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Notes on Deuteromycetes

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Abstract. – The generic name *Aporella* H. SYD. is a homonym and is replaced by *Aporellula* nom. nov. The new species *Marssonina psidii*, *Monostichella appendiculata* and *Myrothecium atroviride* are illustrated, described and compared with related taxa. The new generic name *Rhizosphaerina*, type species *R. variabilis* sp. nov., is introduced and compared with *Rhizosphaera* and *Atichia*.

1. *Aporellula* B. C. SUTTON, nom. nov.

Aporella H. SYD. (1939) *Annls. mycol.* 37: 416, non PODPĚRA (1922) (Musci).
Sp. typ.: *A. erigerontis* (H. SYD.) SUTTON (syn. *Aporella erigerontis* H. SYD.).

Conidiomata eustromatic, separate or aggregated, subcuticular, immersed to semi-immersed, subglobose, initially pale, later dark brown, unilocular; wall of textura angularis; ostiole absent, dehiscence by breakdown of upper wall. – Conidiophores absent. – Conidiogenous cells hyaline, ampulliform to doliiform, discrete, restricted to the basal wall. – Conidia holoblastic, aseptate or with a single basal septum, or with one at each end, hyaline, \pm guttulate, fusiform, base truncate, apex obtuse, straight or curved. – Conidial development: ontogeny holoblastic by apical wall building; maturation synchronous with ontogeny or delayed; delimitation by a transverse septum, secession schizolytic; enteroblastic conidiogenous cell proliferation with successive conidia seceding at the same level.

The generic name *Aporella* is a later homonym of *Aporella* (Musci) PodpĚra, (1922) and is herewith replaced by the new name *Aporellula*. The genus is monotypic. Septation is very indistinct and few conidia show it. Perhaps these conidia are in the initial stages of germination. In many coelomycetes with mature aseptate conidia, more than one septum is laid down prior to and during germination.

***Aporellula erigerontis* (H. SYD.) B. C. SUTTON, comb. nov. – Fig. 1**

Aporella erigerontis H. SYD., *Annls mycol.* 37: 416 (1939).

Conidiomata epiphyllous, up to 100 μ m diam. \times 50 μ m deep. – Conidiogenous cells 8.5 \times 7 μ m. – Conidia 20–25 \times 5.5–7.5 μ m.

On leaves of *Erigeron bonariense*, ECUADOR (IMI 288252, isotype ex W).

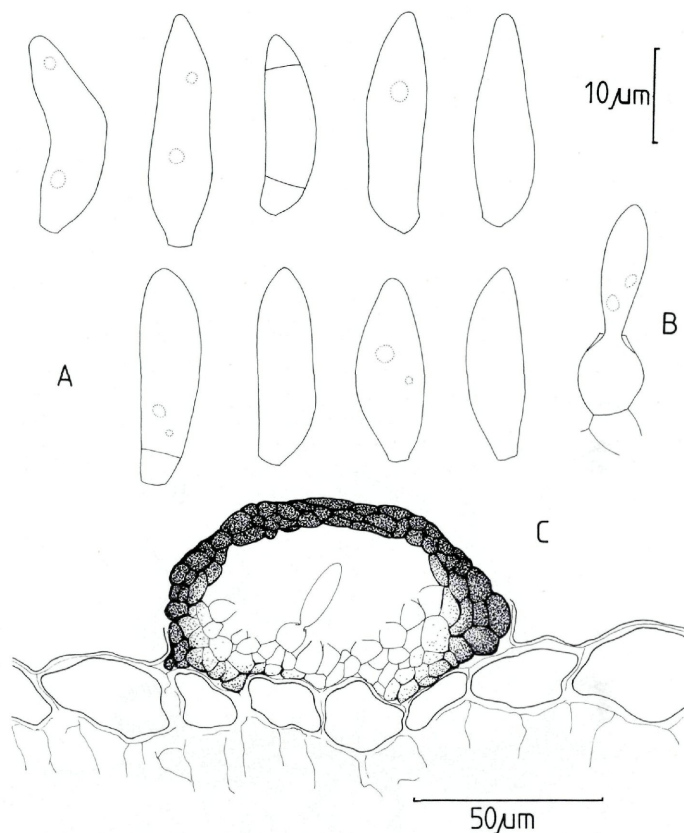


Fig. 1: *Aporellula erigerontis* (isotype). – A. conidia. – B. conidiogenous cell and developing conidium. – C. v. s. conidioma.

2. *Marssonina psidii* B. C. SUTTON, sp. nov. – Fig. 2

Laesiones distinctae absentes. Mycelium immersum ex hyphis hyalinis vel pallide brunneis, ramosis, septatis, in epidermide locatis. Conidiomata acervularia, epiphylla, subcuticularia, atro-brunnea vel nigra, separata vel confluentia, ex 1–3 stratis texturae angularis consistentia; usque ad 10 μm crassis, 200 μm diam. Dehiscens irregularis, cuticula 1–3 stratis textura angulari brunneoli ferenti. Conidiophora absentia. Cellulae conidiogenae cum 1–2 proliferationibus percurrentibus, discretae, ampulliformes vel doliiformes, hyalinae laeves crassis tenuibus vel pallide brunneae

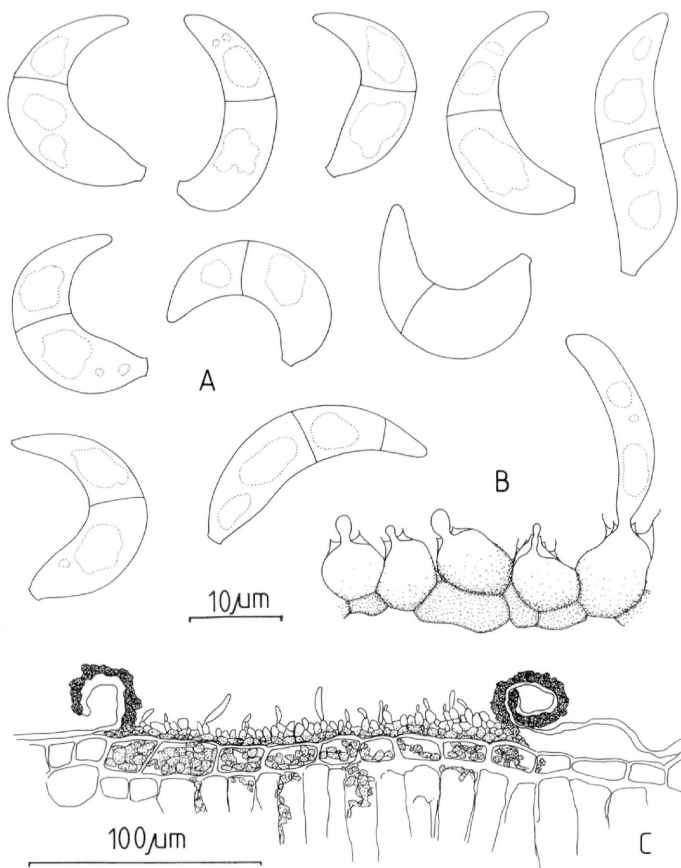


Fig. 2: *Marssonina psidii* (holotype). – A. conidia. – B. conidiogenous cells and developing conidia. – C. v. s. conidioma.

basim versus crassiores et verruculosae, $6.5-11 \times 6-7.5 \mu\text{m}$; canalis et spissescens periclinalis distincti, collo interdum praesenti. Conidia holoblastica, fusiformia, valde curvata, hyalina, 1 (raro 2) euseptata, cellula apicale brevior, cellula basale longior, laevia, basim versus abrupte deminuta, apicem versus gradatim attenuata, guttulata, $16-28.5 \times 6-6.5 \mu\text{m}$. In foliis *Psidii guajavae*, Mandalay, Burma, THAUNG, 30 Mar. 1972, IMI 169371, holotypus.

Distinct lesions are absent. – Mycelium immersed, hyaline to pale brown, branched, septate, concentrated in the epidermis. – Conidiomata acervular, epiphyllous, subcuticular, dark brown to black, separate or sometimes confluent, consisting of 1–3 layers of *textura angularis* up to 10 μm thick, 100 μm diam. Dehiscence irregular, the cuticle carrying away 1–3 layers of darker brown *textura angularis*. – Conidiophores absent. – Conidiogenous cells often with 1–2 percurrent proliferations, discrete, ampulliform to doliiform, either hyaline, thin-walled and smooth or pale brown, thicker-walled and verruculose at the base, $6.5\text{--}11 \times 6\text{--}7.5 \mu\text{m}$; channel and periclinal thickening prominent, occasionally a distinct collarette is present. – Conidia holoblastic, fusiform, strongly curved, hyaline, 1(occasionally 2-) euseptate, the septum differentiating a shorter upper cell and a longer lower cell, smooth, abruptly tapered to a truncate base, gradually tapered to an obtuse apex, guttulate, $16\text{--}28.5 \times 6\text{--}6.5 \mu\text{m}$.

Neither species of *Marssonina* nor related fungi have been described from this host. The species is distinctive on account of the strongly curved conidia and the conidiomatal tissue peeling back with cuticle as it is ruptured. These features in no way conflict with the amended generic limits of the genus proposed by SUTTON & WEBSTER (1984) to accommodate *M. pakistanica*, a species with *Tricellula*-like conidia.

3. *Monostichella appendiculata* B. C. SUTTON, sp. nov. – Fig. 3

Laesiones distinctae, interdum confluentes, circulares deinde irregulares, 0.1–0.6 mm diam. Mycelium immersum, hyalinum vel pallidissime brunneum, ramosum, septatum, inter – et intra-cellulare. Conidiomata acervularia, epiphylla, subcuticularia vel epidermalia, pallide brunnea, separata, ex 3–4 stratis *textura angularis*, usque ad 10 μm profunda, usque ad 120 μm diam. Dehiscens irregularis, cuticula ferenti et discolori. Conidiophora absentia. Cellulae conidiogae lageniformes, hyalinae, tenuitunicatae, laeves, $7\text{--}11.0 \times 5\text{--}6.5 \mu\text{m}$ ad basim, apicem versus $2.5\text{--}3.5 \mu\text{m}$ crassae, saepe sine apparatu apicali, interdum canale lato, spissescenti periclinali minuto sed sine collo. Conidia holoblastica, globosa vel ellipsoidea, hyalina, aseptata, laevia, eguttulata, basim truncata, $14\text{--}21 \times 11\text{--}15 \mu\text{m}$, appendice apicali vel subapicali, cellulosa, non ramosa, filiformi $9\text{--}14 \mu\text{m}$ longa ornata. In foliis vivis *Carpini vimineae*, Gorakhpur, India, KAMAL 104, comm. 22 Nov. 1983, IMI 281879, holotypus.

Lesions distinct, occasionally confluent and spreading along secondary veins, circular when young, becoming more irregular with age, 0.1–0.6 mm diam, surrounded by a very narrow light green chlorotic halo which is only visible by transmitted light, with a brown distinct margin, becoming paler towards the centre. – Mycelium immersed, hyaline to very pale brown, branched, septate, inter- and intra-cellular. – Conidiomata acervular, epiphyllous, subcuticular to epidermal, pale brown, separate, consisting of 3–4 layers of *textura angularis* up to 10 μm deep, up to 120 μm diam.

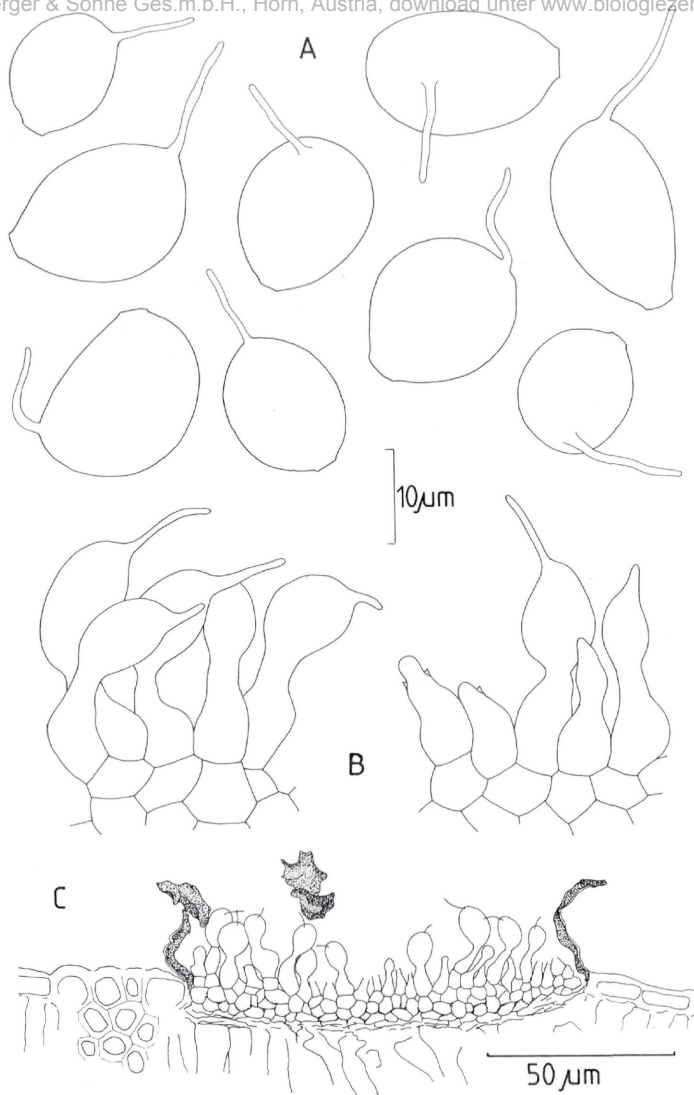


Fig. 3: *Monostichella appendiculata* (holotype). – A. conidia. – B. conidiogenous cells and developing conidia. – C. v. s. conidioma.

Dehiscence irregular, the cuticle being ruptured and discoloured. – Conidiophores absent. – Conidiogenous cells lageniform, hyaline thin-walled, smooth, $7.5\text{--}11.0 \times 5\text{--}6.5 \mu\text{m}$ at the base, narrowing to $2.5\text{--}3.5 \mu\text{m}$ wide at the apex, mostly without apical apparatus, occasionally with a wide cytoplasmic channel, minute periclinal thickening but no collarete. – Conidia holoblastic, globose to ellipsoidal, hyaline, aseptate, smooth, eguttulate, base truncate, $14\text{--}21 \times 11\text{--}15 \mu\text{m}$, with an apical or subapical cellular, unbranched filiform appendage $9\text{--}14 \mu\text{m}$ long.

Placing this species to genus is somewhat problematical because of the combination of conidial morphology and conidiomatal structure. Using the example of *Colletotrichum* CDA. where a species with appendaged conidia such as *C. caudatum* (SACC.) PECK is comfortably accommodated together with species lacking conidial appendages (SUTTON, 1980), there is an acceptable precedent. Species so far described in *Monostichella* v. HÖHN. all have conidia without appendages but SUTTON (1980) has indicated that on the basis of conidial morphology alone the genus is heterogeneous. Rather than introduce another new generic name for this undescribed species it is preferred to place it in *Monostichella* until a complete revision of the group is made. Any such revision would also take into account the genus *Monochaetiella* CASTELLANI, the type species of which, *M. hyparrheniae*, has hyaline fusiform conidia with a short apical cellular appendage and similar conidiogenous cells to *Monostichella appendiculata*. It differs in conidiomatal structure which is simply acervular, the textura angularis being subepidermal. The epidermis and cuticle are ruptured during dehiscence but there is no discolouration of the cuticle. It is this feature which precludes placing this undescribed fungus in *Monochaetiella*.

4. *Myrothecium flavo-virens* B. C. SUTTON, sp. nov. – Fig. 4

Mycelium immersum, hyalinum, laeve, ramosum, septatum, $2\text{--}3 \mu\text{m}$ diam, interdom hypostromate $70 \mu\text{m}$ profundo $\times 30 \mu\text{m}$ crasso formatum. Conidiomata superficialia, separata, cupulata, sessilia vel stipitata, usque ad $140 \mu\text{m}$ diam. $\times 80 \mu\text{m}$ profunda, marginem flavo-virentia, centrum massa conidiorum nitescenti viride nigra; paries basis ex textura angulari, hyalina formatus, marginem versus textura poroecta compositus; hyphae marginales separatae liberae, versus centrum conidiomatis incurvatae sed non obtegentes, rectae vel leviter curvatae, usque ad 4 septatae, non ramosae, apices obtusos versus plus minusve auctae, verrucosae, flavo-virentes, $50\text{--}60 \mu\text{m}$ longae, prope apicem $4\text{--}4.5 \mu\text{m}$ crassae. Conidiophora basim versus ramosa, hyalina vel pallide brunnea, septata, laevia, erecta, \pm recta, marginem conidiomatis usque ad $35 \mu\text{m}$ longa, centro versus $15 \mu\text{m}$ longa $\times 2\text{--}2.5 \mu\text{m}$, basi et lateris parietis conidiomatis formata. Cellulae conidiogenae $7\text{--}15 \mu\text{m}$ longae $\times 2\text{--}2.5 \mu\text{m}$ crassae, apicales, hyalinae vel pallide brunneae, laeves, \pm rectae, loco singulo apicali conidiogeno et collo minuto pigmentoso, canali minuto et spissescenti periclinali instructae, proliferationibus enteroblasticis percurrentibus usque ad

4 collis producentes. Conidia holoblastica, aseptata, brunnea, verruculosa, saepe 2 guttulata, ellipsoidea, basim truncata, in massis viride nigra, $5-6 \times 2-2.5 \mu\text{m}$.

In leguminis *Parsonsiae*, Maijala National Park, Queensland, Australia, SUTTON & ALCORN, 27 Aug. 1981, IMI 263300b, holotypus.

Mycelium immersed, hyaline, smooth, branched, septate, 2–3 μm diam, aggregated beneath conidiomata sometimes to produce a hypostroma up to 70 μm deep \times 30 μm wide. – Conidiomata superficial, separate, cupulate, sessile or stipitate, up to 40 μm diam \times 80 μm deep, yellowish green (RAYNER, 1970) and pruinose at the margin surrounding a central greenish black, shining conidial mass; basal wall composed of hyaline, thin-walled textura angularis, towards the margin composed of textura porrecta; marginal hyphae separate and free, up to 4 septate, unbranched, expanding towards the obtuse apices, distinctly verruculose, yellowish green, 50–60 μm long \times 4–4.5 μm wide near the apex. – Conidiophores repeatedly branched towards the base, hyaline to pale brown, septate, smooth, erect, \pm straight, at the margin of the conidiomata up to 35 μm long, towards the centre up to 15 μm long \times 2–2.5 μm , formed from the base and sides of the conidiomatal wall. – Conidiogenous cells 7–15 μm long \times 2–2.5 μm wide, apical, hyaline to pale brown, smooth, \pm straight, with a single apical conidiogenous locus and minute pigmented collarette, minute channel and periclinal thickening, proliferating enteroblastically to produce up to 4 percurrent collarettes. Occasionally all conidiogenous cells cease to form conidia at the same time and instead produce percurrent vegetative growth with associated deeper pigmentation of the conidiogenous region. This leads to successive zones of sporulation, as seen in *Verticilliodochium* BUBAK (BOOTH, 1978). – Conidia holoblastic, aseptate, brown, verruculose, often biguttulate, ellipsoid, base \pm truncate, greenish black in mass, $5-6 \times 2-2.5 \mu\text{m}$.

TULLOCH (1972) has revised *Myrothecium* TODE: FR. and accepted 13 species. The broad generic limits include cupulate, sporodochial and synnematal forms. Cupulate conidiomata are most typical of *M. gramineum* LIB., *M. leucotrichum* (PECK) TULLOCH and *M. atroviride* (BERK. & BR.) TULLOCH. In all conidiomata, however, differential marginal hyphae are present. Hyaline or dark setae are also sometimes formed. The marginal hyphae surround the central mass of slimy green to black conidia which become hard when dried. Conidia may or may not be pigmented but are formed holoblastically from phialides (sensu SUTTON, 1980) which sometimes percurrently proliferate. In these respects *M. flavo-virens* admirably fits the generic concept. It differs from accepted species in several ways. The yellowish-green pigmentation of the conidiomatal wall and marginal hyphae is quite different from the floccose white hyphae that are typical of all other species. The verruculose marginal hyphae are

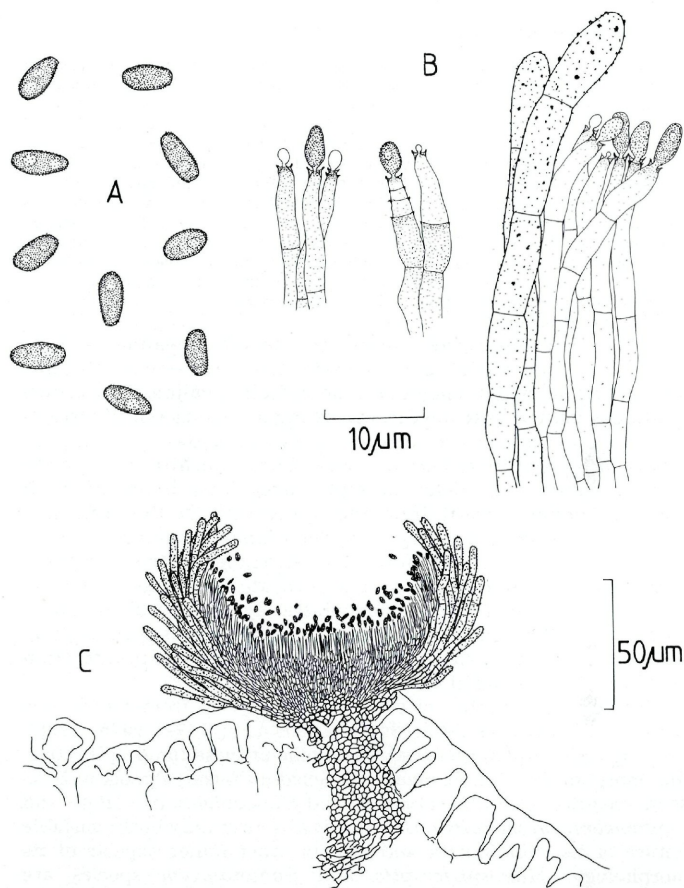


Fig. 4: *Myrothecium flavo-viride* (holotype). A conidia. – B. conidiophores, conidiogenous cells, developing conidia and marginal hyphae. – C. v. s. conidioma.

similar to those in *M. cinctum* (CDA.) SACC. and *M. verrucaria* (ALB. & SCHW.: FR.) DITM.: FR. but are erect rather than sinuous. The pigmentation and size of conidia is quite different from any known species, most closely approaching those of *M. verrucaria* but lacking the fan-tailed appendage.

5. *Rhizosphaerina* B. C. SUTTON, gen. nov.

Mycelium immersum, ramosum, septatum, hyalinum. Conidiomata superficialia et sporodochialia, semi-immersa et acervularia, in matrice gelatinosa initio hyalina, deinde brunnea inclusa, eustromatica, ex textura oblita/intricata consistantia, hyalina vel atro brunnea; a rupto matricis vel epidermidis dehiscentia. Conidiophora hyalina vel brunnea, septata, ad septis constricta, irregulariter ramosa, cum luminibus deminutis, ex cellulis superioribus stromatum formata. Cellulae conidiogenae in conidiophoris incorporatae, determinatae, terminales vel intercalares, doliiformes vel ampulliformes. Conidia holoblastica, brunnea, aseptata, verruculosa, ellipsoidea, parietibus tenuibus, basim versus truncata. Conidiogenesis: ontogenesis conidiorum holoblastica constructione ad parietes apicales, maturatio conidiorum tarde evoluta, limes conidiorum uno septo duplici, secessio schizolytica, proliferatio cellulae conidiogenae enteroblasticae conidiis additis ad positiones easdem successivas producens, regeneratio et collum non visis.

Sp. typ.: *R. variabilis*.

Mycelium immersed, branched, septate, hyaline. — Conidiomata superficial and sporodochial, semi-immersed, immersed and acervular, enclosed in an initially hyaline, later brown gelatinous matrix, eustromatic, consisting of textura oblita/intricata, hyaline to dark brown; dehiscence by breakdown of gelatinous matrix or by rupture of host tissues. — Conidiophores hyaline to brown, septate, constricted at septa, irregularly branched, with reduced lumina, formed from the upper cells of the stroma. — Conidiogenous cells integrated, determinate, terminal or intercalary, doliiform to ampulliform. — Conidia holoblastic, aseptate, verruculose, ellipsoid, thick-walled, truncate at the base. — Conidial development: conidia holoblastic by apical wall building, maturation after secession, delimitation by a transverse septum, secession schizolytic, enteroblastic conidiogenous cell proliferation with conidia seceding at the same level.

There are a number of coelomycetes known from *Eucalyptus* with small brown conidia (SUTTON, 1971a, b; 1974; 1975; 1980). Although *Rhizosphaerina* resembles some of these fungi in its conidial morphology, e. g. *Fairmaniella leprosa* (FAIRM.) PETRAK & SYD., some species of *Coniothyrium* CDA. and *Microsphaeropsis* HÖHN. and *Leptomelanconium australe* SUTTON, it differs mainly in the variable nature of its conidiomata and also in other minor aspects of its morphology. *Microsphaeropsis* and *Coniothyrium* species are characterized by pycnidial conidiomata whereas *Fairmaniella* and *Leptomelanconium* are acervular. *Rhizosphaerina* has two distinct types of conidiomata, both of which incorporate a pigmented gelatinous matrix covering the conidial mass. This is hygroscopic at high humidity. The less frequently seen conidioma is typically acervular and resembles similar structures in *Fairmaniella* and *Leptomelanconium* except for the gelatinous covering. It is also hygroscopic. The more frequent type is superficial and connected to the substrate by hyaline mycelium through the host stromata. Superfi-

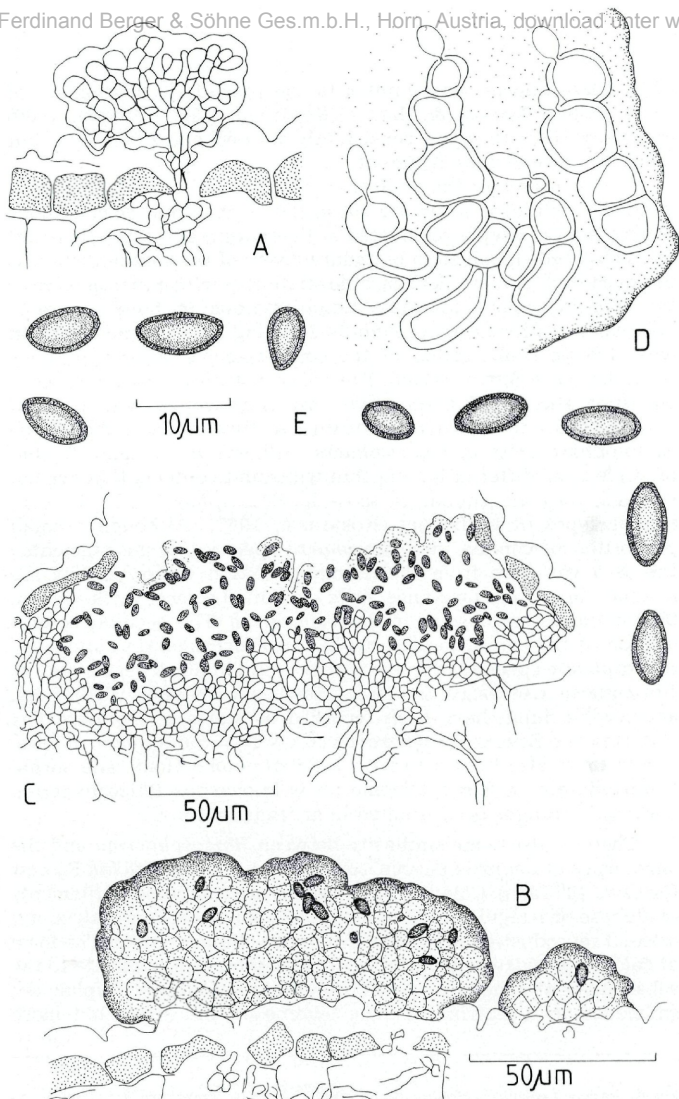


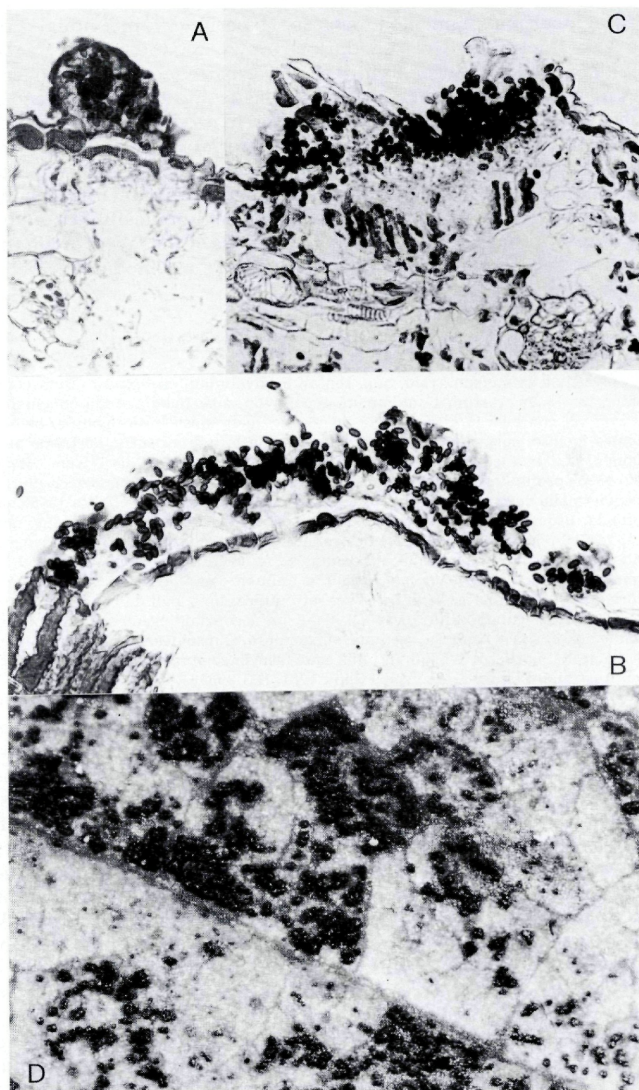
Fig. 5: *Rhizosphaerina variabilis* (holotype). - A. immature conidia. - B. mature superficial conidiomata. - C. mature immersed conidia. - D. conidiogenous cells and developing conidia. - E. conidia.

cially these appear very similar to the pycnidial conidiomata of *Rhizosphaera* MANGIN & HARIOT (KOBAYASHI, 1967; SUTTON, 1980) especially since they are consistently formed above stomata, but their structure is quite different.

In *Rhizosphaera* the wall of the conidioma is 1 cell thick and distinctly cellular in structure but in *Rhizosphaerina* the gelatinous matrix is more deeply pigmented at the margin and since there are no hyphal cells involved in boundary layers of the conidiomata it is not pycnidial. A more demonstrable similarity with *Rhizosphaera* is the conidiogenous apparatus. Conidiogenesis in both genera is holoblastic with successive conidia seceding at the same level and enteroblastic proliferation of the conidiogenous cells to produce phialides *sensu* SUTTON (1980). The cells constituting the conidiogenous apparatus in *Rhizosphaerina* are thick-walled with reduced lumina similar to the cells constituting *textura oblita*. Although the conidiophore cells in *Rhizosphaera kalkoffii* BUBAK and *R. pini* (CDA.) MAUBL. differ in having thin walls and contents that are not reduced, they are similar to those in *Rhizosphaerina* in the very similar types of branching (KOBAYASHI, 1967). Although a small proportion of conidia in *Rhizosphaera* species become pigmented this is a variation from the normal situation where conidia are hyaline. In no circumstance have conidia become thick-walled, brown and verruculose as in *Rhizosphaerina*. The peculiar configuration of the conidiogenous hyphae in *Rhizosphaerina* and some *Rhizosphaera* species is similar to that found in black yeasts such as *Hormonema* LAGERBERG & MELIN (HERMANIDES-NUJHOF, 1977). Such anamorphic fungi have been recorded as states of *Dothiora* FR., *Pringsheimia* SCHULZ, *Guignardia* VIALA & RAVAZ and *Sydowia* BRES. The latter is also known to have a *Sclerophoma* HÖHN. anamorph. Unfortunately neither a teleomorph is known for *Rhizosphaerina* nor has the fungus been isolated in artificial culture.

There is also some similarity between *Rhizosphaerina* and the anamorphs of *Seuratia* PATOUILLARD which belong in *Atichia* FLOTOW (MEEKER, 1975 a, b). Colonies in this genus are composed of filaments of globose or irregular cells in a hygroscopic gelatinous matrix and asexual reproduction is by means of multicellular conidia. The form of colonies is extremely variable; they may be wholly adnate to the substrate or attached by a basal disc if larger. Cells and hyphae are embedded in a matrix which is hyaline on the inside but more

Fig. 6: *Rhizosphaerina variabilis* (holotype). — A. v. s. immature superficial conidiomata. — B. v. s. mature superficial conidioma. — C. v. s. mature immersed conidioma. — D. surface view of individual conidiomata at various stages of maturity.
— A. C, $\times 250$; D, $\times 25$.



cartilaginous and pigmented towards the periphery; individual cells are also thicker-walled and darker brown on their outer faces. Conidia in *Atichia* differ from those in *Rhizosphaerina* in ontogeny and morphology in that they are holoblastic and the conidiogenous cells do not show percurrent proliferation to produce a succession of conidia at one level. Conidia are of indeterminate growth but are basically triradiate and variable in pigmentation. MEEKER (1975a) has described and illustrated the wide range in conidial morphology seen in the genus. In *Rhizosphaerina* the single unicellular conidia are formed in succession from individual cells of the mycelium in the gelatinous matrix. Such differences preclude accomodating *Rhizosphaerina* in *Atichia*.

***Rhizosphaerina variabilis* B. C. SUTTON, sp. nov. – Fig. 5–6**

Mycelium immersum, ramosum, septatum, hyalinum, ex textura oblita compositum, 3.5–5 μ m crassum. Conidiomata hypophylla, superficialia et sporodochialia, solitaria vel confluentia et complexa, in matrice gelatinosa initio hyalina, deinde brunnea inclusa, eustromatica, pulvinata vel punctiformia, nitentia, postremo atro brunnea, ex textura oblita supra stomatibus superposita, 35–110 μ m diam. \times 22–45 μ m profunda; a rupto matricis dehiscentia. Aliquot conidiomata acervularia, subepidermalia cum matrice gelatinosa pallide brunnea, ex textura oblita 15–30 μ m profunda, usque ad 220 μ m diam.; a rupto epidermide dehiscentia. Conidiophora initio hyalina, deinde pallide vel medie brunnea, septata, ad septis constricta, irregulariter ramosa, luminibus cellularum deminutis, ex cellulis superioribus stromatum formata, usque ad 35 μ m longa \times 4–8 μ m lata. Cellulae conidiogena in conidiophoris incorporatis, determinatis, terminales vel raro intercalares, pallide vel medio brunnea, doliformis vel ampulliformes, 5–8 \times 4–8 μ m, loco conidiogeno singulo apicale. Conidia holoblastica, brunnea, aseptata, verruculosa, ellipsoidea, parietibus tenuibus basi truncata, 6.5–9.5 \times 4–5 μ m. In foliis emortuis? *Eucalypti*, Mt Coot-tha, Queensland, Australia, SUTTON & ALCORN, 1 Sept. 1981, IMI 263561, holotypus.

Mycelium immersed branched, septate, hyaline, extensively ramifying in the host tissues, composed of thick-walled textura oblita, 3.5–5 μ m wide. – Conidiomata superficial and sporodochial, solitary or confluent to produce composite conidiomata, enclosed in an initially hyaline, later brown, gelatinous matrix, eustromatic, pulvinate to punctiform, shining, eventually dark brown, consisting of textura oblita radiating out and above from the stomata, 35–110 μ m diam. \times 22–45 μ m deep, attached to the substrate by mycelium through the stomata; dehiscence by breakdown of the gelatinous matrix coincident with conidial production. A small proportion of conidiomata are acervular, subepidermal, usually separate not confluent, with a less distinct pale brown matrix, and a well-defined basal stroma of textura oblita, 15–30 μ m deep, up to 220 μ m diam., dehiscence by rupture of the host epidermis. – Conidiophores in young conidiomata hyaline, becoming pale to medium brown with age, septate, markedly constricted at the septa, irregularly branched but tending to fan out from the base of the

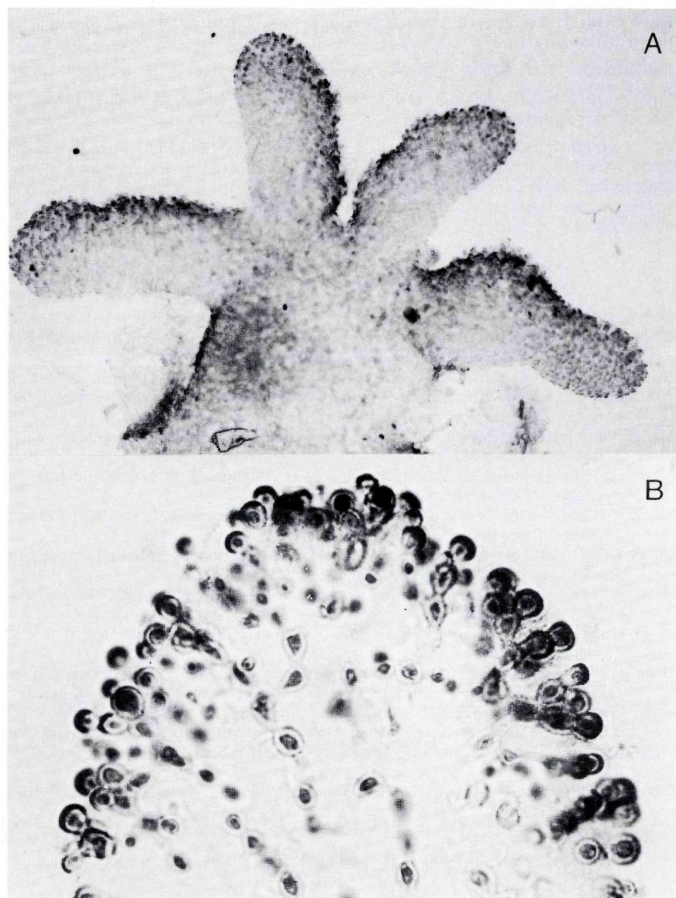


Fig. 7: *Atichia* state of *Seuratia millardetii* (IMI 274557). – A. gross features of thallus, $\times 100$. – B. section showing internal and peripheral structure. $\times 650$.

conidioma, with reduced lumina, formed from the upper cells of the stroma, up to 35 μm long \times 4–8.5 μm wide. – Conidiogenous cells integrated, determinate, terminal or more rarely intercalary, pale to medium brown, doliiform, 5–8 \times 4–8 μm , with a single apical conidiogenous locus. – Conidia holoblastic, brown, aseptate, verruculose, ellipsoid, thick-walled, truncate at the base, 6.5–9.5 \times 4–5 μm , to a limited extent spreading over the surface of the substratum.

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Artikel/Article: [Notes on Deuteromycetes. 324-338](#)