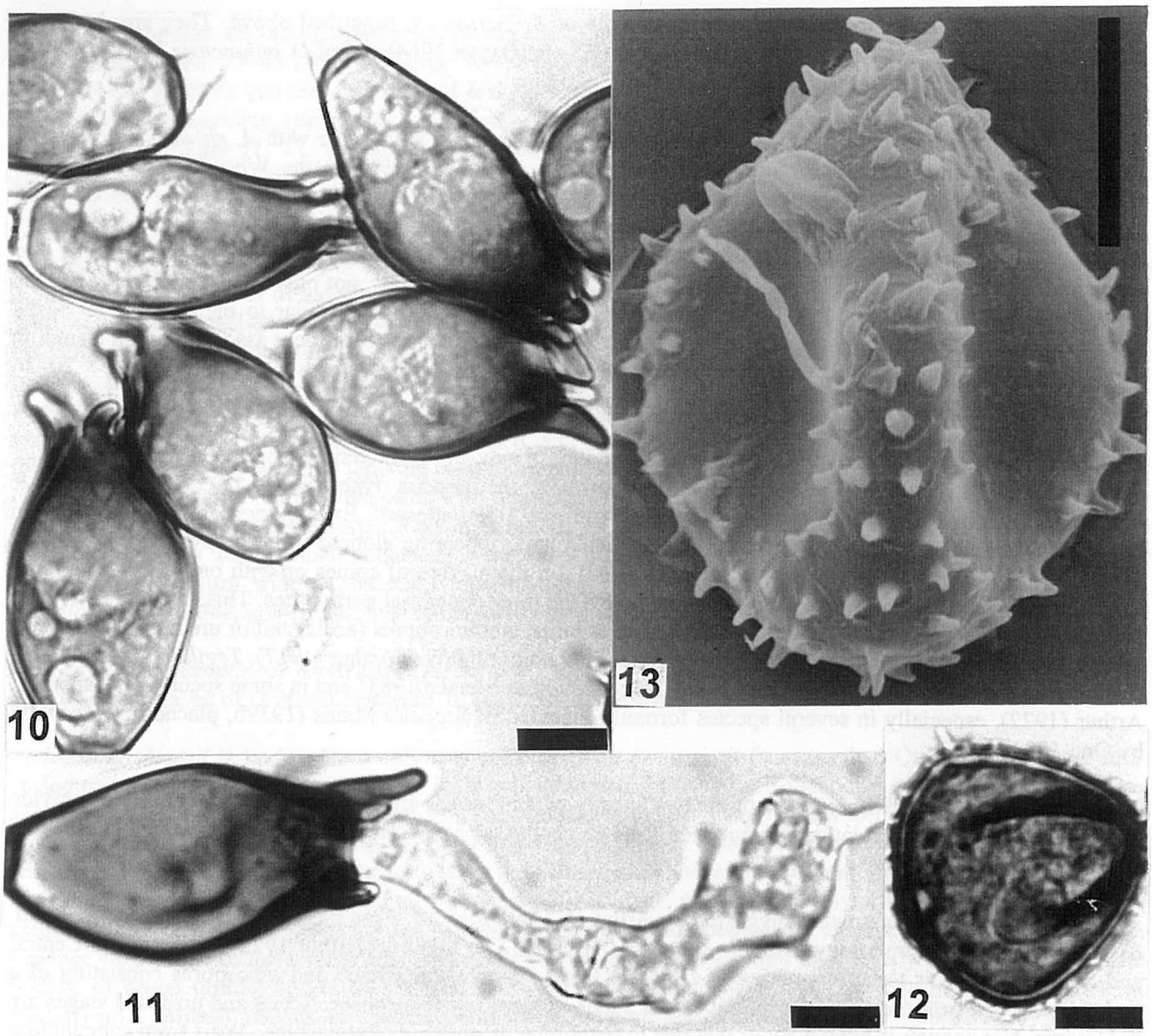
Irregularly shaped urediniospores (aecial and/or uredinial) may be characteristic for the genus *Dicheirinia*. Cummins (1935) described the aecial urediniospores of the generic type species, *D. binata* (Berk. & M.A. Curtis) Arthur 1907 as '... obovoid-globoid or with one side flattened'. Examination of the type specimen has shown that most spores are flattened in the vertical plane, appearing globose in face view and oval in side view (Fig. 21). There is also a smooth patch 15 (–20) µm diam., free of spines or with only a few scattered spines, on one face in the lower half of the spore below the three equatorial germ pores. This has not been noted previously for this species. Asymmetrical triangular or lobed urediniospores (aecial and/or uredinial) are known in several other rusts. For example, they are common in species of *Olivea* Arthur (1917), *Tegillum* Mains (1940) (included in *Olivea* by Cummins & Hiratsuka 1983 and Ono & Hennen 1983) and in some species of *Maravalia* Arthur (1922), especially in several species formerly included in *Scopella* Mains (1939b, placed in *Maravalia* by Ono 1984).

These observations on urediniospores of the two species of *Atelocauda* and some species of *Dicheirinia* provide additional evidence for a relationship between the two genera, as proposed by Arthur & Cummins (1933) and discussed by Cummins (1937).

Diabole and *Pileolaria* were also suggested by Arthur & Cummins (1933) as possible relatives of *Atelocauda*, based on teliospore morphology. *Diabole cubensis* (Arthur & J.R. Johnson) Arthur 1922 on *Mimosa* in Central and South America is the only species of *Diabole*. It has subcuticular pycnia and teliospores consisting of a pedicel bearing 2 or 3 short apical cells each with a pair of verrucose teliospores. Aecial and uredinial stages are not known. Not enough is known about this rust to determine its possible relationships. Apart from subcuticular pycnia, it has little in common with *Atelocauda* on Fabaceae and is perhaps closer to some other rusts of Mimosaceae. This will be considered in more detail elsewhere under a treatment of the genus *Uromycladium*.

Thirumalachar & Kern (1955) reduced *Atelocauda* to synonymy under *Pileolaria*. The type species, *P. terebinthi* Cast. 1842, and about twenty other species, occur on hosts in the Anacardiaceae, although some *Acacia* rusts were placed in *Pileolaria* by Dietel (1921, see below). Pycnia are subcuticular and teliospores globose to globose-depressed with verrucose walls. Urediniospores, when present, are commonly broadly fusiform, with longitudinal or spiral ridges or lines of warts. Leaving aside the *Acacia* rusts (considered below), these rusts of Anacardiaceae are morphologically quite distinct in both urediniospore and teliospore characters from *Atelocauda* on Fabaceae and are not considered here as closely related. Savile (1989) placed these two genera in different tribes of the Raveneliaceae, *Pileolaria* being grouped with *Uropyxis* and several other genera in the Uropyxidiae, and *Atelocauda* with *Dicheirinia*, *Ravenelia* and other genera in the Raveneliae. This classification is provisionally accepted here.

Finally, *Uredo ierensis* W.T. Dale (1955) has been reported on *Lonchocarpus* spp. in the West Indies, Mexico, El Salvador, Guatemala and Brazil (Baxter 1968, Cummins 1978, Dale 1955, Léon Gallegos & Cummins 1981). It was described by Dale (1955) with '... uredospores broadly ellipsoid, globoid or triangular-globoid in front view, 16–23 × 20–28 µ, more or less invaginate in side view' and with 2 or 3 approximately equatorial germ pores. Although this suggests some similarity in spore size and germ pores to the aecial urediniospores of *A. incrustans*, examination of portion of the type collection has shown that it is quite distinct. The taxonomic position of *U. ierensis* will be discussed elsewhere.

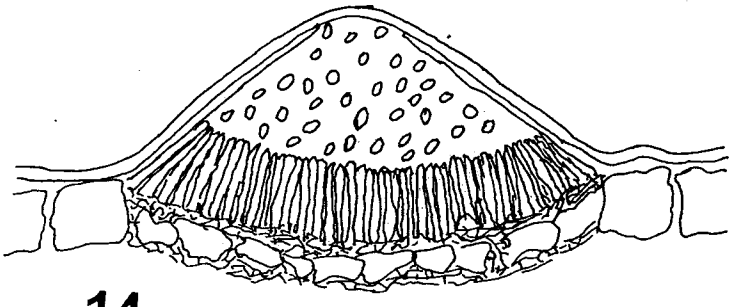


Figs 10–13. *Atelocauda shivasii* ex DAR 68494 (holotype). **Fig. 10.** Apically digitate teliospores. **Fig. 11.** Germinating teliospore with basidium. **Fig. 12.** Lobed aecial urediniospore. **Fig. 13.** SEM of aecial urediniospore showing smooth patches (hilum at top of spore). Bars: 10 µm.

Specimens examined: *Dicheirinia binata* (Berk. & Broome) Arthur: **Nicaragua**, on leaf of undetermined host [considered to be *Erythrina* by later workers *e.g.* Arthur 1925, Cummins 1978], date and collector not given, II, III, K(M) 64036, Holotype (microscope slide as DAR 72258).
Dicheirinia ormosiae (Arthur) Cummins: **Dominican Republic**, *Santo Domingo*, on leaves of *Ormosia krugii*, 3 Mar. 1930, *E. Ekman 3186*, II, III, IMI 101491, ex Herb. Ciferri, (microscope slide as DAR 72193); **Dominica**, Castle Bruce, on leaves of suspected *Ormosia krugii*, 2 Jan. 1972, *C. Critchett*, II, IMI 163804 (microscope slide as DAR 72194).
Uredo ierensis W.T. Dale: **Trinidad**, Quaré Valley, on leaves of *Lonchocarpus latifolius* (Willd.) Humb., Bonpl. & Kunth, 16 Dec. 1945, *W.T. Dale 771*, II, Isotype, PUR F11665 (microscope slides as DAR 74665).

The species of *Atelocauda* on *Acacia*, and *Racospermyces gen. nov.* (Uredinales)

Five *Acacia* rusts are placed currently in *Atelocauda*. Four, described originally as species of *Uromyces*, were transferred to the genus (Cummins & Hiratsuka 1983, Ono 1984) and a fifth, *A. angustiphylloda*, described from *Acacia koa* in Hawaii (Gardner 1991). With the exception of the microcyclic *A. angustiphylloda*, all have aecial uredinia or uredinia or both, as well as pycnia and telia. The aecial urediniospores and urediniospores are usually similar, but not necessarily identical, variable in shape but often fusiform to oval with a raised surface reticulum and several germ pores, variously arranged but commonly in an approximately equatorial band.



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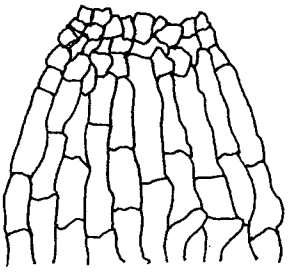

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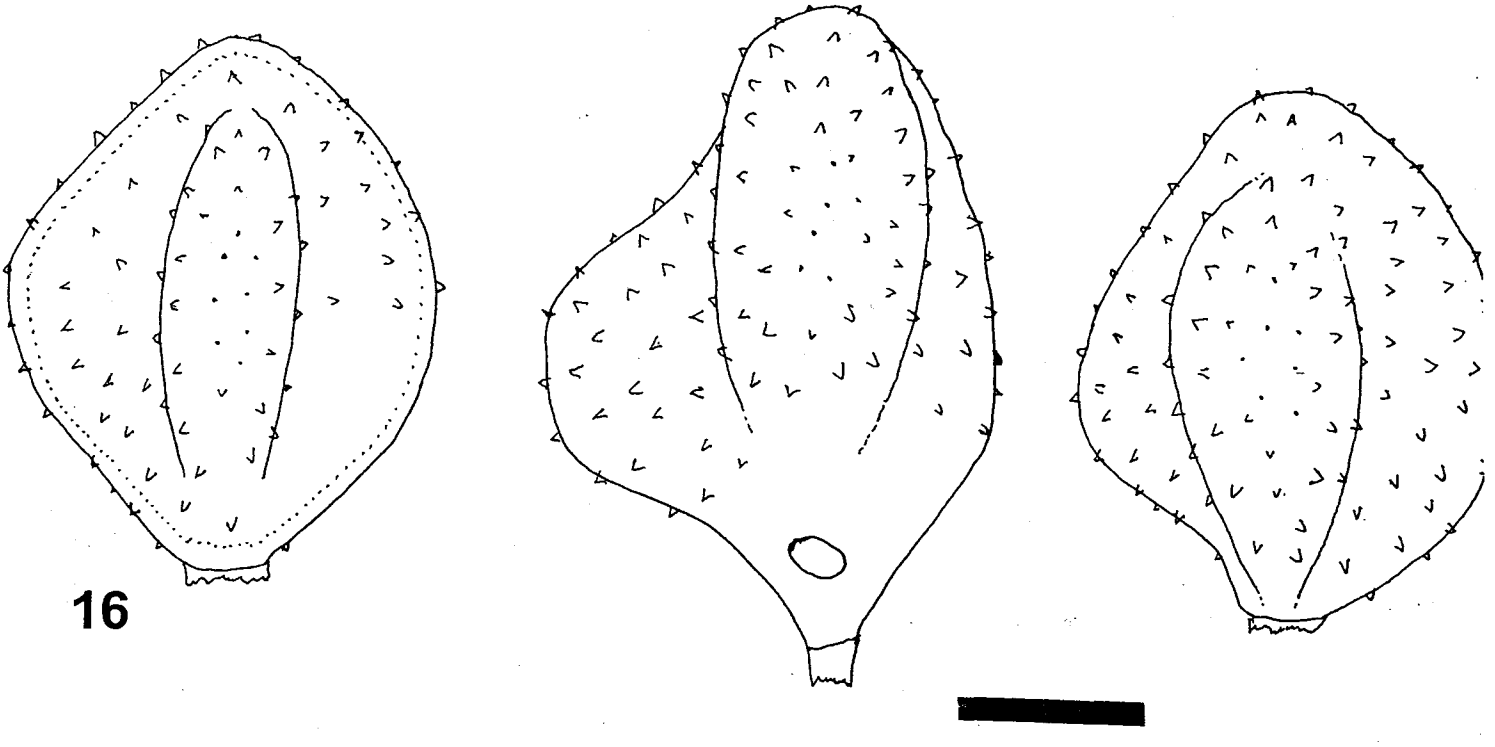

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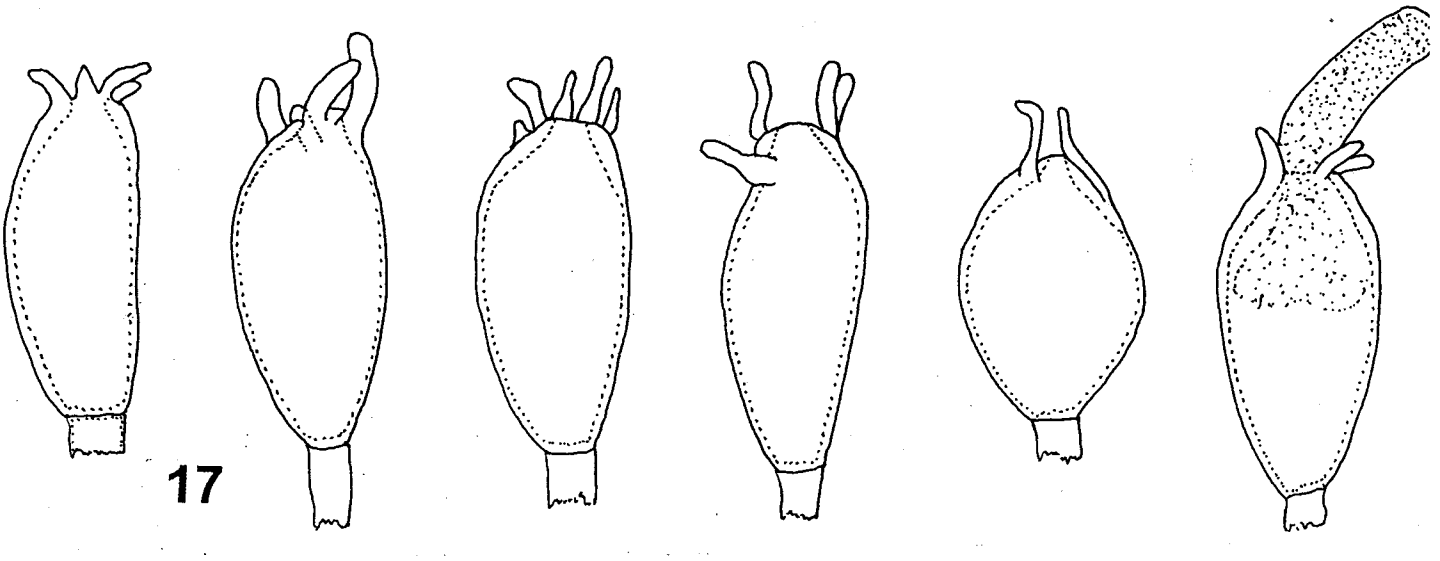

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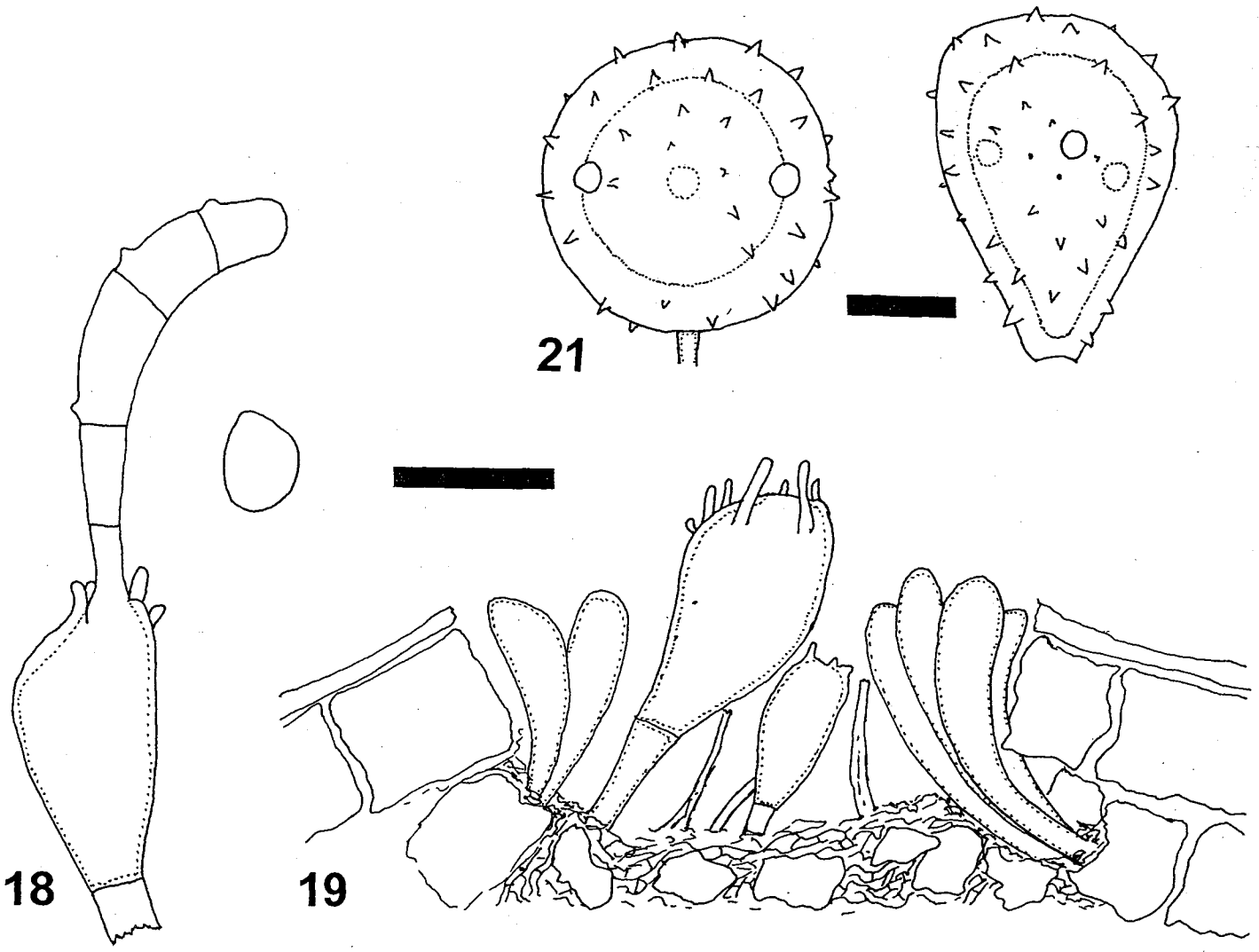
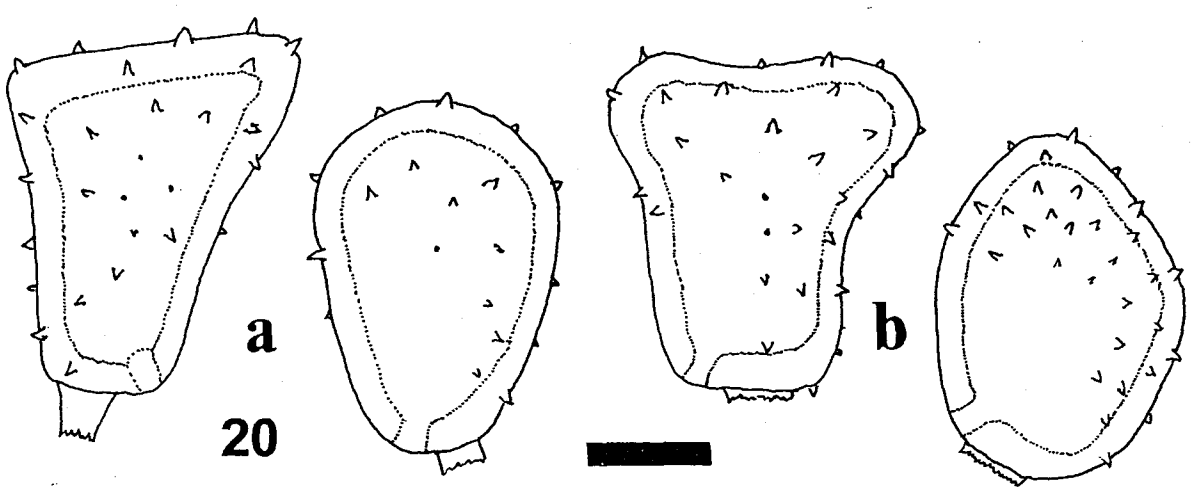
Figs 14–17. *Atelocauda shivasii* ex DAR 68494 (holotype). **Fig. 14.** Subcuticular pycnium. **Fig. 15.** Portion of pycnial peridium in surface view. **Fig. 16.** Three lobed aecial urediniospores, showing smooth patch and basal pore. **Fig. 17.** Six teliospores, one germinating, with apical pore and appendages. Bar: **Fig. 14** = 50 µm. **Fig. 15** = 25 µm. **Fig. 16** = 10 µm. **Fig. 17** = 20 µm.





Figs 18 & 19. *Atelocauda shivasii* ex DAR 68494 (holotype). **Fig. 18.** Teliospore with basidium and one basidiospore. **Fig. 19.** Section of telium showing marginal paraphyses. Bar: 20 µm.
Fig. 20. *Dicheirinia ormosiae.* Four angular urediniospores with basal germ pore and smooth patch (a) from IMI 101491 (b) from IMI 163804. Bar: 10 µm.
Fig. 21. *Dicheirinia binata* ex K(M) 64036 (holotype). Urediniospores in face and side views, with three equatorial germ pores and smooth patch. Bar: 10 µm.

Teliospores are hyaline at first, pale golden brown when mature, usually darker in the upper half, from subglobose to fusiform or elongated oval, germinating through an often indistinct pore in a thin apex or in a subapical position at the side of an apically thickened wall. This germ pore is less distinct than that in the apex of teliospores of the two species of *Atelocauda* accepted above but much more critical work to compare the development of teliospore germ pores in these two groups is needed. Apical digitate or tuberculate appendages of varying form and extent are usually present.

With their type 5 subepidermal pycnia, reticulate aecial urediniospores and urediniospores, and pale teliospores, these *Acacia* rusts are quite distinct from the puccinioid genus *Uromyces*, with type 4 pycnia (Hiratsuka & Hiratsuka 1980) and from *Atelocauda s. str.*, as defined above. In the absence of any suitable genus to contain them, the new genus *Racospermyces* is described. With the exception of the generic type, the species are dealt with in chronological order of date of original description.

Racospermyces J. Walker *gen. nov.*
Etymology. *Racosperma*, genus plantarum ex *Acacia* segregatum, species hospites horum uredinalium sunt, et *-myces*, fungus.

Pycnia subepidermalia, determinata, peridiata, aparaphysata, hymenio applanato vel parum concavo. *Uredinia aeciales* subepidermalia, erumpentes, pycniis concomitata. *Urediniosporae aeciales* pedicellatae, non-lobatae, concinnae, pariete reticulato, poris germinationibus pluribus aequatoriis vel aliter dispositis. *Uredinia* subepidermalia, erumpentes. *Urediniosporae* urediniosporis aecialis similes. *Telia* subepidermalia, erumpentia, saepe solida. *Teliosporae* unicellulares, pedicellatae, ad maturitatem pallide aureofuscae, pariete laterale tenui, paries ad apicem saepe incrassatus et plerumque appendicibus digitatis vel tuberculatis, porus germinationis praesens sed saepe obscurus, germinatio plerumque sine dormienti nunc per apicem, nunc, ubi apex incrassatus, per parietem lateralem proxime sub apice incrassato. *Paraphyses* saepe in soris adsunt, anguste clavatae vel cylindricae, hyalinae vel pallide flavae, interdum apice incrassato, interdum ramoso.

Typus generis hic designatus: *Racospermyces digitatus* (G. Winter) J. Walker *comb. nov.*
Basionym: *Uromyces digitatus* G. Winter, *Revue de Mycologie* **8,** 209 (1886).

Pycnia subepidermal, determinate, peridiate, aparaphysate, with a flat or slightly concave hymenium (type 5, Hiratsuka & Hiratsuka 1980). *Aecial uredinia* subepidermal, erumpent, accompanying pycnia. *Aecial urediniospores* pedicellate, not lobed, symmetrical, with reticulate wall, several germ pores equatorial or otherwise arranged. *Uredinia* subepidermal, erumpent. *Urediniospores* similar to aecial urediniospores. *Telia* subepidermal, erumpent, often firm. *Teliospores* unicellular, pedicellate, pale golden brown at maturity, side wall thin, often thickened apically and commonly with digitate or tuberculate appendages, germ pore present but usually obscure, germination without a rest period, either through the apex or, when apically thickened, through the side wall below the apical thickening. *Paraphyses* often present in sori, narrowly clavate to cylindrical, hyaline to pale yellowish, sometimes apically thickened, occasionally branched.

Racospermyces digitatus (G. Winter) J. Walker
Uromyces digitatus G. Winter, *Revue de Mycologie* **8,** 209 (1886).
Atelocauda digitata (G.Winter) Cummins & Y. Hirats., *Illustrated Genera of Rust Fungi*, revised edition, 147 (1983).
Melampsora phyllodiorum Berk. & Broome, *The Transactions of the Linnean Society of London*, ser. 2, **2,** 67 (1882), based on aecial uredinia.
Uromyces phyllodiorum (Berk. & Broome) McAlpine, *The Rusts of Australia* 95 (1906).
Pileolaria phyllodiorum (Berk. & Broome) Dietel, *Annales Mycologici* **19,** 302 (1921).
Uromyces phyllodii Cooke & Massee *in* Cooke, *Grevillea* **17,** 70 (1889) (as '*phyllodiae*'), based on aecial uredinia.

Pycnia mainly on hypertrophied host organs, such as bullate lesions up to 10 (–15) mm diam. and 2–4 mm high on phyllodes, smaller on leaflets of bipinnate wattles, and on small galls on twigs and pods, more rarely on small, unthickened lesions, subepidermal, pale amber but darker (often almost black) around the ostiole, 100–200 µm diam., 60–70 µm high, with a basal layer of sporogenous cells 20–25 µm high, 2 µm wide, *peridium* of a single layer of vertical, septate hyphae, surrounded by aecial uredinia and/or telia. *Pycniospores* subglobose to broadly oval, 2–4 µm diam. or up to 4–5 µm. *Aecial uredinia* with pycnia mainly on hypertrophied lesions, on some host species with pycnia occasionally on smaller unthickened lesions 3–4 × 1–2 mm, pale cinnamon-brown to pale reddish brown, singly to 250 µm diam., often several fused into a soral network between the pycnia, with a cinnamon-brown granular-powdery spore mass. *Aecial urediniospores* pale golden yellow to

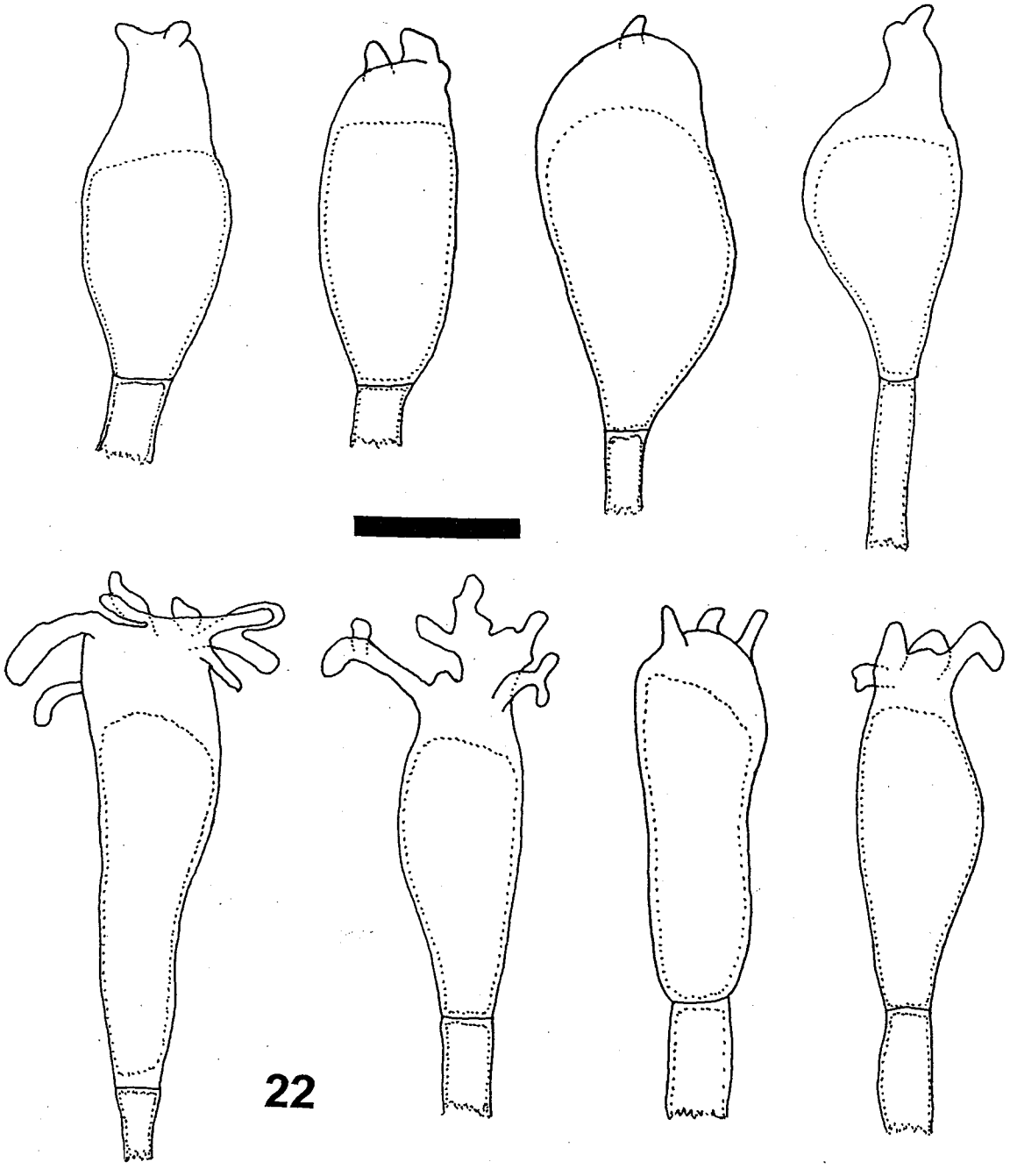
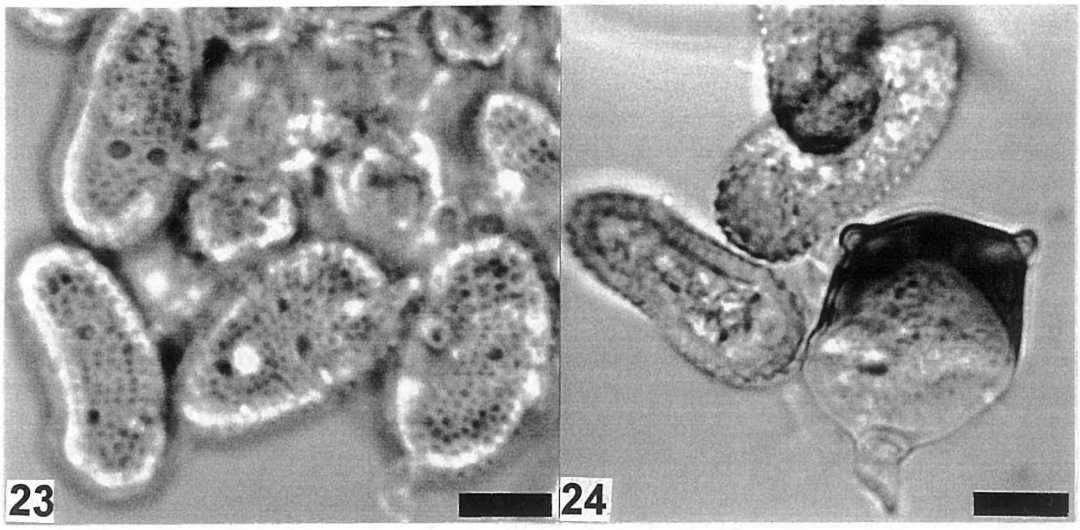


Fig. 22. *Racospermyces digitatus*. Variation in teliospores from six hosts. Top row: *Acacia aulacocarpa* s.l. BRIP 8769; *A. aulacocarpa* s.l. BRIP23284; *A. aulacocarpa* s.l. BRIP 6041; *A. concurrens* BRIP 23071. Bottom row: *A. deanei* BRIP 14106; *A. irrorata* BRIP 14165; *A. notabilis* ex B (type; slide as DAR 30659); *A. podalyriifolia* BRIP 6056. Bar: 20 µm.



Figs 23 & 24. *Racospermyces bicinctus*. **Fig. 23.** Reticulate urediniospores with two rows of germ pores ex MEL 2061107. **Fig. 24.** Teliospore and urediniospores ex MEL 2061113. Bars: 10 µm.

golden brown, variable in shape, oval to obovate to clavate, (26–) 30–42 (–46) × (16–) 18–22 (–24) µm, wall 2–4 µm thick at the sides, from unthickened to 9–12 µm thick at the apex, reticulate with roughly hexagonal areolae to 2 µm diam., germ pores 3–5 equatorial or rarely subequatorial, base not protruding or protruding up to 4–6 µm. *Uredinia* unaccompanied by pycnia, on non-hypertrophied phyllode or leaf lesions 1–2 (–3) mm diam., brown, often with a thin very dark brown to almost black line-like margin or scattered or loosely clustered on unspotted areas of phyllodes or leaves, sori pale cinnamon-brown to reddish brown, to 250 µm diam. singly, sometimes two or more coalescing into a larger composite sorus, granular-powdery. *Urediniospores* similar to aecial urediniospores but usually slightly larger, (28–) 33–45 (–55) × 16–24 (–28) µm, wall 2–4 µm thick at sides, from unthickened to 5–11 µm thick at apex, germ pores 3–6, equatorial or rarely subequatorial, base usually protruding from slightly to 4–6 (–8) µm. *Telia* either accompanying pycnia and then often developing in aecial uredinia, or alone, raised, single or in loose groups, often solid, pale reddish brown to reddish cinnamon, sometimes slightly glistening, often with a whitish bloom of basidia and basidiospores, to 250 µm diam. *Teliospores* (Fig. 22) at first hyaline and thin-walled, at maturity wall pale golden yellow to pale golden brown, very variable in shape, size, apical wall thickening and the development of apical appendages, often broadly fusiform to clavate, mainly (30–) 35–55 (–65) × (11–) 16–26 (–28) µm but some larger forms seen, wall (1–) 1.5–2 µm thick at sides, apical thickening developing as the spores mature, mainly from slight to 4–16 (–18) µm, some to 24 µm or thicker, with (0–) 1–7 apical finger-like appendages which are straight or curved or reflexed, (2–) 4–10 (–18) × 2–4 (–6) µm, germinating through either an apical pore in thin apices or through a pore just below the apical thickening in other spores, pore developing just before germination. *Paraphyses* of variable development within and between collections, in aecial uredinia, uredinia and telia, cylindrical, thin-walled, 50–80 × 6–8 µm, some thinner filaments often present.

This description is a composite one, based on a series of 34 Australian collections covering 12 named *Acacia* spp. (nine phyllodinous and three bipinnate), three undetermined species (all phyllodinous) plus the type collections of all names listed in the synonymy. It does not include any overseas collections, or Australian collections of extreme forms, which will be dealt with elsewhere. Studies so far indicate that, as currently conceived, *R. digitatus* is a complex of several closely related taxa, differing in spore morphology, life cycles, host range and probably geographic distribution. Some of the variation seen in teliospore morphology on six host species is shown in Fig. 22. The synonymy given above is also a composite one, as there is no certainty at present that the aecial uredinial fungi described as *Melampsora phyllodiorum* and *Uromyces phyllodii* belong to the same taxon as *Uromyces digitatus* G. Winter *s. str.* The type collection of *U. digitatus* is in poor condition but shows non-hypertrophied phyllode spots bearing true urediniospores and teliospores. The relationship of the fungus described by Winter (1886) on *A. notabile* to recent collections on this and other *Acacia* spp. requires further investigation. Work on all these problems is in progress and results will form the subject of a future paper dealing with variation within *R. digitatus s. lat.* These investigations will include study of the fungi from outside Australia currently placed within *R. digitatus e.g.* the rust of *A. koa* in Hawaii (Hodges & Gardner 1984) and those causing damage to several *Acacia* spp. in Papua New Guinea, China and other countries of South-

East Asia (Old, See, Sharma & Yuan 2000). Only a selected list of specimens examined is given here until studies on the host ranges and distributions of these *R. digitatus* variants are completed.

Some specimens examined: **Australia**: *South Australia*, near Gawler, on phyllodes of *Acacia notabilis* F. Muell., 1 July 1885, II, III, *J.G.O. Tepper*, Holotype of *Uromyces digitatus* G. Winter, two fragments in B (microscope slides as DAR 29789 (no rust), DAR 30659): *Queensland*, Brisbane, on phyllodes of *Acacia* sp., no date given, 0, II[I], III (few, immature), *F.M. Bailey 269*, Holotype of *Melampsora phyllodiorum*, K (microscope slides as DAR 28715); duplicate, Isotype, as VPRI 5779 (microscope slides as DAR 74663); *Queensland*, Brisbane, on phyllodes of *Acacia* sp., no date given, 0, II[I], *F.M. Bailey 643*, Isotype of *Uromyces phyllodii* (as '*phyllodiae*'), VPRI 5781 (microscope slides as DAR 74664); *Queensland*, Brisbane hilly country, on phyllodes of *A.* sp. aff. *A. aulacocarpa* Cunn. ex Benth., April 1911, II, III, *E. Jarvis*, BRIP 6041 (microscope slides as DAR 72323); *Queensland*, Marcus Beach, on phyllodes of *A. aulacocarpa*, 17 Aug. 1972, II, III, *J.L. Alcorn 72/114*, BRIP 8769 (microscope slides as DAR 72333); *Queensland*, near Mission Beach, on phyllodes of *A. aulacocarpa*, 5 Apr. 1995, 0, II, III, *I. Hood*, BRIP 23284 (microscope slides as DAR 72340); *Queensland*, Indooroopilly, on phyllodes of *A. concurrens* Pedley, 30 Sept. 1996, II, III, *D.E. Shaw Q 1413a*, BRIP 23071 (microscope slides as DAR 74659); *Queensland*, Indooroopilly, on leaves, twigs and pods of *A. deanei* (R. Baker) Welch, Coombs & McGlynn, 30 Aug. 1983, 0, II[I], II, III (microscope slides as DAR 74654); *New South Wales*, Batemans Bay, 18 Mile Peg Road, on twigs, leaves and pods of *A. irrorata* Sieber ex Sprengel subsp. *irrorata*, 14 May 2000, 0, II[I], III, *J.A. Simpson*, DAR 72322; *Queensland*, Brisbane, on phyllodes of *A. podalyriifolia* Cunn. ex D. Don., 19 June 1930, II, III, *R.J. McAllister*, BRIP 6056 (microscope slides as DAR 72324).

Racospermyces bicinctus (McAlpine) J. Walker *comb. nov.*
Basionym: *Uromyces bicinctus* McAlpine, *The Rusts of Australia* 93 (1906).
Pileolaria bicincta (McAlpine) Dietel, *Annales Mycologici* **19**, 302 (1921).
Atelocauda bicincta (McAlpine) Cummins & Y. Hirats., *Illustrated Genera of Rust Fungi*, revised edition, 147 (1983).

Lesions on pods and phyllodes, from 2–3 mm to 10 mm wide, grey with a thin, dark brown margin, either amphigenous or hologenous on phyllodes. *Pycnia* on both pod and phyllode lesions, subepidermal, amber in colour, 110–120 µm wide, 60 µm high, with a basal layer of sporogenous cells 20–25 µm high, 2 µm wide, *peridium* of a single layer of vertical hyphae; *pycniospores* broadly oval, hyaline, 2–2.5 × 1–1.5 µm. *Aecial uredinia* in association with pycnia, either surrounding them or on the opposite side of the phyllode, to 250 µm diam., subepidermal. *Aecial urediniospores* golden brown, mainly obovate, with a finely reticulate surface, 24–39 (–44) × (13.5–) 15.5–22 (–26) µm, germ pores indistinct but at least 3–5 present in one row. *Uredinia* on pods and phyllodes, subepidermal, to 2–3 mm diam., surrounded by a rim of torn host epidermis and cuticle. *Urediniospores* (Figs 23–26) pale cinnamon in mass, pale golden brown singly, narrowly clavate to narrowly (occasionally broadly) obovate or cylindrical, straight or rarely slightly curved, sometimes slightly constricted in the middle, (24–) 28–33 × (11–) 13–15 (–16) µm, an occasional spore to 20 µm wide seen, wall 2–2.5 µm thick at the sides, sometimes thickened to 3–4 µm at the apex, with a finely reticulate surface which is coarser towards the apex of the spore, germ pores most commonly in two rows each of (3 or) 4 pores, rarely 5 in one row, usually one row in the top half of the spore and the other in the lower half, but sometimes one row almost equatorial and the other depressed, a few spores with only one equatorial band of pores and rarely pores in two closely intermingling rows, giving the impression of several scattered pores, germ pores 1.5–2 µm diam., without a cap, hilum unthickened, not protruding, often concave, 4–5 µm wide. *Teliospores* (Figs 24, 25, 27) sparse, usually borne in the same sori as urediniospores, very pale yellowish at the base and sides, golden brown in the apical third, obovate to broadly clavate to almost rectangular, 26–44 × 18–22 µm, wall thin (1.5–2 µm) at the sides, thickened to 7–11 µm at the apex which usually has from (1–) 2–5 (–6) short digitations from 2–6 (–8) µm long, 2–3 µm wide at the base and tapering to a rounded apex, no germ pore detected, hilum 4 µm wide, often with a fragment of pedicel to 6–8 µm long attached.

This is a rare species of *Racospermyces*, represented only by specimens collected in the 1800s (earliest in 1860) on *Acacia fasciculifera* in the Rockhampton district of Queensland. The two collections in VPRI, which were the basis of McAlpine's (1906) original description, were taken from botanical specimens of the host in MEL. No other collections of this rust have been found in BRIP or the Queensland Forestry Herbarium. Examination of the two collections in VPRI and of several botanical sheets of *A. fasciculifera* in MEL collected at Rockhampton in the 1800s has revealed the presence of spore stages additional to the uredinia and telia described by McAlpine (1906). Of eleven botanical specimens of *A. fasciculifera* in MEL examined, the rust was found sparingly on four. As well as uredinia and telia, pycnia and aecial uredinia were observed for the first time. Lesions were very sparse and badly damaged and, due to flaking of layers of host tissue, some pycnia on

these old lesions appeared almost superficial. In the very few aecial urediniospores observed, only a single equatorial row of germ pores could be seen, thus differing from the urediniospores which characteristically have two rows of pores. However, fresh collections with abundant spores are needed to determine if this is a true difference between the two spore stages. Of the known species, *R. bicinctus* is most similar to the newly described *R. tierneyi*; both have short, compact teliospores much thickened at the apex and with apical digitations. These are less numerous and shorter in *R. bicinctus* than in *R. tierneyi*. They also have urediniospores of similar size but those of *R. bicinctus* have the germ pores in two rows whereas the 4–8 pores of *R. tierneyi* are arranged in one equatorial band.

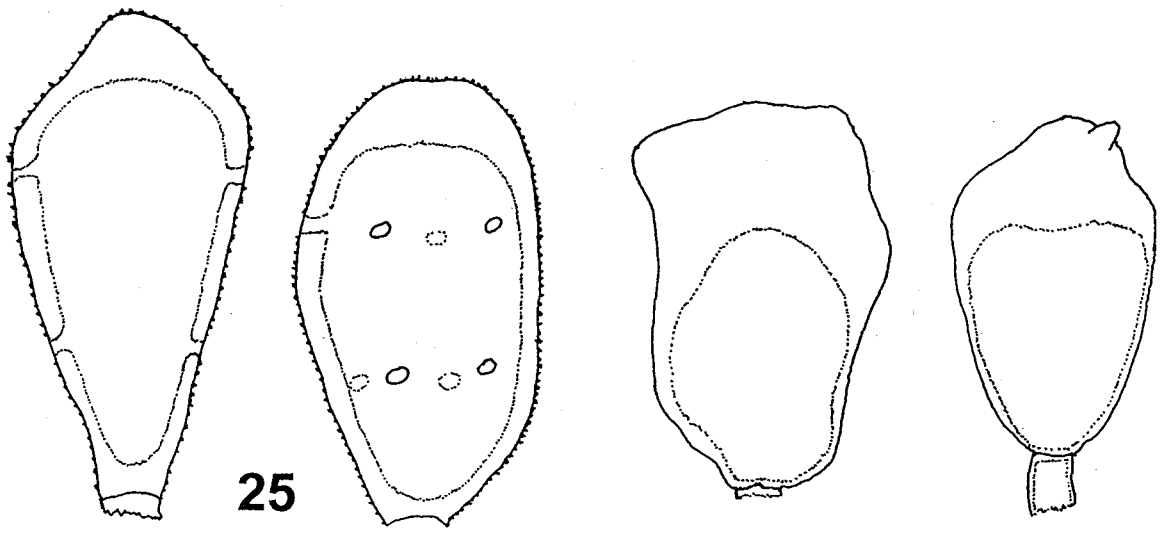
There are two collections in the McAlpine herbarium that McAlpine examined but neither is marked 'type' nor gives any indication (such as 'n. sp.') that McAlpine considered it as type. In the original description, he gave the following details: 'On phyllodes and pods of *Acacia fasciculifera* F.v.M. Queensland – Rockhampton, 1867 (from host plant in the National Herbarium, Melbourne)'. Both VPRI 5751 and VPRI 5752 are portions of collections from plants in MEL but only one (VPRI 5751) bears the date '1867' and it is also the only one of the two that shows any rust. It is thus chosen as the lectotype of the name *Uromyces bicinctus* McAlpine. The collections in MEL from which VPRI 5751 and VPRI 5752 were taken are not known. Of the thirteen collections of *A. fasciculifera* from the mid-1800s examined, three (MEL 2061105, 2061109 and 2061110) were dated 1867 but rust was not found on them.

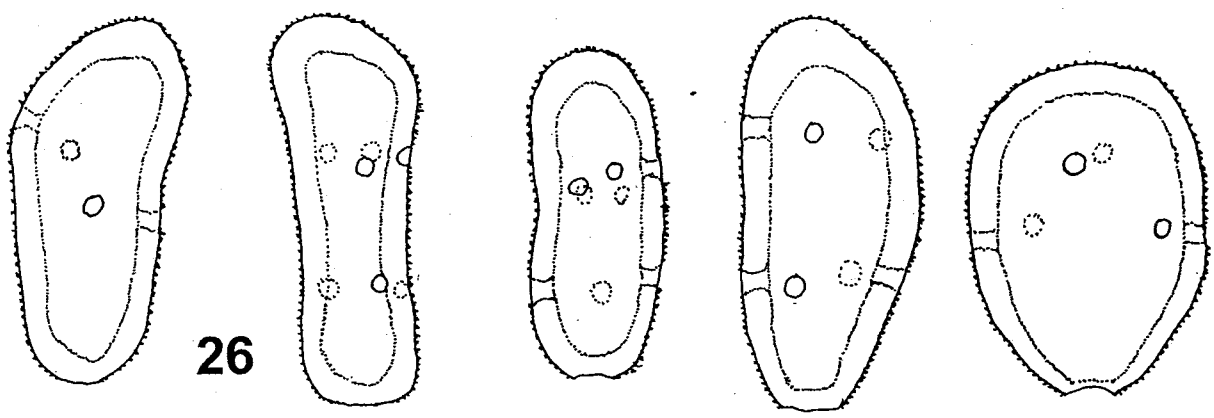
Lectotypus hic designatus: **Australia**: *Queensland*, Rockhampton, on phyllodes and pods of *Acacia fasciculifera* Benth., 1867, II, III, *G.H. Robinson* (from specimen in National Herbarium), VPRI 5751 (formerly as 539/05) (microscope slide as DAR 72203, isolectotype).

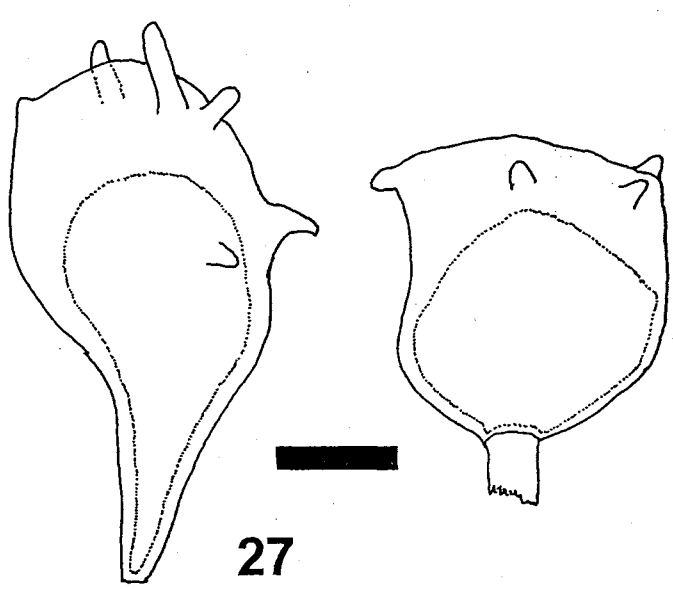
Other specimens examined: **Australia**: *Queensland* (all on phyllodes and pods of *A. fasciculifera)*, Rockhampton, no date, no rust found, *G.H. Robinson* (from a botanical collection in MEL), VPRI 5752 (formerly 538/05) (microscope slide as DAR 72202); Rockhampton, ?1860, II, *M.A. Thozet*, MEL 2061107 (microscope slide as DAR 72198); Rockhampton, no date, 0, dubious II^{I}, badly eroded, *M.A. Thozet*, MEL 2061111 (microscope slide as DAR 72199); Rockhampton, no date, 0, II^{I}, *P.O'Shanesy*, MEL 2061112 (microscope slide as DAR 72200); Rockhampton, no date, II, III, *J. Dallachy*, MEL 2061113 (microscope slide as DAR 72201).

Racospermyces hyalosporus (Sawada) J. Walker *comb. nov.*
Basionym: *Uromyces hyalosporus* Sawada, *The Botanical Magazine (Tokyo)* **27** (No. 313–324), 19 (1913).
Maravalia hyalospora (Sawada) Dietel, *Annales Mycologici* **22,** 270 (1924).
Poliotelium hyalosporum (Sawada) Mains, *Bulletin of the Torrey Botanical Club* **66,** 175 (1939) (as '*hyalospora*').
Atelocauda hyalospora (Sawada) Ono, *Mycologia* **76,** 909 (1984).

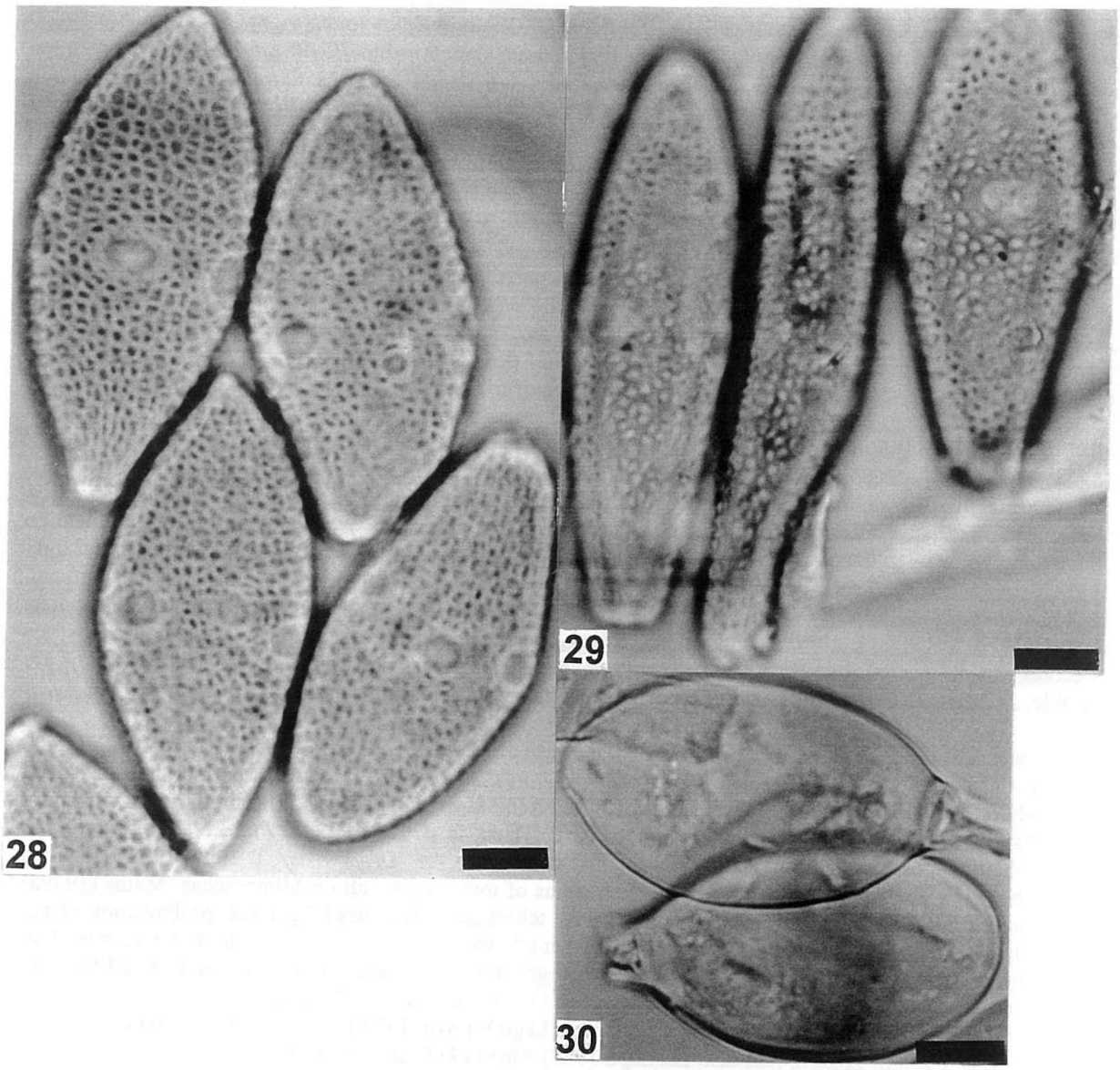
Phyllode lesions from minute (0.25–1 mm diam.) (Fig. 31) to large bullate lesions to 5 mm diam., slightly raised on the upper surface and concave on the lower, often clustered into larger groups which twist and distort the phyllode. *Pycnia* (Figs 31, 33) present on most lesions, only on upper surface, subepidermal, 110–150 (–160) µm diam., 110–150 µm high, with a basal layer of sporogenous cells 20–25 µm high, 2 µm wide, *peridium* (Fig. 34) of vertical septate hyphae with rectangular cells 4–8 × 3–4 µm. *Pycniospores* subglobose to broadly oval, 3–4 µm diam. *Aecial uredinia* (Fig. 31) subepidermal, later erumpent, 300–400 µm diam., pale reddish brown, mainly epigenous and arising between the pycnia on the outer half of the lesion, occasionally amphigneous, containing both aecial urediniospores and teliospores. *Aecial urediniospores* (Figs 28, 35) pedicellate, golden yellow, commonly fusiform to broadly fusiform to oval or occasionally narrowly clavate, (42–) 46–70 (–75) × (20–) 22–28 (–29) µm, wall 2.5–3.0 µm thick at the sides, often slightly thicker in the equatorial region, a minority of spores to 4–6 (–7) µm thick at the apex, finely reticulate with areolae to 1 µm across, randomly arranged, germ pores 4–5 (–6), prominent, 2–2.5 µm diam., often in a slight depression and in an equatorial band, hilum 2.5–6.5 µm diam., depending on spore shape and degree of basal narrowing. *Uredinia* not common, epigenous, less commonly amphigenous or hologenous, on minute lesions or on unspotted phyllode tissue, small, 0.25–0.5 mm diam., slightly raised, usually slightly elongated along the phyllode, single or commonly in elongated clusters up to 5 × 1 mm of 5–15 sori running along the phyllode between the veins, containing both urediniospores and teliospores. *Urediniospores* (Figs 29, 32) similar to aecial urediniospores but tending to be longer and thinner, (57–) 61–75 × 22–26 µm, commonly thickened to (4–) 5–7 µm at the apex which is often narrowed and broadly papillate. *Telia* developing in aecial and uredinial uredinia, 0.25–0.5 mm diam. singly, often several clustered. *Teliospores* (Figs 30, 37) at first hyaline, later pale golden yellow, oval to ovate or broadly obovate, apex broadly rounded or occasionally narrowed, 44–50 × 15–24 µm, borne







Figs 25 & 26. *Racospermyces bicinctus*. **Fig. 25.** Two urediniospores showing two rows of germ pores and two teliospores ex VPRI 5751 (lectotype). **Fig. 26.** Five urediniospores showing variation in shape and germ pore arrangement ex MEL 2061107. Bar: 10 µm.
Fig. 27. *Racospermyces bicinctus*. Two teliospores ex MEL 2061113. Bar: 10 µm.



Figs 28–30. *Racospermyces hyalosporus*. **Fig. 28**. Four reticulate aecial urediniospores ex DAR 65442. **Fig. 29**. Three reticulate urediniospores ex DAR 65443. **Fig. 30**. Two teliospores ex DAR 65442. Bars: 10 µm

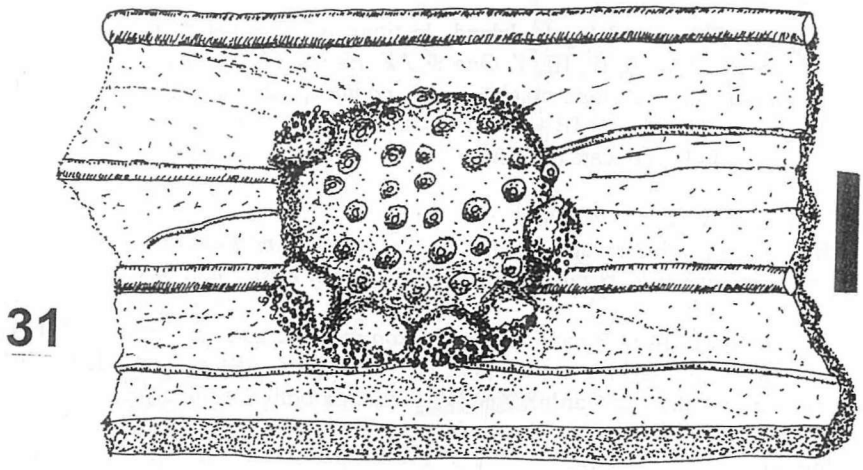


Fig. 31. *Racospermyces hyalosporus*. Very small, young, bullate phyllode lesion with central pycnia and marginal aecial uredinia ex DAR 65442. Bar: 0.5 mm.

sympodially from a basal sporogenous cell, pedicel thick, 10–12 µm wide in young spores, elongating to 50–60 µm long and 4–6 µm wide in mature spores, breaking and a fragment up to 30–40 µm long often remaining attached, wall 1–2 µm thick at sides, much thinner across 4–6 µm of the apex through which germination occurs. Remnants of shrivelled basidia often present with teliospores. *Paraphyses* (Fig. 36) common in aecial uredinia, uredinia and telia, hyaline to faintly tinted yellowish, 90–110 µm long, either narrow cylindrical and 6–8 µm wide or more commonly clavate and 10–18 µm wide in their upper half and tapering to a broadly rounded apex, wall thin 1–2 µm, sometimes slightly thicker at the apex.

Sawada (1913) described this rust from phyllodes, pods and shoots of *Acacia confusa* Merrill in Taiwan (formerly Formosa). On the same host, it has been recorded from Japan (Honshu, Okinawa, Ogasawara) (Hiratsuka *et al.* 1992) and continental China (Cummins & Ling 1950, as *Poliotelium hyalosporum*). The centre of distribution of *Acacia confusa* is the Philippines but as far as can be determined, the rust has not been recorded on it there. It is the only known host. In Taiwan, Sawada (1913) and Hirane (1934) reported serious deformation of young shoots, especially of young trees in nurseries, with tubercular lesions on phyllodes. These often coalesce into large masses, deforming infected host organs. Sawada (1913) described only uredinia and telia but Hirane (1934) found pycnia on the tubercular lesions in association with both aecial uredinia and telia. He also reported on phyllodes smaller uredinia and telia not associated with pycnia. The rust is thus a full-cycled species, with pycnia, aecial uredinia, uredinia and telia. The most recent description is that given by Hiratsuka *et al.* (1992, p. 374) which agrees in essentials with that given above, except that they do not mention uredinia. In the three collections examined, sori unassociated with pycnia were not common, being found only in DAR 65443. These sori contained mainly teliospores but some urediniospores were also present. Urediniospores were slightly longer and usually slightly narrower at the base than aecial urediniospores. Sawada (1913) listed over thirty localities in Taiwan from which the rust had been studied, but no type collection was designated. It will thus be necessary to select a lectotype from whatever Sawada collections are available. Attempts to borrow them for the present investigation have been unsuccessful.

Racospermyces is the fifth genus to which this rust has been assigned. *Uromyces*, a puccinioid rust with type 4 pycnia, is unsuitable. Dietel (1921) considered placing *U. hyalosporus* in *Pileolaria*, to which he transferred several other *Acacia* rusts but later (Dietel 1924) disposed it in *Maravalia*, because of its similarity in teliospore characteristics with the type species, *M. pallida* Arthur & Thaxt. in Arthur 1922 on *Pithecellobium latifolium* (L.) Benth. (Mimosaceae) from Trinidad. In his conspectus of *Uredinales*, Dietel (1928) retained *U. hyalosporus* in *Maravalia*, which he considered a genus of four species, all on Mimosaceae. Mains (1939a) revised *Maravalia* and retained in it only species whose teliospores germinated by apical prolongation of the spore, without an evident germ pore. As he considered that teliospores of *U. hyalosporus* showed evidence of an apical pore, he transferred this rust to *Poliotelium* (a segregate genus from *Uromyces* based on a life cycle without uredinia, erected by Sydow 1922). However, as Ono (1984) noted, *U. hyalosporus* must be excluded from *Poliotelium* as the generic type species, *P. iresines* (Lagerh.) Syd. 1922 has type 4 pycnia and is a species of *Uromyces*, *U. iresines* Lagerh. (see also Laundon 1965). Ono (1984) also showed that *U. hyalosporus* differs in its reticulate aecial urediniospores from the 31 species he accepted in *Maravalia* and, with some reservations, and because of the inclusion of other *Acacia* rusts by Cummins & Hiratsuka (1983), he placed *U. hyalosporus* into *Atelocauda*. The reasons for excluding it from this genus have been fully detailed here.

Specimens examined: **Japan**: *Okinawa*, Ishigaki Island, Institute of Tropical Agriculture, on phyllodes of *Acacia confusa* Merrill, 10 Sept. 1983, 0, II^{I}, III, *Y. Ono & J.F. Hennen 1285*, DAR 65441 (duplicate of IBA 2826); Iriomote Island, Shirahama, Taketomi-machi, on *A. confusa*, 12 Sept. 1983, 0, II^{I}, III, *Y. Ono & J.F. Hennen 1300*, DAR 65442 (duplicate of IBA 2842); Okinawa Island, Nago, on *A. confusa*, 7 Feb. 1985, 0, II^{I}, II, III, *Y. Ono 1607*, DAR 65443 (duplicate of IBA 3079).

Racospermyces koae (Arthur) J. Walker *comb. nov.*
Basionym: *Uromyces koae* Arthur *in* F. Stevens, *Bernice P. Bishop Museum Bulletin* **19,** 118 (1925).
Atelocauda koae (Arthur) Cummins & Y. Hirats., *Illustrated Genera of Rust Fungi*, revised edition, 147 (1983).

Racospermyces koae is known only from Hawaii on *Acacia koa* var. *koa* and var. *latifolia*. It has been studied comprehensively and its life cycle clarified by Gardner (1978, 1981), Gardner & Hodges (1985), Gardner, Miller & Kuhlman (1979) and Hodges & Gardner (1984). Although both urediniospores and teliospores were described originally for *R. koae* (Stevens 1925), the urediniospores described in Stevens (1925) are now known to be the aecial urediniospores of *R. digitatus* (Hodges & Gardner 1984). *Racospermyces koae* has pycnia, aecial urediniospores and teliospores in its life cycle and no true urediniospores have so far been discovered. It infects juvenile leaves, phyllodes and shoots, on which it causes severe distortion and is common on young

plants (Hodges & Gardner 1984). A full description is given by Hodges & Gardner (1984) and the spore surface morphology of *R. koae* and some other *Acacia* rusts is compared by Gardner & Hodges (1985).

Specimens examined: **United States of America**: *Hawaii*, Oahu, Tantalus, on phyllodes of *Acacia koa* A. Gray, no date given, III, *North*, PUR F2888, Holotype (microscope slide as DAR 30666).

Racospermyces angustiphyllodius (D.E. Gardner) J. Walker *comb. nov.*
Basionym: *Atelocauda angustiphyllodia* D.E. Gardner, *Mycologia* **83,** 650 (1991) (as '*angustiphylloda*').

This rust is also known only from Hawaii, on *Acacia koa* var. *latifolia*, on which it is associated with witches' broom development. It is fully described and illustrated by Gardner (1991). Phyllodes of brooms are reduced in size and brooms may be up to 1 m or more in length (Gardner 1991). The rust is considered by Gardner (1991) to be a microcyclic form of *R. digitatus*, producing only pycnia and telia on distorted phyllodes and branches. From the description and illustration, its teliospores are virtually indistinguishable from those produced by *R. digitatus* in Hawaii. Gardner considered that this microcyclic rust merited recognition as a separate species. Its behaviour in the field is distinctive, being limited to *A. koa* var. *latifolia*, endemic to the island of Hawaii, on which it produces much larger witches' brooms than *R. digitatus* on the same host. So far, no specimens have been seen and it will be considered in more detail in current studies of the *R. digitatus* complex.

The original spelling of the specific epithet has been changed. The generic name *Atelocauda* is feminine. The original feminine epithet '*angustiphylloda*' (narrow-phylloded) denotes the much narrowed phyllodes of the witches' brooms produced by this rust. As this epithet is derived from '*angustus*' (narrow) and '*phyllodium*' (phyllode), its termination is altered and the spelling becomes '*angustiphyllodia*', by analogy with '*angustifolia*' (narrow-leaved) and in accord with Art. 32.5 of the ICBN (Greuter *et al.* 2000). When transferred to the masculine *Racospermyces*, this becomes '*angustiphyllodius*'.

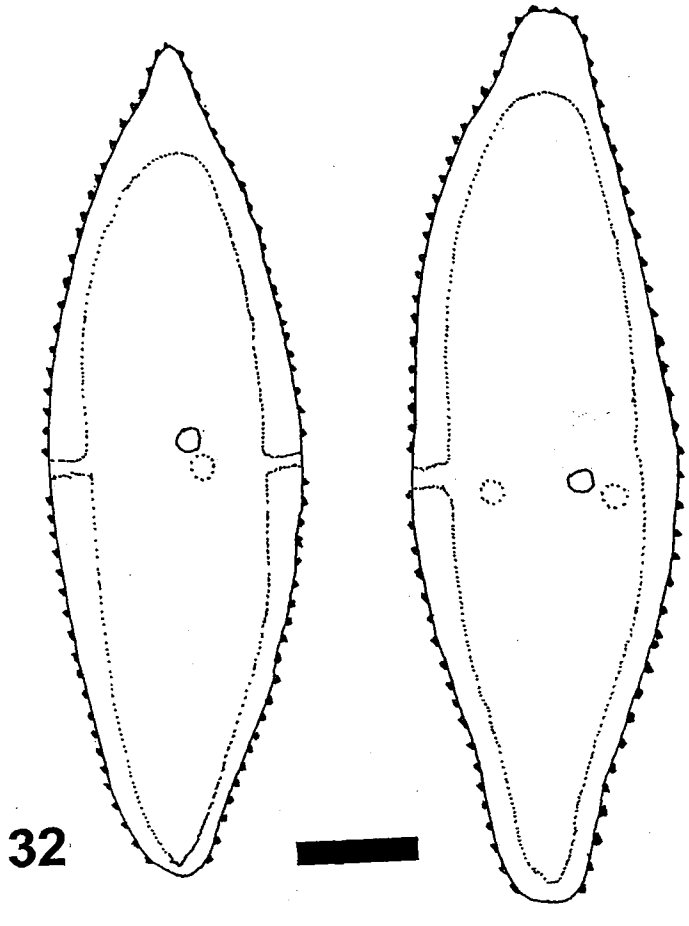
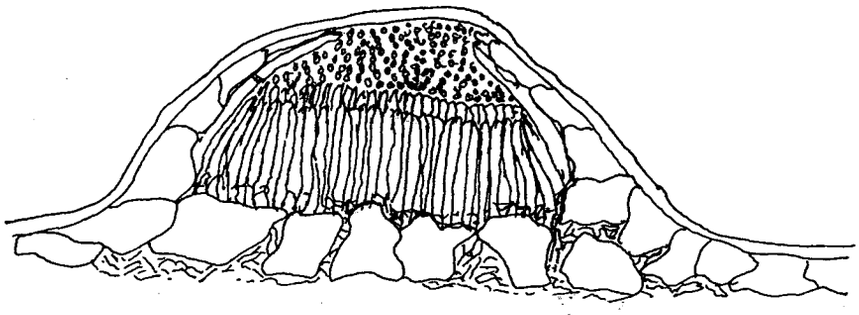


Fig. 32. *Racospermyces hyalosporus*. Two urediniospores from small sori unaccompanied by pycnia ex DAR 65443. Bar: 10 µm.



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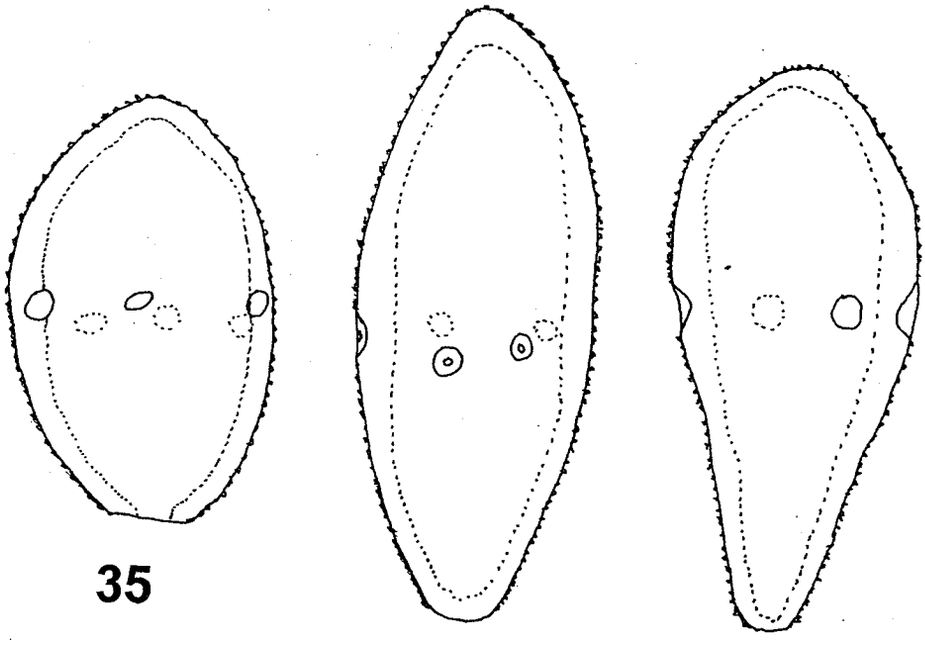

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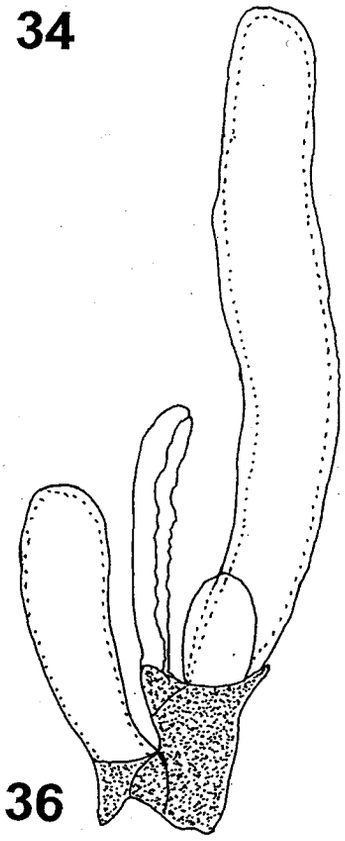

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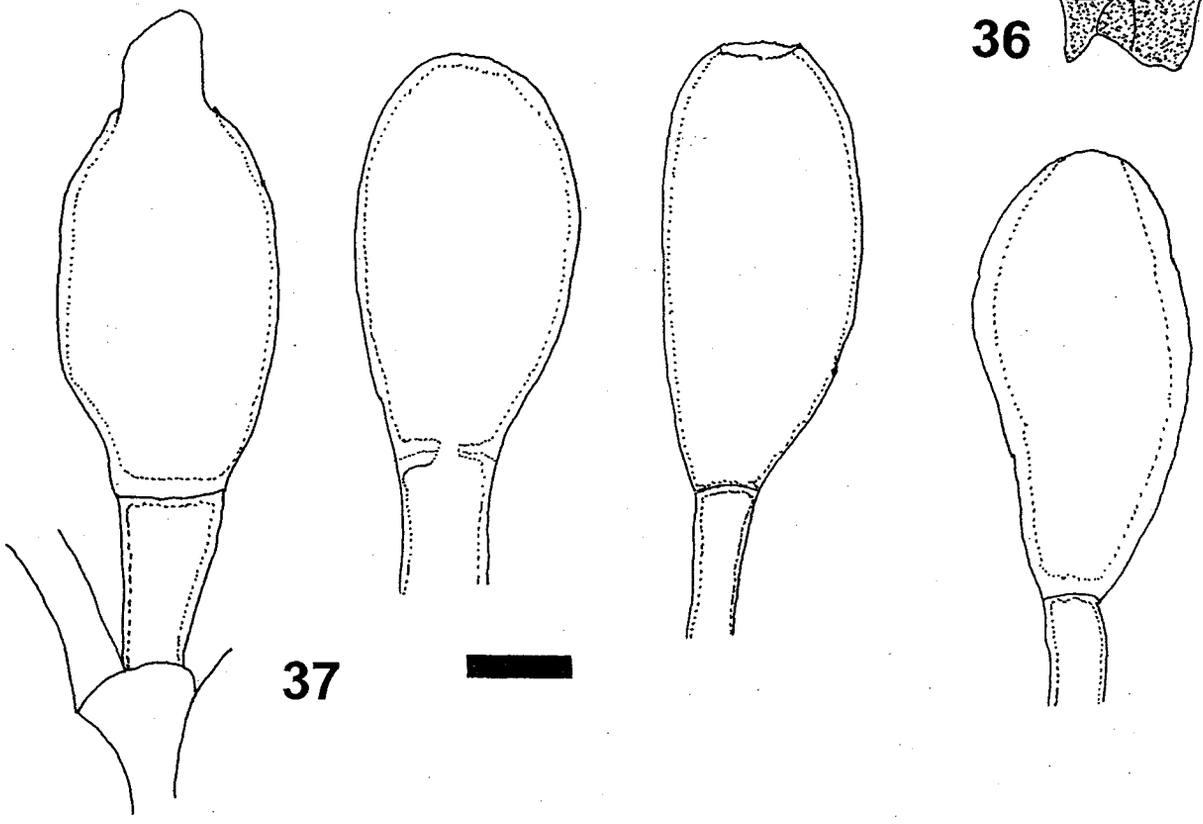

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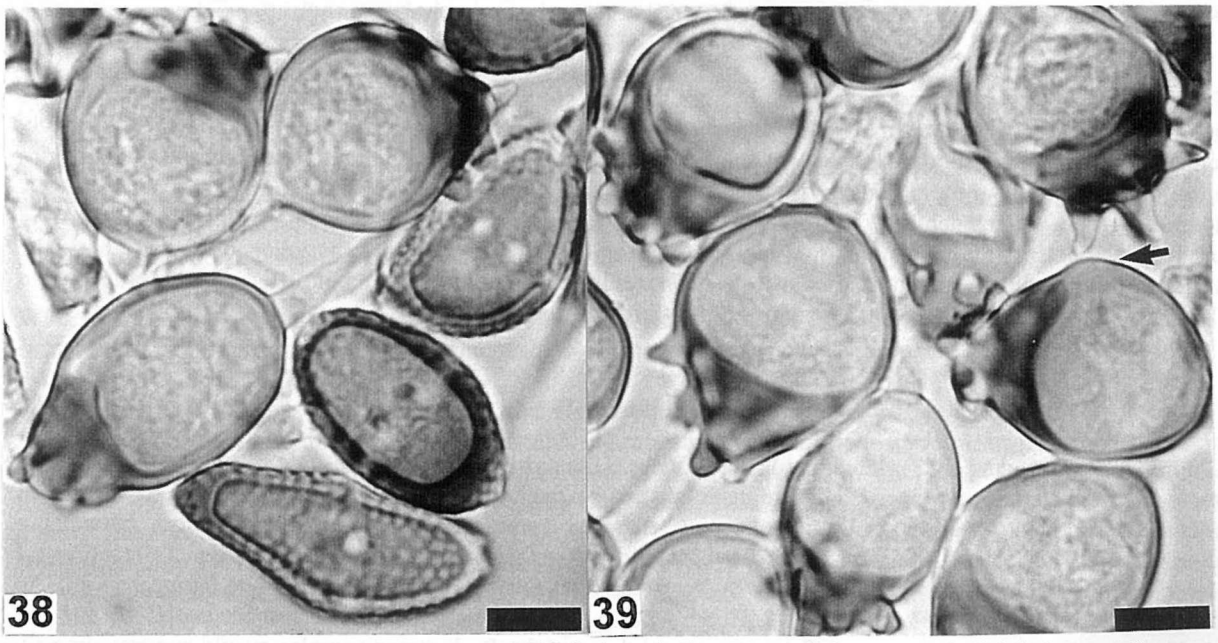
Figs 33–37 (page 22). *Racospermyces hyalosporus*, all ex DAR 65441. **Fig. 33.** Subepidermal pycnium. **Fig. 34.** Fragment of pycnial peridium in surface view. **Fig. 35.** Three aecial urediniospores. **Fig. 36.** Paraphyses and basal cells. **Fig. 37.** Four teliospores, one showing sympodial development from basal cell. Bar: **Fig. 33** = 30 µm. **Fig. 34** = 12 µm. **Figs 35–37** = 10 µm.

Racospermyces tierneyi J. Walker & R.G. Shivas *sp. nov.*
Etymology: John William Tierney, 1952–1991, uredinalium *Acaciae* collector et studens queenslandensis, beatus.

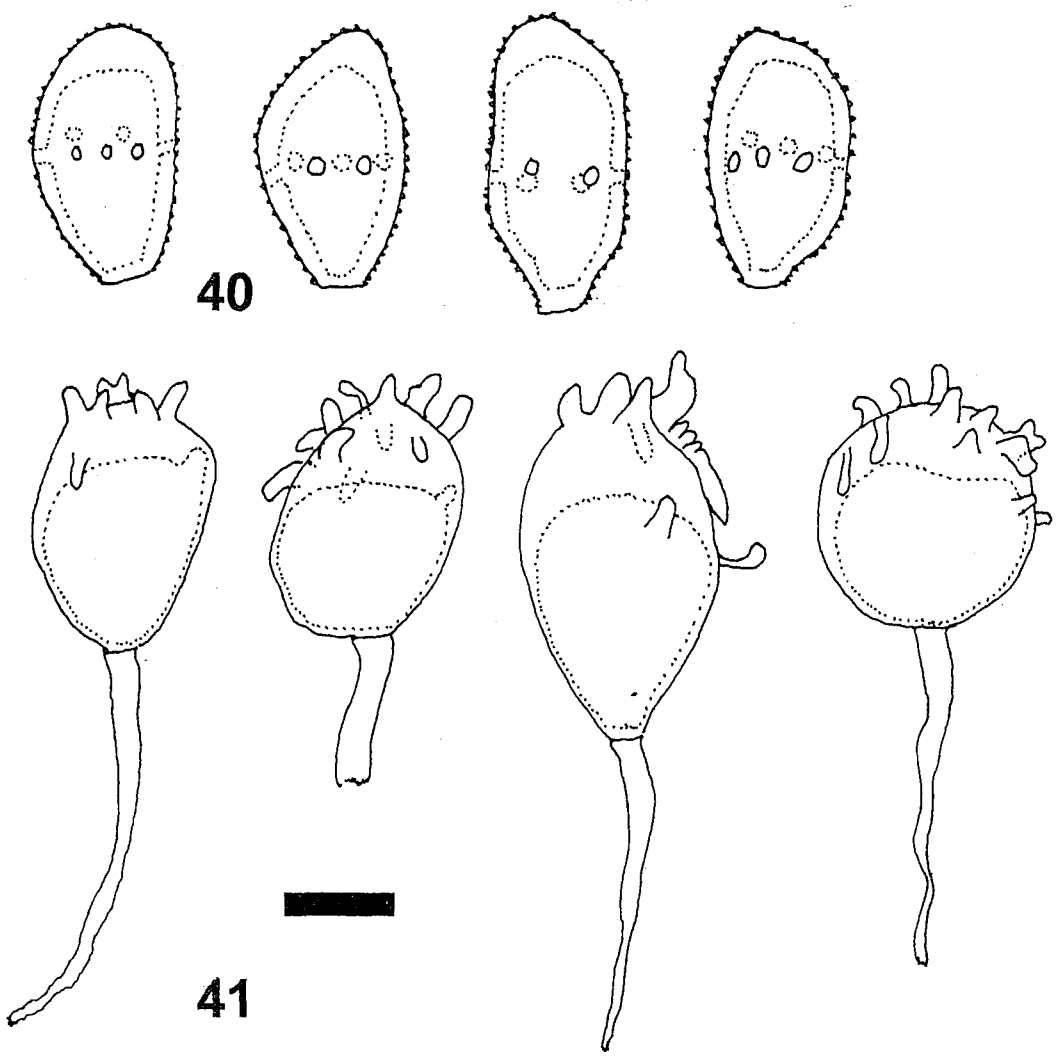
Pycnia non visa. *Sori* amphigeni, subepidermales, ferruginei, parum elongati secus phyllodium, 0.5 mm longi, 0.25 mm lati singulatim, saepe 3–5 sori laxe aggregati, in phyllodiis super aream 2 cm longam et 2 cm latam dispersi, urediniosporas et teliosporas continentes. *Paraphyses* non visae. *Urediniosporae* formae variabilis, cylindraceae, fusiformes vel late fusiformes, obovatae vel interdum clavatae, aureae vel pallide ferrugineae, 26–33 (–36) × 13–17 (–18) µm, pariete 2–2.5 µm crasso ad latera, 4.5–5.0 µm ad apicem, reticulato cum areolis 1–1.5 µm latis, pori germinationes (4–) 5–8 aequatorii, hilum 4–5 µm latum, leniter vel manifeste protrudens. *Teliosporae* subglobosae, ovatae vel obovatae, ferrugineae, ad apicem fuscatae, 27–37 (–41) × 20–23 (–26) µm, pariete ad latera tenuissimo 1 µm, ad apicem multo incrassato 7–13 µm, teliosporae ad apicem 4–12 appendices digitiformes 2–8 µm longas ferentes, porus germinationis unus in pariete subapicale, pedicellus ad 50–55 µm longus cum fragmentum breve vel 40 µm longum saepae remanens affixum. Teliosporae in soro saepe germinantes basidia et basidiosporas producentes.

Holotypus hic designatus: **Australia**: *Queensland*, in regione Tambo, Castlevale, in phyllodiis *Acaciae harpophyllae* F. Muell. ex Benth., 6 June 2000, II, III, *G. Pegg*, DAR 72315 (isotypus hic designatus BRIP 27071).

Pycnia not seen. *Sori* amphigenous, subepidermal, light reddish brown, slightly elongated along the phyllode, to 0.5 mm long and 0.25 mm wide singly, often 3–5 sori loosely clustered, sori scattered over an area roughly 2 × 2 cm, containing urediniospores and teliospores. *Paraphyses* not seen. *Urediniospores* (Figs 38, 40) variable in shape, cylindrical, fusiform to broadly fusiform, obovate to sometimes clavate, golden to pale reddish brown, 26–33 (–36) × 13–17 (–18) µm, with wall 2–2.5 µm thick at sides, 4.5–5.0 µm at apex, reticulate with areolae 1–1.5 µm wide, germ pores (4–) 5–8, equatorial, hilum 4–5 µm wide, slightly or prominently protruding. *Teliospores* (Figs 38, 39, 41) subglobose, ovate to obovate, light reddish brown, darker at the apex, 27–37 (–41) × 20–23 (–26) µm, with wall thin 1 µm at sides, much thickened to 7–13 µm at apex, bearing 4–12 apical digitate appendages 2–8 µm long, a single germ pore in the subapical wall just below the apical thickening, pedicel to 50–55 µm long, with a short fragment or up to 40 µm long remaining attached. Teliospores often germinating in the sorus, producing basidia and basidiospores, which are shrivelled in the one specimen examined.



Figs 38–39. *Racospermyces tierneyi*, all ex DAR 72315 (holotype). **Fig. 38.** Urediniospores and slightly longer teliospores. **Fig. 39.** Teliospores showing apical appendages and one with germ pore in earliest stages of germination (arrow). Bar: 10 µm.



Figs 40 & 41. *Racospermyces tierneyi*, all ex DAR 72315 (holotype). **Fig. 40.** Four urediniospores. **Fig. 41.** Four teliospores. Bar: 12 µm.

Racospermyces tierneyi is known so far only from the type specimen. It is quite distinct from the other species of *Racospermyces* in its short narrow urediniospores with 4–8 equatorial germ pores and in the squat, strongly apically thickened teliospores with several apical appendages. The sori are often restricted laterally by the close longitudinal veins of the phyllode and in width usually fill only one or two neighbouring interveinal spaces. They arise from a plectenchymatous stromatic mass that extends up to 200 µm deep into the phyllode tissue and the long pedicels of the teliospores fan out from the top of the sorus carrying the teliospores well above the surface of the phyllode. It is most similar to *R. bicinctus* in teliospore characters but differs from this species in the single equatorial row of several germ pores in its urediniospores.

Discussion

Cummins & Hiratsuka (1983) stated that 'Teliospores are the most important spore state in generic distinctions'. *Atelocauda* and *Racospermyces* cannot be distinguished by their teliospores alone. Although no discussion of reasons was given, their similarity in teliospore characters was obviously one of the factors influencing Cummins & Hiratsuka (1983) to place all these fungi together in the genus *Atelocauda*. Teliospores of *A. incrustans* have a tuberculate ornamentation very similar to that of teliospores of *R. koae* (compare Fig. 3 in the present paper with Fig. 7 of Gardner & Hodges 1985) and, in the absence of other spore states, the striking similarity of the digitate teliospores of *A. shivasii* and those of the *R. digitatus* complex would suggest strongly that they belonged to the same genus. However, it is felt that, in establishing sound generic distinctions in the *Uredinales*, **all** spore states together with the life cycles, host ranges and distributions of the rusts should be

taken into account. In the present case, it is considered that the similarity in teliospores does not constitute a sound reason for placing these fungi in the one genus. The cumulative differences in urediniospores (aecial and uredinial) and in pycnial type, together with the different host families (subfamilies of some authors) are sufficient to regard the two groups of rusts as distinct genera.

Treating these rusts in this way gives rise to certain biogeographical hypotheses:

(i) The genus *Atelocauda* is of Central American origin and in the same group (?clade) as the genus *Dicheirinia* with several species in the region. Both the type species of *Atelocauda*, *A. incrustans* and some species of *Dicheirinia* occur on the genus *Lonchocarpus* and the possible connection between them suggested by Arthur & Cummins (1933) and Cummins (1937) has been dealt with above. A similar resemblance in urediniospore characters between the Australian *A. shivasii* and the Central American *D. ormosiae*, both on *Ormosia*, has been shown here. The occurrence of *A. shivasii* on *Ormosia* in Queensland is considered another example of the relationship between the floras and the fungi of the Central and South American and Australasian regions detailed earlier by Walker (1996).

(ii) *Racospermyces* is confined to hosts in the group of *Acacia* species accepted by Pedley (1986, 1989) (but not by some other authors, see Maslin 1989) as belonging to the segregate genus *Racosperma* Mart. *Racospermyces* has probably arisen in the Australasian region from rust ancestors of African origin, arriving with ancestral *Acacia* spp. of the *Racosperma* group (Pedley 1986, Walker 1996). All species of *Racospermyces* occur on phyllodinous hosts, with the exception of some members of the *R. digitatus* complex which infect several bipinnate wattles. Species such as *Racospermyces hyalosporus* and *R. koae* have developed on *Acacia* (*Racosperma* group) dispersed in the Asian and Pacific area.

(iii) The six species of *Racospermyces* are all variations on the *R. digitatus* theme and originated from it. As currently conceived, *R. digitatus* is a complex of related taxa, with varying morphologies, life cycles and host ranges. It is in an active state of differentiation and, as a complex, has the largest number of recorded hosts (over 30 species) of any *Racospermyces*. The three species, *R. angustiphyllodius*, *R. bicinctus* and *R. tierneyi*, each have only one known host and teliospores with apical thickening and varying development of digitate appendages. They are probably *R. digitatus* variants that have become relatively recently recognisable as distinct species on their particular hosts. In Hawaii, Hodges & Gardner (1984) considered that *R. koae* arose from a macrocyclic form of *R. digitatus,* which they suggested as the original colonizing species from which all the Hawaiian rusts of endemic *Acacia* spp. have evolved. *Racospermyces hyalosporus* differs from the other species in having non-ornamented teliospores, not thickened apically. However, its mature teliospores closely resemble immature thin-walled, non-ornamented teliospores of the *R. digitatus* complex, some of whose variants produce mature teliospores with none or very few short appendages. Production of pycnia and reticulate aecial uredinia on bullate lesions distorting host organs is similar in both species. It is suggested that *R. hyalosporus* is an *R. digitatus* derivative, which has retained pale, thin-walled teliospores, posssibly as a beneficial adaptation to moist tropical conditions (see Savile 1980).

(iv) Cummins & Hiratsuka (1983, 1984) placed *Atelocauda* (including the *Acacia* rusts here disposed in *Racospermyces*) with *Pileolaria* and *Uromycladium* in the Pileolariaceae. *Dicheirinia* was included with several other genera in Raveneliaceae. As shown above, *Atelocauda* in the strict sense defined here shows no similarity to *Pileolaria* but is close to *Dicheirinia* and should be included in the same family. It is thus redisposed here in Raveneliaceae. The familial position of the various species of *Racospermyces* will be considered later together with a detailed treatment of the genus *Uromycladium.*

With modern DNA techniques, it should be possible to test aspects of these hypotheses and uncover further evidence to help determine the precise relationships of the genera and species discussed here.

Teliospore germ pores in *Atelocauda* and *Racospermyces*

Preliminary observations on herbarium specimens indicate differences in teliospore germ pores in these two genera. In the two species of *Atelocauda*, the germ pore in mature spores is distinct, well-developed, penetrates the spore wall and is similar to that seen in many other rusts, such as species of *Uromyces* and *Puccinia*. In mature teliospores of *Racospermyces* spp., a germ pore in ungerminated spores is either not obvious or is recognised only by a small bulge of cytoplasm into the spore wall at the germination site. The pore appears to form shortly before germination, in the wall just to one side of the apical thickening or, in *R. hyalosporus*, through the thin apex. The basidial initial develops by penetration through the spore wall and not by apical elongation of the spore into a basidium. Much more work with fresh material and spores germinated experimentally is needed to categorise accurately any differences in germ pores between the two genera.

Keys

Key to genera *Atelocauda* and *Racospermyces*

In the key to rust genera provided by Cummins & Hiratsuka (1983), these two genera fall into Section VIII. With the inclusion of *Racospermyces*, their key needs to be modified as follows from step 16:

16 Teliospores depressed-globoid, verrucose or reticulate ..... *Pileolaria*

16 Teliospores subglobose to broadly ellipsoidal or longer, smooth or with digitate appendages or block-like warts **17**

17 Urediniospores (aecial and uredinial) triangular to lobed or irregular, with echinulate walls, and one or more germ pores variously arranged. Pycnia type 7. Known hosts in Fabaceae *s. str.* ..... *Atelocauda*

17 Urediniospores (aecial and uredinial) regularly oval, ovate, obovate to fusiform, with reticulate walls, and several germ pores usually in one or two rows. Pycnia type 5. Known hosts in Mimosaceae ..... *Racospermyces*

Key to species of *Atelocauda*

1 Teliospores with block-like or shortly digitate tubercles, at apex and in a few rows down the side. Aecial urediniospores lobed, with three germ pores, one in apex of each lobe. Wall completely echinulate. On *Lonchocarpus*, Central America. 0, II^{I}, III ..... *A. incrustans*

1 Teliospores without tubercles but with 4–6 digitate apical appendages. Aecial and uredinial urediniospores longitudinally lobed with one basal germ pore. Wall partly echinulate, with smooth patch 11–16 µm diam. above germ pore. On *Ormosia*, Australia (Queensland). 0, II^{I}, II, III ..... *A. shivasii*

Key to species of *Racospermyces*

1 Teliospores without ornamentation or appendages, apex unthickened; urediniospores (aecial and uredinial) fusiform, often over 60 µm long. On *Acacia confusa*, China, Japan, Taiwan. 0, II^{I}, II, III ..... *R. hyalosporus*

1 Teliospores with tuberculate ornamentation or digitate appendages, apex often thickened; urediniospores (aecial and uredinial), when present, variable in shape, ellipsoidal, oval to ovate or obovate, fusiform, rarely to 50 µm long **2**

2 Teliospores ornamented with several short tubercles at apex and extending in a few vertical rows down most spores. On *Acacia koa*, Hawaiian Islands. 0, II^{I}, III ..... *R. koae*

2 Teliospores with digitate appendages apical to subapical, not extending in vertical rows down the spore **3**

3 Teliospores mainly with length:breadth less than 2:1, apex much thickened, urediniospores (aecial and uredinial) only slightly shorter than teliospores **4**

3 Teliospores mainly with length:breadth 2:1 to 3:1 or more, apex slightly to much thickened; urediniospores (aecial and uredinial), when present, generally much shorter than teliospores **5**

4 Urediniospore germ pores mostly in two distinct rows of (3 or) 4 pores each. On *Acacia fasciculifera*, Australia (Queensland). 0, II^{I}, II, III ..... *R. bicinctus*

4 Urediniospore germ pores mostly in one equatorial row of (5–) 6–8 pores. On *Acacia harpophylla*, Australia (Queensland). II, III ..... *R. tierneyi*

5 Urediniospores (aecial and uredinial) present, on spots, tuberculate swellings, galls and compact witches' brooms. On *Acacia* spp., widespread in Australasia, South-East Asia and the Hawaiian Islands. 0, II^{I}, II, III ..... *R. digitatus s. lat.*

5 Urediniospores (aecial and uredinial) not known. Pycnia and telia on elongated witches' brooms and phyllode spots. On *Acacia koa* var. *latifolia*, Hawaiian Islands (Hawaii, Gardner 1991). 0, III ..... *R. angustiphyllodius*

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