

Colletogloeopsis, a new coelomycete genus to accommodate anamorphs of two species of *Mycosphaerella* on *Eucalyptus*

P.W. Crous and M.J. Wingfield

Abstract: Species in *Colletogloeopsis* are characterized by having acervular conidiomata, and brown, verruculose, thick-walled, aseptate conidia that are formed on brown, verruculose conidiogenous cells that proliferate sympodially or percurrently. *Colletogloeum nubilosum*, the anamorph of *Mycosphaerella cryptica*, is transferred to *Colletogloeopsis*. *Colletogloeopsis molleriana* is described for the anamorph of *Mycosphaerella molleriana*, formed from single ascospore isolations obtained from collections of *Eucalyptus globulus* leaves from Portugal and California, United States. *Mycosphaerella molleriana* is redescribed and distinguished from *Mycosphaerella nubilosa*, which was earlier regarded to be synonymous with the former.

Key words: *Colletogloeum*, *Mycosphaerella* leaf blotch, systematics.

Résumé : Les espèces du *Colletogloeopsis* se caractérisent par des conidiomata acervulés, ainsi que des conidies brunes, verruqueuses et aseptées qui se forment sur des cellules conidiogènes brunes et verruqueuses qui prolifèrent de façon sympodiale ou percurrente. Les auteurs transfèrent le *Colletogloeum nubilosum*, anamorphe du *Mycosphaerella cryptica*, au *Colletogloeopsis*. Ils décrivent le *Colletogloeopsis molleriana* comme anamorphe du *Mycosphaerella molleriana*; il est formé d'isolats à ascospores simples obtenus à partir d'une collection sur feuilles de l'*Eucalyptus globulus*, provenant du Portugal et de la Californie aux États-Unis. Ils redécrivent le *M. molleriana* pour le distinguer du *Mycosphaerella nubilosa*, qui a été auparavant considéré comme synonyme du premier.

Mots clés : *Colletogloeum*, tache foliaire du *Mycosphaerellea*, systématique.

[Traduit par la rédaction]

Introduction

Several species of *Mycosphaerella* Johanson have been associated with *Mycosphaerella* leaf blotch (MLB) disease of *Eucalyptus* spp. both in Australia, where these trees are native, and elsewhere where they are commercially propagated (Carnegie et al. 1994; Crous and Wingfield 1996). One of the most often cited *Mycosphaerella* spp. occurring on eucalypts is *M. molleriana* (Thüm.) Lindau. Although this species has been associated with MLB on many species of *Eucalyptus* from several countries (Crous et al. 1991, 1995b; Carnegie and Keane 1994), it appears that most records are not conspecific with the type of *M. molleriana* (Crous and Alfenas 1995; Crous and Wingfield 1996). *Mycosphaerella molleriana*, which is similar to *Mycosphaerella nubilosa* (Cooke) Hansf. and *Mycosphaerella cryptica* (Cooke) Hansf., was described as a species of *Sphaerella* from *Eucalyptus globulus* Labill. in Portugal by Von Thümen (1881). Based on leaf symptoms, pseudothecial

distribution, and general morphology, Crous et al. (1991) considered *M. nubilosa* to be a synonym of *M. molleriana*, but distinct from *M. cryptica*. In recent years, we collected several fresh field specimens that enabled us to study cultural features and mode of ascospore germination. Based on these studies, we concluded that our earlier interpretation (Crous et al. 1991) of *M. molleriana* was incorrect, and that it includes several distinct taxa (Crous and Wingfield 1996). Because *M. molleriana* was the first species of *Mycosphaerella* to be described from *Eucalyptus* (Corlett 1991) and this tree genus has become increasingly important to the international paper and pulp industry, it is imperative that the taxonomy of this frequently cited species of *Mycosphaerella* be clarified.

Sphaerella nubilosa Cooke was originally described from eucalypt leaves in Australia (Cooke 1893), and later transferred to *Mycosphaerella* (Hansford 1957). *Colletogloeum nubilosum* Ganap. & Corbin was described as the anamorph of *M. nubilosa* (Cooke) Hansf. (Ganapathi and Corbin 1979). This anamorph-teleomorph connection was incorrect, however, because *Colletogloeum nubilosum* was later shown to be the anamorph of *M. cryptica* (Park and Keane 1982). In the description of *Colletogloeum nubilosum*, Ganapathi and Corbin (1979) noted that there were several morphological features that were inconsistent with the type species of *Colletogloeum* Petr., or with other species of the genus. In the present study, *Colletogloeum*-like anamorphs were observed in cultures derived from single ascospores obtained

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from *Eucalyptus* leaves with symptoms morphologically similar to the type of *M. molleriana*.

The coelomycete genus *Colletogloeum* has been linked to two distinct loculoascomycete genera, *Coccoidella* Höhn. and *Mycosphaerella*. However, neither of the anamorphs linked to these teleomorphs appear to be congeneric with the type species, *Colletogloeum sissoo* (Syd.) B. Sutton, which has hyaline, 1- to 4-septate, smooth conidia. *Colletogloeum perseae* Sivan. (teleomorph: *Coccoidella perseae* Sivan.) is distinct from *Colletogloeum sissoo* by having rostrate conidia with a long, apical, branched or unbranched appendage (Sivanesan 1987). *Colletogloeum nubilosum* (teleomorph: *Mycosphaerella cryptica*) differs from *Colletogloeum sissoo* in producing aseptate, brown, verruculose conidia that are formed on brown, verruculose conidiogenous cells that proliferate percurrently or sympodially. In a recent revision of species complexes within *Colletogloeum*, Morgan-Jones and Phelps (1995) noted that this genus is heterogenous, and that features such as conidium morphology may have to be examined more closely to accurately define taxonomic groups.

The anamorph obtained for *M. molleriana* in the present study is morphologically similar to *Colletogloeum nubilosum*. The two taxa form a group distinct from *Colletogloeum* which is characterized by the production of brown, verruculose, thick-walled, aseptate conidia, from sympodially or percurrently proliferating brown, verruculose, conidiogenous cells. To determine the appropriate generic placement, several other generic names were considered. These taxa cannot be accommodated in *Lecanostictopsis* B. Sutton & Crous, which includes species with verruculose to tuberculate conidiogenous cells, conidiophores, and conidia, and a dark brown conidioma consisting of dense hyphal elements. They differ from species of *Lecanosticta* Syd. because of their aseptate conidia, and sympodial as well as percurrent proliferation. Similarly, they are distinguished from species of *Ahmadia* Syd. by having subepidermal conidiomata, and from *Marssonina* Magnus and *Cryptocline* Petr. by having medium brown, verruculose, conidiogenous cells and conidia. None of these genera share all the characteristics of the *Colletogloeum*-like anamorphs of *Mycosphaerella*, and they differ in either conidial or conidiophore morphology, pigmentation, or mode of conidiogenesis. The *Colletogloeum*-like fungi from *Eucalyptus* appear to represent a group intermediate between *Colletogloeum* and *Lecanostictopsis*. For these reasons, it is our opinion that these two species are best accommodated in a separate genus, which is described here.

Materials and methods

Leaves of *E. globulus* with MLB symptoms were collected from plantations in southern Portugal and from shade-tree plantings near Berkeley, California. Leaves were tightly packed between sheets of paper and transported to the laboratory. Lesions were excised from leaves, and single ascospores were placed on 2% malt extract agar (Biolab Diagnostics, Midrand, JHB, South Africa) (MEA) as described in Crous et al. (1991). Germinating ascospores were examined after 24 h, illustrated, then transferred to MEA. Cultures were incubated for 2 weeks at 25°C in the dark, then subcultured onto divided plates with one half containing carnation-leaf agar (CLA) (Crous et al. 1992) and the other MEA, incubated at 25°C under continuous near-ultraviolet light. Linear growth on agar for each culture was determined after 1 month as explained in Crous

and Wingfield (1996). Colony colors (top and bottom) were determined using the color charts of Rayner (1970). All measurements were made of fungal structures mounted in lactophenol. Thirty measurements of each structure were taken, whenever sufficient material was available; extremes are given in parentheses.

Taxonomy

Colletogloeopsis Crous et M.J. Wingf. gen.nov.

Mycelium internum et externum, pallide ad mediobrunneum, septatum, ramosum, laevigatum. Acervuli atrobrunnei ad atrii, subcuticulares, erumpentes. Conidiogenae cellulae doliiformes ad subcylindraceae vel irregulares, parietibus tennibus, brunneae, verruculosae, proliferationibus sympodialibus vel compluriente enteroblasticis et percurrentibus. Conidia solitaria, aseptata, mediobrunnea, verruculosa, subcylindracea ad ellipsoidea, recta ad parum curvata; apex obtusus, basis truncata, margine fimbriato. Status teleomorphicus *Mycosphaerella*.

TYPE SPECIES: *Colletogloeopsis nubilosum* (Ganap. et Corbin) Crous et M.J. Wingf. comb.nov.

Mycelium internal and external, light to medium brown, septate, branched, smooth. Acervuli dark brown to black, subcuticular, erumpent. Conidiogenous cells arising from upper cells of the stroma, doliiform to subcylindrical or irregular, thick-walled, brown, verruculose, proliferating sympodially or several times enteroblastically and percurrently. Conidia single, aseptate, medium brown, verruculose, subcylindrical to ellipsoidal, straight to slightly curved, apex obtuse, base truncate with a marginal frill, occasionally with a lateral protuberance that can develop into a secondary conidium. Teleomorph *Mycosphaerella*.

Colletogloeopsis nubilosum (Ganap. et Corbin) Crous et M.J. Wingf. comb.nov. Fig. 1
= *Colletogloeum nubilosum* Ganap. & Corbin, Trans. Br. Mycol. Soc. 72: 237. 1979 (basionym)

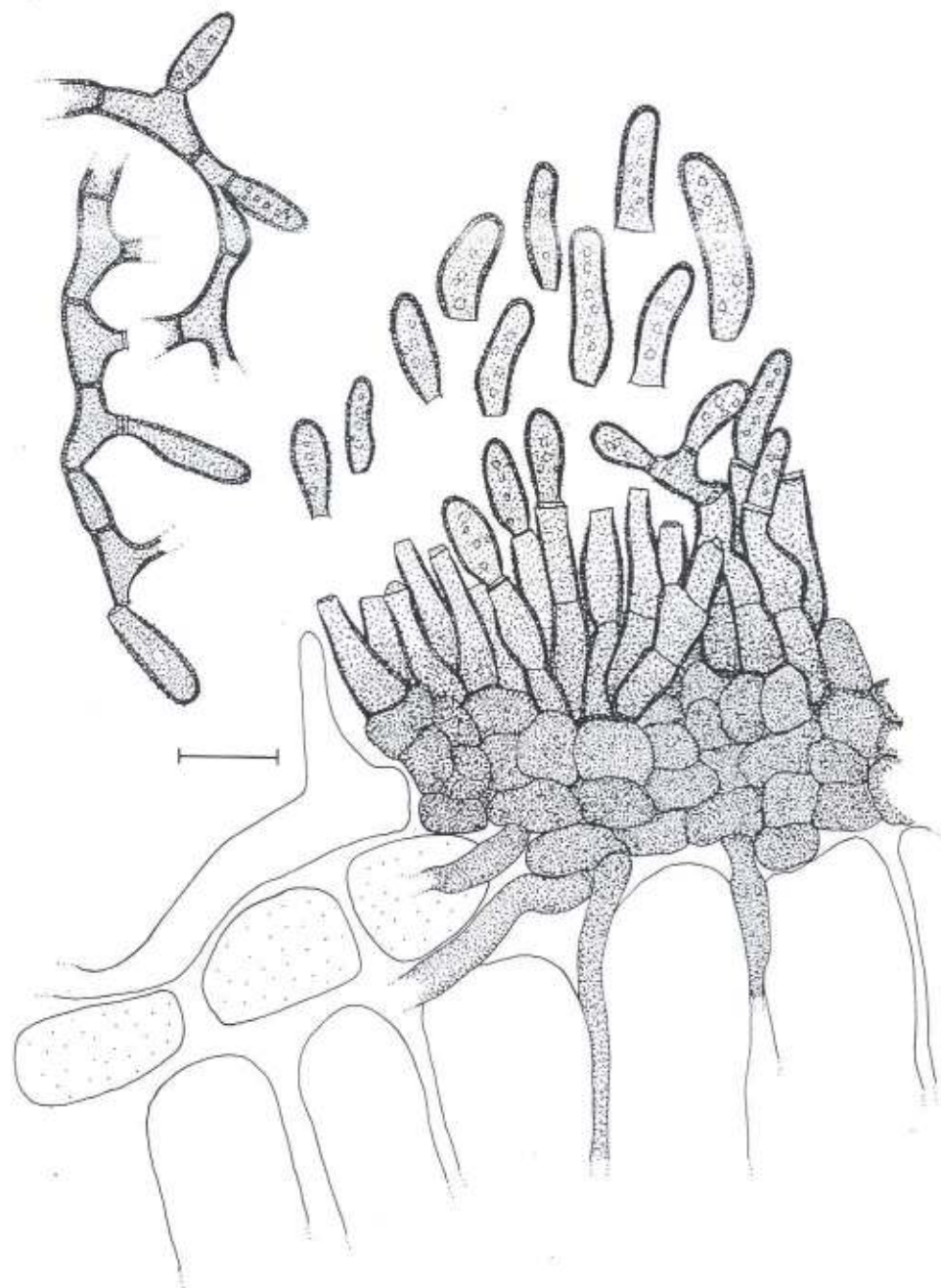
TELEOMORPH: *Mycosphaerella cryptica* (Cooke) Hansf., Proc. Linn. Soc. N.S.W. 81: 35, 1956

Mycelium internal and external, light to medium brown, septate, branched, smooth, hyphae 3–5 µm wide. Acervuli amphigenous, dark brown to black, subcuticular, erumpent, up to 150 µm wide and 100–200 µm high. Conidiogenous cells arising from upper cells of the stroma, doliiform to subcylindrical or irregular, 5–10 × 4–7 µm, thick-walled, brown, verruculose, proliferating sympodially or 1–4 times enteroblastically and percurrently. Conidia single, aseptate, medium brown, verruculose, subcylindrical to ellipsoidal, straight to slightly curved, apex obtuse, base truncate with a marginal frill, (8.5–)10–15(–18) × 4–5(–6) µm, occasionally with a lateral protuberance that can develop into a secondary conidium.

HOLOTYPE: NEW ZEALAND: Auckland, leaves of *Eucalyptus delegatensis*, A. Ganapathi, April 1977, PDD 37677.

HOSTS: *Eucalyptus agglomerata*, *E. baxteri*, *E. bicostata*, *E. blakelyi*, *E. bosistoana*, *E. botryoides*, *E. bridgesiana*, *E. brookeriana*, *E. camaldulensis*, *E. camphora*, *E. cladocalyx*, *E. consideniana*, *E. cytellocarpa*, *E. dalrympleana*, *E. delegatensis*, *E. dendromorpha*, *E. diversicolor*, *E. dives*,

Fig. 1. *Colletogloeopsis nubilosum*. Hyphae producing conidia, and a vertical section through an acervulus on *Eucalyptus delegatensis* (holotype, PDD 37677). Scale bar = 10 μ m.



E. dunnii, *E. elata*, *E. fastigata*, *E. fraxinoides*, *E. globoidea*, *E. globulus*, *E. gomphocephala*, *E. haemastoma*, *E. gonio-calyx*, *E. gunnii*, *E. macrorhyncha*, *E. marginata*, *E. melliodora*, *E. micrantha*, *E. microcorys*, *E. muellerana*, *E. nitens*, *E. nitida*, *E. obliqua*, *E. ovata*, *E. pauciflora*, *E. phaeotricha*, *E. polyanthemos*, *E. quadrangulata*, *E. radiata*, *E. regnans*, *E. saligna*, *E. sideroxylon*, *E. sieberi*, *E. smithii*, *E. tereticornis*, and *E. viminalis* (Crous et al. 1995a).

DISEASE: Leaf spot, cankers on shoots, twigs, and petioles; causing leaf drop and twig dieback.

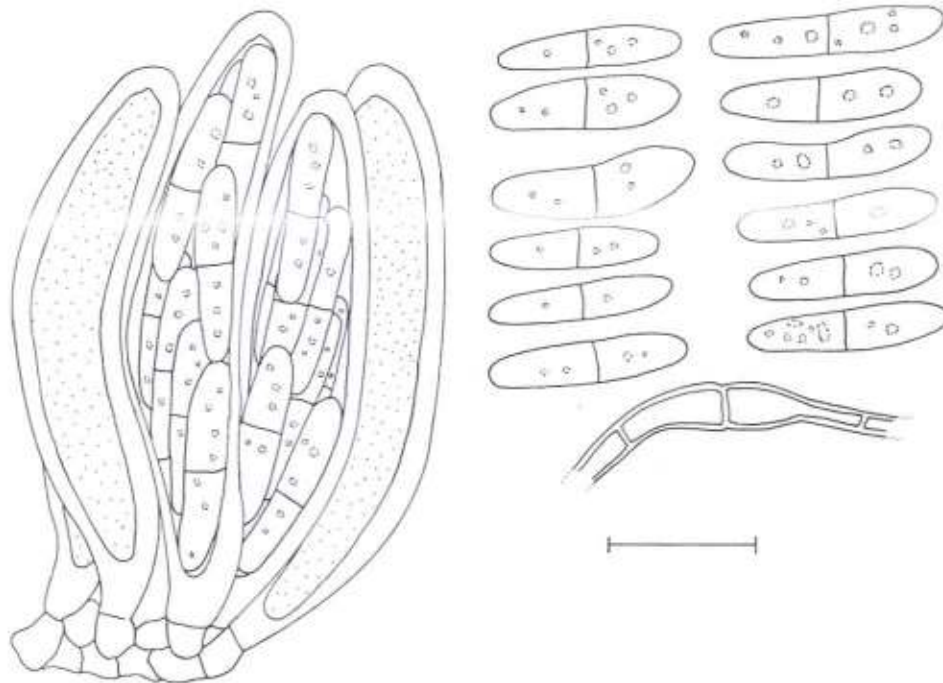
GEOGRAPHIC DISTRIBUTION: Australia, New Zealand, Chile (Crous et al. 1995a; Wingfield et al. 1995).

NOTES: *Mycosphaerella cryptica* was originally confused

with *M. nubilosa* (Ganapathi and Corbin 1979). However, these species can easily be distinguished based on their ascospore morphology (ascospores being constricted at their septa in *M. cryptica*, but not in *M. nubilosa*), mode of ascospore germination (germ tubes growing perpendicular to the long axis of the spore in *M. cryptica*, and parallel to the axis in *M. nubilosa*), leaf symptomatology, and cultural characteristics (Park and Keane 1982). Cultures of *M. cryptica* on MEA are dark green and grow slowly (5–10 mm in 2 months), whereas those of *M. nubilosa* are dark green to black, and have a faster linear growth (15–20 mm in 2 months) (Crous et al. 1995a, 1995b).

Mycosphaerella molleriana has also been confused with

Fig. 2. *Mycosphaerella molleriana*. Asci, ascospores, and germinating ascospore on *Eucalyptus globulus* (isotype, BPI 608879). Scale bar = 10 μm .



M. nubilosa, but as a result of the collection of new material and the establishment of cultures the two species can now be distinguished. To assist mycologists and forest pathologists in identifying this species, the following description is provided.

Mycosphaerella molleriana (Thüm.) Lindau in Engler & Prantl., *Natürlichen Pflanzenfamilie*, 1: 424. 1897

Figs. 2–4

Sphaerella molleriana Thüm., *Inst. Coimbra*, 28: 31. 1881

Mycosphaerella molleriana (Thüm.) Woronow, *Tr. Tiflissk. Bot. Sada*, Ser. 2, 3: 138. 1923

ANAMORPH: *Colletogloeopsis molleriana* Crous et M.J. Wingf. sp. nov. (Figs. 3, 4)

Mycelium internum et externum, pallide ad mediobrunneum, septatum, ramosum, laevigatum, 1.5–3.5 μm latum. Acervuli plerumque hypophyllosi, atrobrunnei ad atrii, subcuticulares, erumpentes, ad 150 μm lati. Conidiogenae cellulae doliiformes ad subcylindraceae vel irregulares, 4–20 \times 3.5–5 μm , parietibus tennibus, brunneae, verruculosae, proliferationibus sympodialibus vel compluriente enteroblasticis et percurrentibus. Conidia solitaria, aseptata, mediobrunnea, verruculosa, subcylindracea ad ellipsoidea, recta ad parum curvata, interdum protuberatione conidium secundarium producenti; apex obtusus, basis truncata, margine imbriato, (7–)9–12(–13) \times (2.5–)3–3.5(–4) μm . Status teleomorphyicus *Mycosphaerella molleriana*.

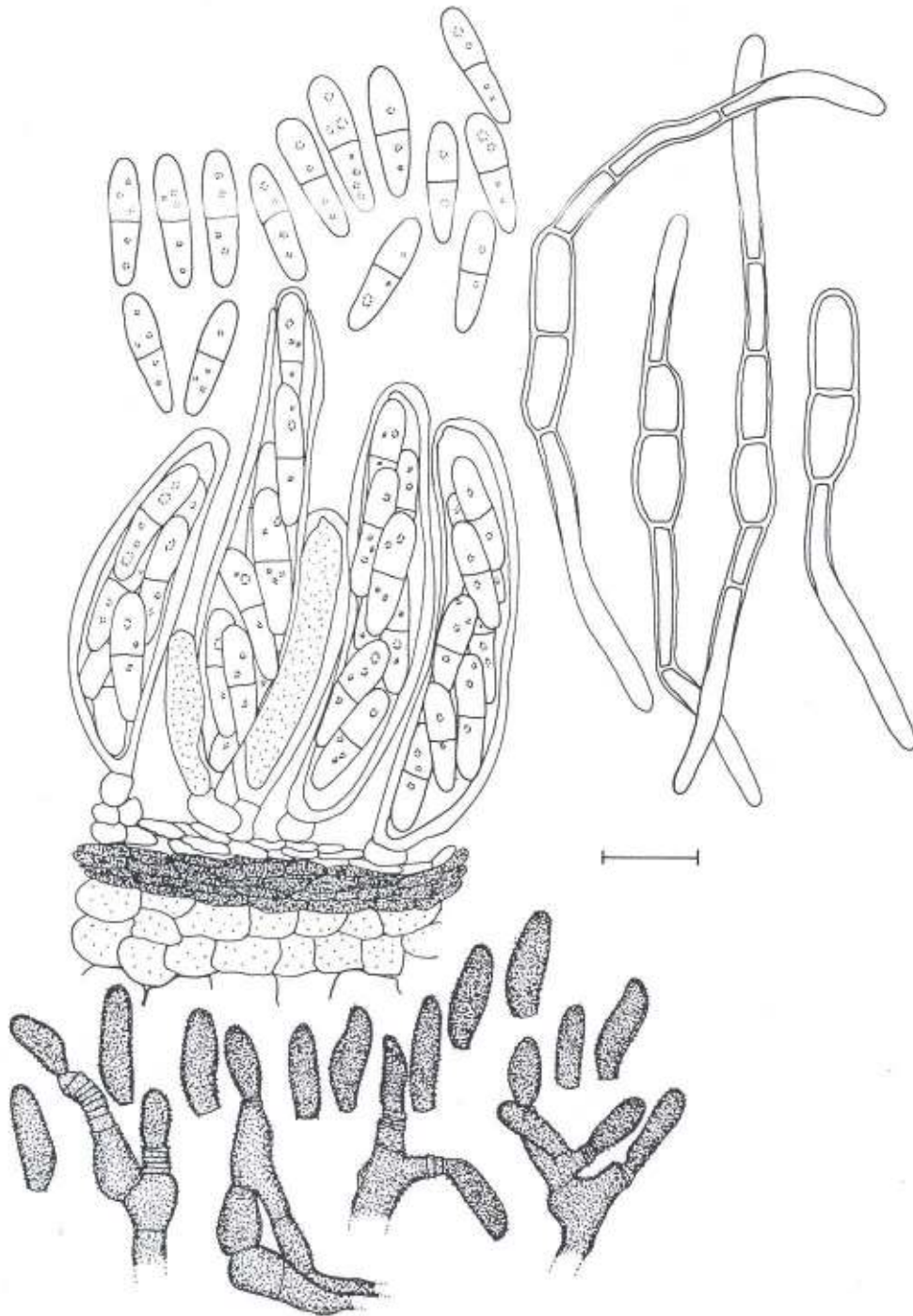
HOLOTYPE: PORTUGAL: Abrantes, leaves of *E. globulus*, July 1995, leg. S. McCrae (PREM 54395, cultures ex type STE-U 1214-1216).

Leaf spots amphigenous, subcircular to irregular, becoming confluent, 2–10 mm diameter, light brown, becoming

darker brown towards the raised, medium brown border on the upper surface, which is concolorous on the lower surface; margin absent. Pseudothecia predominantly hypophyllous, single or aggregated, 5–30 per colonized square millimetre, black, subepidermal, becoming erumpent, globose, 70–110 μm wide, 60–110 μm high; apical ostioles 10–15 μm diameter, becoming papillate; walls consisting of 2–3 layers of medium brown *textura angularis*, subhymenial layer basal, consisting of 1–2 layers of hyaline cells. Asci fasciculate, bitunicate, obovoid to narrowly ellipsoidal, straight or incurved, 8-spored, 30–45 \times 9–13 μm . Ascospores bi- to multi-seriate, overlapping, hyaline, guttulate, thin-walled, straight to curved, fusoid–ellipsoidal with obtuse ends, widest in middle of apical cells, medianly 1-septate, not or very slightly constricted at septum, tapering toward both ends, but with slightly more prominent taper towards lower end (11–)12–14(–17) \times (2.5–)3.5–4(–4.5) μm . Spermogonia not observed. Mycelium internal and external, light to medium brown, septate, branched, smooth, hyphae 1.5–3.5 μm wide. Acervuli predominantly hypophyllous, dark brown to black, subcuticular, erumpent, up to 150 μm wide. Conidiogenous cells arising from upper cells of the stroma, doliiform to subcylindrical or irregular, 4–20 \times 3.5–5 μm , thick-walled, brown, verruculose, proliferating sympodially or several times enteroblastically and percurrently. Conidia single, medium brown, verruculose, subcylindrical to ellipsoidal, straight to slightly curved, occasionally with a lateral protuberance that can develop into a secondary conidium; apex obtuse, base truncate with a marginal frill, (7–)9–12(–13) \times (2.5–)3–3.5(–4) μm ; conidia rarely becoming 1-septate in culture.

ASCOSPORE GERMINATION ON MEA: Germinating from one or both ends with germ tubes parallel to the long axis of

Fig. 3. *Mycosphaerella molleriana* and its anamorph *Colletogloeopsis molleriana* from California. Asci and ascospores on *Eucalyptus globulus*; germinating ascospores, conidia, and conidiogenous cells on MEA (PREM 54394). Scale bar = 10 μ m.



the spore, not darkening upon germination, becoming constricted at median septum of ascospore with slight distortion (Crous and Wingfield 1996), with ascospore cells becoming up to 5 μ m wide upon germination, and frequently developing a lateral branch from the original spore 24–48 h after germination.

CULTURES: Colonies 19–29 mm diameter on MEA after 1 month at 25°C in the dark, margin feathery, aerial mycelium absent to sparse, iron grey, 25^{mm}k (bottom), oli-

vaceous grey 23^{mm}i (top), colony sectored; anamorph forming in sectors with grey aerial mycelium after 2 weeks at 25°C on MEA.

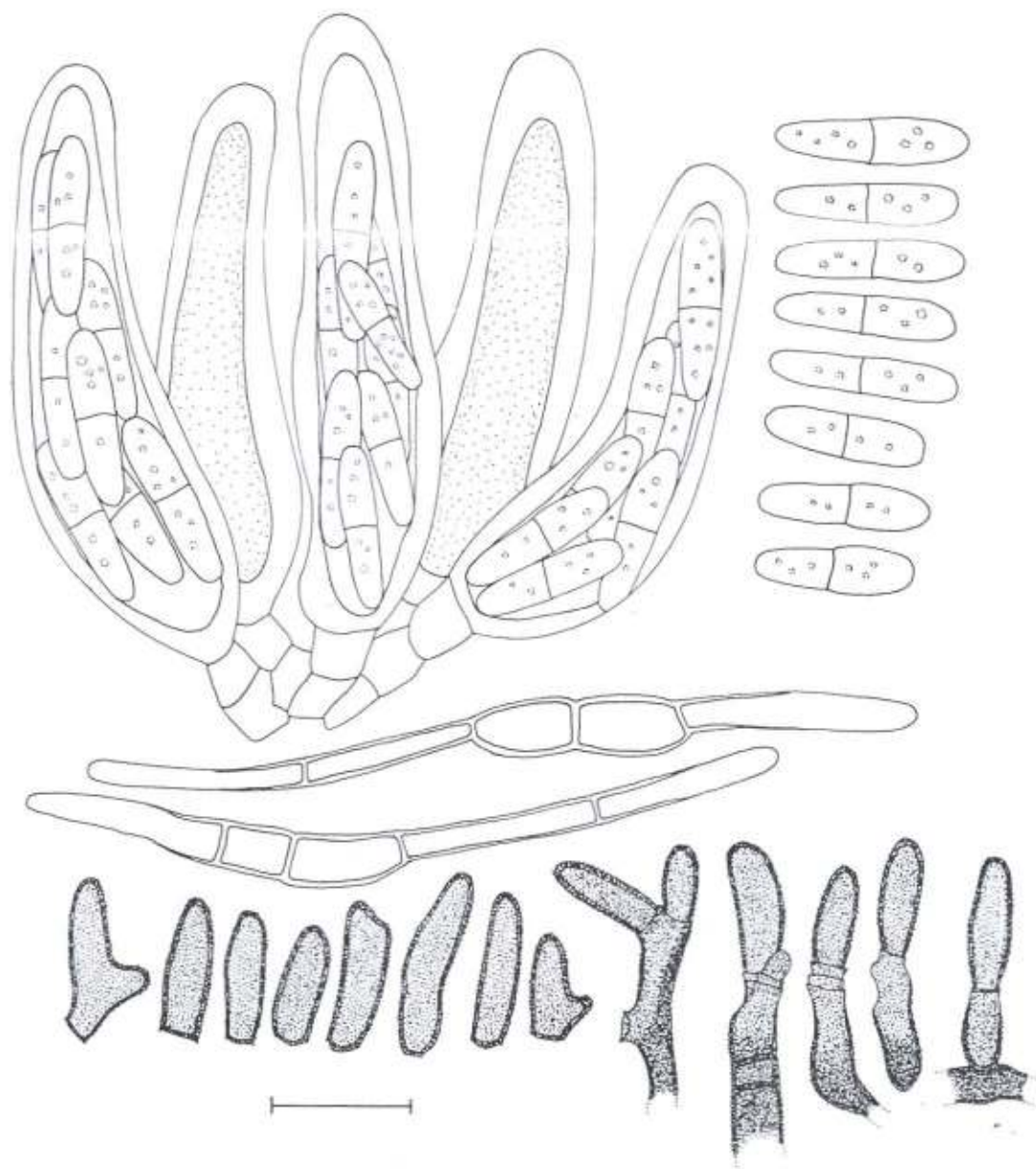
CARDINAL TEMPERATURE REQUIREMENTS FOR GROWTH: Above 5°C min., 20–25°C optimum, below 30°C max.

HOST: *Eucalyptus globulus*.

GEOGRAPHIC DISTRIBUTION: California, U.S.A.; Abrantes and Lusitania, Portugal.

SPECIMENS EXAMINED: PORTUGAL: Lusitania, leaves

Fig. 4. *Mycosphaerella molleriana* and its anamorph *Colletogloeopsis molleriana* from Abrantes, Portugal. Asci and ascospores on *Eucalyptus globulus* (PREM 54393); germinating ascospores, conidia, and conidiogenous cells on MEA (PREM 54395). Scale bar = 10 μm .

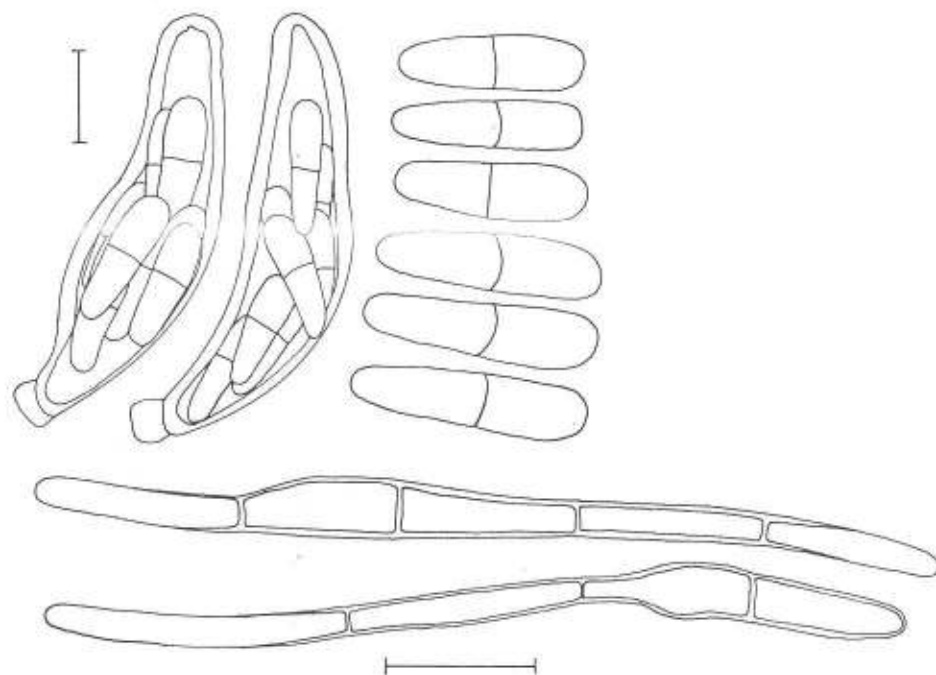


of *E. globulus*, July 1879, leg. Fr. Moller, K? (holotype of teleomorph), BPI 608879 (isotype); Abrantes, leaves of *E. globulus*, July 1995, leg. S. McCrae (holotype of anamorph) (PREM 54393, cultures ex type STE-U 1214-1216). U.S.A.: California, leaves of *E. globulus*, June 1994, leg. M.J. Wingfield (PREM 54394, cultures STE-U 780-782, 784, 785).

NOTES: Although *M. molleriana* has been reported from numerous hosts in several countries (Crous et al. 1995b), we have been able to confirm its occurrence only from *E. globulus* in Portugal (from where it was originally described) and California. Although ascospores of the type and isotype collections lodged, respectively, at K and BPI are slightly larger ((10-12)-12-14(-17) \times (2.5-3)-3.5(-4.5) μm) than those

in the recent collections from Abrantes, Portugal ((8-12)-14(-15) \times 3-3.5(-4) μm), and California ((11-12)-13(-15) \times (2.5-3)-3.5 μm), the average range of all three collections is 12-14 \times 3-3.5 μm . Furthermore, all three collections are similar in leaf symptomatology, pseudothecial distribution, ascus shape and size, and ascospore shape and mode of germination. Although no cultures are available from the type collection, germinating ascospores were observed that had exuded from pseudothecia on leaves of the isotype. Those ascospores had germinated from both ends, with germ tubes parallel to the long axis of the spore, a slight distortion of the original spore body, and a constriction at the median septum, typical of our collections from Portugal and California. This information is a result of

Fig. 5. *Mycosphaerella nubilosa*. Asci and ascospores on *Eucalyptus globulus* from Australia; germinating ascospores on MEA. Scale bar = 10 μm .



extensive collections within Portugal, California, and South Africa, from where *M. molleriana* had earlier been reported (Crous et al. 1991, 1995b; Carnegie and Keane 1994).

Based on leaf symptomatology, ascus, and ascospore shape, Crous et al. (1991) placed *M. nubilosa* in synonymy with the earlier described name, *M. molleriana*. Subsequent collections of *M. nubilosa* from Australia and *M. molleriana* from Portugal have shown that, although these two species induce similar host symptoms on juvenile leaves and share a similar ascus and ascospore morphology, as well as mode of ascospore germination, they are distinct taxa. Cultures of *M. molleriana* are relatively fast growing and are 19–29 mm diameter after 1 month, whereas those of *M. nubilosa* are only 15–20 mm diameter after 2 months. Furthermore, *M. molleriana* readily produces a *Colletogloeopsis* anamorph in culture which is absent in cultures of *M. nubilosa*. Finally, there is also a slight difference in the ascospore shape between *M. nubilosa*, in which they are obovoid and widest near the apex (Fig. 5), and *M. molleriana*, in which ascospores are fusoid–ellipsoidal and widest in the middle of the apical cell (Figs. 2–4). Considering current species concepts within *Mycosphaerella* spp. occurring on *Eucalyptus* and results of this study, our original interpretation of *M. molleriana* and *M. nubilosa* was incorrect (Crous et al. 1991, 1995b). With the recent description of yet more species in this complex (Carnegie and Keane 1994), detailed studies of Australian material will be required to further resolve the species boundaries of *M. nubilosa*.

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