

Contribution to the taxonomy and pathogenicity of fungicolous *Verticillium* species. I. Taxonomy

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Abstract

The genus *Verticillium* is divided into four sections (two new) and a residual group. The new section *Nigrescentia* comprises the well-known plant-pathogenic and some other saprophytic species with dark resting structures. The new section *Albo-erecta* is characterized by white (or yellowish) colonies and erect conidiophores and contains mainly fungicolous species. Seven (two new) species and two new varieties are described and keyed out. Three other species have known teleomorphs of *Nectriopsis* (one new and two new combinations). This genus had been merged with *Nectria* by Samuels, but its retention is justified, as the original and the here described fungicolous (and myxomyceticolous) species are more suitably accommodated in *Nectriopsis* than in *Hypomyces*.

The common causal agent of dry bubble in *Agaricus bisporus*, *Verticillium fungicola* var. *fungicola*, is redescribed and defined more narrowly than by Gams (1971) by its maximum growth temperature below 27 °C. A similar fungus with a maximum growth temperature near 33 °C, causing brown spots in *A. bitorquis*, is described as *V. fungicola* var. *aleophilum*. Isolates from wild agarics with a strongly reduced growth at 24 °C and a maximum below 27 °C, a yellowish mycelium and inconspicuous sclerotia, are described as *V. fungicola* var. *flavidum*. *V. biguttatum* W. Gams, sp. nov., with cylindrical biguttulate conidia, is a common soil fungus and hyperparasite of *Rhizoctonia solani*. *Gliocladium microspermum* (Sacc.) W. Gams, comb. nov., the anamorph of *Nectriopsis broomeana* (Tul.) W. Gams, comb. nov., which is intermediate between *Gliocladium* and *Verticillium*, is included because of its fungicolous habit.

Additional keywords: mycoparasites, hyperparasites, *Verticillium fungicola*, *Verticillium biguttatum*, *Nectriopsis (Hypomyces) tremellicola*, *Nectriopsis (Hypomyces) broomeana*, *Nectriopsis tubariicola*, *Gliocladium microspermum*, *Agaricus*, *Rhizoctonia solani*, mushroom diseases, dry bubble.

Introduction

Since the introduction of *Agaricus bitorquis* as a commercially grown mushroom, cultivated at higher temperatures than *A. bisporus*, the range of pathogens and competitors has changed (Van Zaayen and Van der Pol-Luiten, 1977; Upstone and Carter, 1979). *Verticillium fungicola* (Preuss) Hassebr. (syn. *V. malthousei* Ware), the causal agent of dry bubble, is a major pathogen of *A. bisporus*, but of minor importance in *A. bitorquis* (Poppe, 1972), probably because of its temperature relation-

ships (Dieleman-van Zaayen, 1975). Another *Verticillium* causing a brown spot disease on *A. bitorquis* has recently appeared (Van Zaayen, 1981 a, b). A comparison of this fungus with *V. fungicola* and some other fungicolous *Verticillium* species with regard to morphology and temperature relationships is the scope of the present study.

A taxonomic revision of the genus *Verticillium* Nees : Fr.* is overdue but will present a task requiring a period of some years. The group of species with darkening resting structures is relatively well-known and species are clearly delimited (Isaac, 1967; Domsch et al., 1980). Gams (1971) singled out a rather homogeneous group of species with procumbent or prostrate conidiophores as Section *Prostrata* W. Gams. These species probably all represent anamorphs of Clavicipitaceae, while the remaining species are at least partly connected with Hypocreaceae.

This does not imply that all the remaining species should be comprised in one section, *Verticillium*. For reasons which will be explained in this and subsequent publications, we here propose a further subdivision of the genus into four sections and a residual group according to the following key. The most important species of the new Section *Albo-erecta* and an additional *Gliocladium*-like anamorph, all fungicolous, will then be described in detail.

The following descriptions are based on streak-inoculated cultures grown in Petri dishes on 2% malt extract agar (MEA) at about 20 °C. Microscopic preparations were mounted in lactic acid containing 'Waterman' black ink or aniline blue.

Key to the sections of *Verticillium*

1. Conidiophores and conidia intensely orange-brown; conidiophores always erect
 1. Section *Verticillium*
Conidiophores and conidia hyaline, yellow or pale pink; darkening hyphae, conidiophores, chlamydospores or microsclerotia sometimes present; conidiophores erect or prostrate 2
2. Darkening hyphae, conidiophores, chlamydospores or microsclerotia present; conidiophores erect
 2. Section *Nigrescentia*
Darkening structures absent; conidiophores erect or prostrate 3
3. Conidiophores at least partly prostrate, i.e. phialides arising singly or in small groups from arched, undifferentiated hyphae; colonies white or yellow, sometimes with red discoloration of the agar
 3. Section *Prostrata*
Conidiophores typically erect, not prostrate (or only at a late stage) 4
4. Colonies pure white or yellow (exceptionally livid-vinaceous), never pink, rather fast-growing, reaching between 1.8 and 3.5 cm diam at 20 °C in 10 days
 4. Section *Albo-erecta*

* Author's citations changed according to the new Art. 13 of the International Code of Botanical Nomenclature (see Greuter, 1981).

Colonies with pink or orange hues and/or very slowly or faster growing

5. Residual group

1. Section **Verticillium**: Only species *V. tenerum* (Nees : Fr.) Link* (synonymy in Domsch et al., 1980, and Subramanian, 1971; teleomorph *Nectria inventa* Pethybr.). This fungus is very distinct by its pigmentation, though it is rather variable in its growth habit; this fact accounts for a large number of synonyms.

2. Section **Nigrescentia** W. Gams, *sect. nov.*

Conidiophora erecta sed saepe *Acremonii* modo simplicia. Structurae fuscae praesentes velut hyphae plus minusve inflatae vel conidiophora vel chlamydosporae vel microsclerotia. Species typica *Verticillium nigrescens* Pethybr.

Conidiophores erect, with few branches and phialides in whorls, often almost unbranched or solitary phialides like in *Acremonium*. Dark resting structures present, either dark, more or less inflated hyphae and dark conidiophores or chlamydospores or microsclerotia. Type species *V. nigrescens* Pethybr., other species: *V. albo-atrum* Reinke & Berth., *V. dahliae* Kleb., *V. nubilum* Pethybr., *V. tricorpus* Isaac and *V. theobromae* (Turconi) Mason & Hughes.

3. Section **Prostrata** W. Gams 1971. Mycelium consisting of thin-walled hyphae, white or yellowish, forming a cottony cushion. Erect conidiophores, if present, thin-walled and hardly differentiated from vegetative hyphae. Phialides verticillate or solitary, aculeate, mostly arising from prostrate hyphae of the aerial mycelium. In contrast with those of *Acremonium*, phialides arising from single, not conglutinated aerial hyphae (fasciculate hyphae occurring rarely), at the base usually narrower than the subtending hyphae and very thin-walled. Conidia adhering in slimy heads, often few elongate conidia attached transversely to the phialide tips, or sometimes in dry chains. Hyaline dictyochlamydospores (*Diheterospora* type) occurring in some species. Type species: anamorph of *Cordyceps militaris* (L.) Link.

Eighteen species (aggregates), including the commonest *V. lecanii* (Zimm.) Viègas and *V. psalliotae* Treschow, were treated by Gams (1971). Some more species have been described from nematodes and rotifers, partly in the genus *Diheterospora* Kamyschko ex Barron & Onions (Barron, 1980).

4. Section **Albo-erecta** W. Gams, *sect. nov.*

Conidiophora erecta, distincta, compluries verticillata. Structurae fuscae absentes. Coloniae albae vel flavae, nec roseae, fere celeriter crescentes, magis quam 1.8 cm et minus quam 3.5 cm diam. post 10 dies 20 °C. Chlamydosporae vulgo absentes. Species typica *Verticillium fungicola* (Preuss) Hassebr.

Conidiophores erect, differentiated from the vegetative hyphae in wall thickness, repeatedly verticillate. Dark resting structures absent. Colonies densely floccose to cottony, at least in the centre, white to yellowish, never pink or orange, rather fast-growing, reaching between 1.8 and 3.5 cm diam at 20 °C in 10 days. Colony reverse colourless (livid-vinaceous in *Nectriopsis tremellicola*). Conidia mostly forming globose slimy heads, sometimes fasciculate and somewhat transverse in young cultures. Chlamydospores generally absent.

5. The difficult **residual group** will be treated in a later study.

Temperature relationships

Streak-inoculated cultures on 2% MEA were incubated at the temperatures indicated in Fig. 1, ± 0.5 °C, in darkness. Colony diameters were determined after several lengths of time. A measurement of the diameter after 4 days proved to give the significant information and the average values calculated for several isolates of each taxon are presented in Fig. 1. All isolates of the six taxa, which are listed in the text, followed the same pattern with very little variation.

The thermal death points were determined after Van Zaayen and Rutjens (1981) as the minimal lethal temperature applied to an aqueous conidial suspension for 30 min.

Fig. 1. Colony diameters of three species and three varieties of *Verticillium* after 4 days growth on MEA.

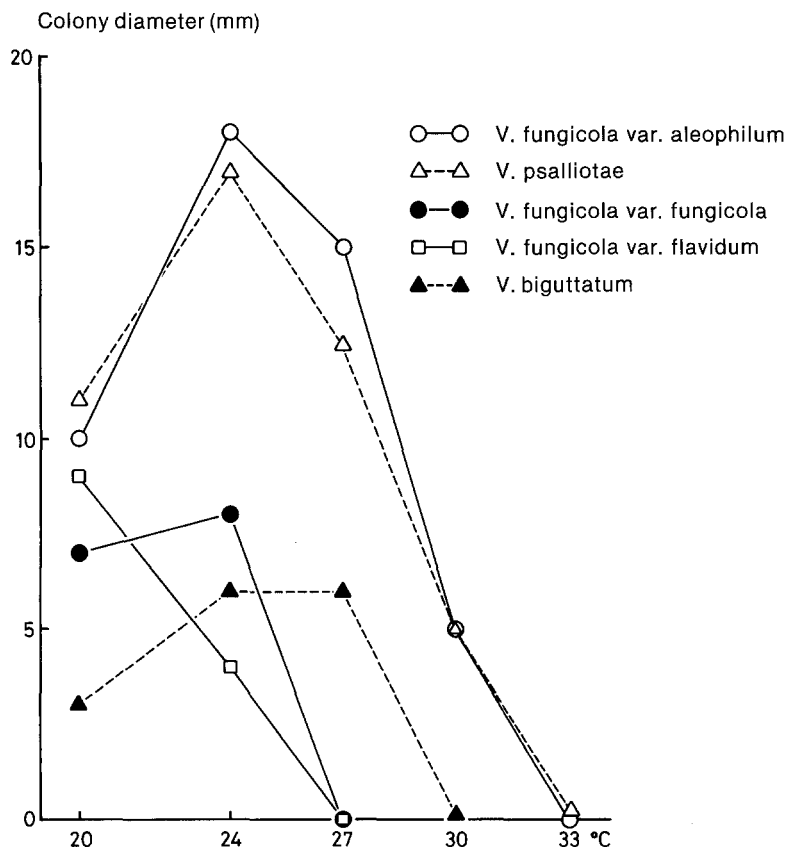


Fig. 1. Kolonie diameters van drie soorten en drie variëteiten van *Verticillium* na 4 dagen op mout agar.

Descriptions of the species

1. *Verticillium fungicola* (Preuss) Hassebrauk var. *fungicola* – Phytopath. Z. 9: 514. 1936 (autonym of the variety automatically established here) – Fig. 2.

- ≡ *Acrostalagmus fungicola* Preuss, Linnaea 24: 126. 1851.
- = *Cephalosporium costantinii* F. E. V. Smith, Trans. Br. mycol. Soc. 10: 90. 1924.
- = *Verticillium malthousei* Ware, Ann. Bot. 47: 781. 1933.

Description (translated from Gams, 1971, and supplemented): Colonies on MEA reaching (1.8–)2.3–2.8 cm diam in 10 days at about 20 °C, white to pale cream-coloured, dusty to velvety, partly (especially in degenerating cultures) cottony. Reverse uncoloured or pale yellowish. Octahedral crystals often abundantly produced in the substrate. Odour indistinct. Vegetative hyphae 0.7–2.5 µm wide. Sporulation very abundant, conidiophores arising typically from submerged hyphae. Conidial heads of single phialides often coalescing to form large slimy masses. Conidiophores erect, 3.5–4 µm wide at the base, thick-walled, with 2–5 (– over 10 in old colonies) whorls of 3–7 phialides, later also procumbent. Phialides forming an oblique angle with the conidiophore stipe, 14–20 (– 35) µm long, from 2.0–2.5 µm gradually tapering to 0.5–1.0 µm at the tips. Conidia adhering in slimy, globose heads, long ellipsoidal to almost cylindrical, but often with conically tapering but ultimately rounded tips, the basal end indistinctly truncate; sometimes curved along the longitudinal axis, asymmetrically biconvex to concave-convex or slightly sickle-shaped, smooth-walled, 3.8–7.2 × 1.2–2.4 µm, length/width ratio 2.5–4.5, with 1–2 or more inconspicuous guttules. On mushrooms the ellipsoidal form may dominate, *in vitro* the fusiform shape is commonly present. Chlamydospores absent. Teleomorph unknown.

Temperature optimum for growth 20–24 °C, no growth occurring at 27 °C (Fig. 1). Thermal death point of conidia 38–39 °C (Van Zaayen and Rutjens, 1981).

Some of the isolates mentioned by Gams (1971) under *V. fungicola* have to be reassigned as follows: CBS 504.48 is *V. psalliotae*. CBS 300.70A is *V. fungicola* var. *aleophilum*. CBS 300.70D is *V. fungicola* var. *flavidum*.

Additional isolates: CBS: 733.74, from *Agaricus bisporus*, Horst (L.), resistant to benomyl, comm. G.J. Bollen, 1974. – CBS 648.80, from dark spots on *Agaricus bisporus* (cv. Les Miz 60), Horst (L.), A. van Zaayen, 1980.

This is the well-known causal agent of the dry bubble disease (Dutch: droge molen) of the cultivated mushroom, *Agaricus bisporus*. After the study by Gams (1971) this species was also described by Gray and Morgan-Jones (1980). The illustrations given here for the other varieties could equally stand for var. *fungicola*, whilst Fig. 2 shows just the extremes of conidial shapes observed in material assigned to var. *fungicola*.

The use of temperature relationships as a criterion in species delimitation allows a much sharper differentiation than the morphological criteria used by Gams (1971) alone. It is now possible to predict the pathogenicity of new isolates of this complex from a simple temperature test.

Acrostalagmus fungicola was originally described by Preuss (l. c.) from unidentified agarics; identification at variety level is not possible from the herbarium material. For convenience the mushroom pathogen is assigned here to the type variety.

Fig. 2. *Verticillium fungicola* var. *fungicola*. a. CBS 648.80, b. conidia of type material in Herb. Preuss (B), c. CBS 440.34 (type isolate of *V. malthousei*).

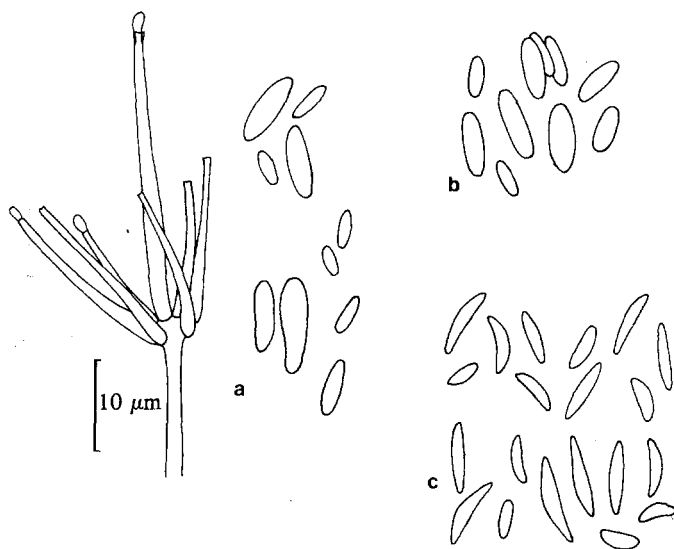


Fig. 2. *Verticillium fungicola* var. *fungicola*. a. CBS 648.80, b. conidiën van type materiaal in Herb. Preuss (B), c. CBS 440.34 (type cultuur van *V. malthousei*).

V. fungicola var. *fungicola* is normally very sensitive to benomyl with an ED_{50} of about $1\mu\text{g ml}^{-1}$ (Holmes et al., 1971), but completely resistant strains appeared in 1974 which are still equally vital and pathogenic (e.g. CBS 733.74) (Bollen and Van Zaayen, 1975).

2. *Verticillium fungicola* var. *aleophilum* W. Gams & Van Zaayen, var. nov. — Fig. 3.

A varietate *fungicola* differt conidiis semper rectis, $4.5-8.0 \times 1.5-2.5\mu\text{m}$, et temperatura maxima crescentiae circa 30°C . Typus CBS 357.80, isolatus ex *Agarico bitorqui* in quo maculas brunneas format, Helden in Neerlandia, 1979. Etym.: Greek *alea* = warmth.

Colonies on MEA reaching 2.5–3.0 cm diam in 10 days at about 20°C , white, thinly floccose to slightly cottony; reverse uncoloured. Odour indistinct. Octahedral (sometimes also prismatic) crystals abundant. Vegetative hyphae 1–3 μm wide, sometimes swollen to 3–4.5 μm wide. Sporulation abundant, conidiophores generally arising from submerged hyphae; conidiophores erect, up to over 400 μm tall, about 2.5(–3.5) μm wide at the base, thick-walled, bearing many whorls of 3–10 phialides. Phialides 15–30 μm long, from 1.5–2.2 μm gradually tapering to 0.8–1.2 μm . Conidia forming globose heads, long ellipsoidal to almost cylindrical but often with conically tapering but ultimately rounded tips, equal at both ends, usually straight, smooth-walled, of very irregular size, $4.5-8.0 \times 1.5-2.5\mu\text{m}$, length/width ratio 2.7–4.5, with two or more inconspicuous guttules. On mushrooms the conidia are of similar, generally straight, shape and size. Chlamydo-spores absent. Teleomorph unknown.

Fig. 3. *Verticillium fungicola* var. *aleophilum*. a. CBS 357.80, b. CBS 519.81.

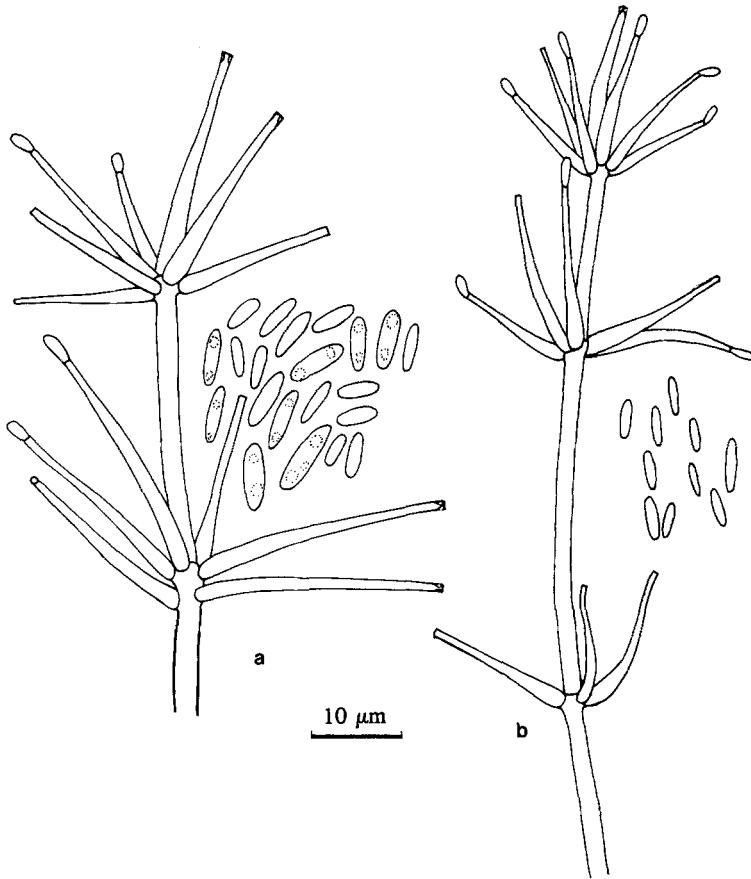


Fig. 3. *Verticillium fungicola* var. *aleophilum*. a. CBS 357.80, b. CBS 519.81.

Temperature optimum 24–27 °C, no growth occurring at 33 °C (Fig. 1). Thermal death point of conidia 42 °C.

Material examined: CBS 357.80, type isolate, and CBS 507.81A, mushroom farm in Helden-Panningen (L.), Nov. 1979 and July 1981. – CBS 507.81B and C, mushroom farms in Kessel and Horst (L.), 1981 (all from brown spots on *Agaricus bitorquis*). – CBS 519.81, from brown spots in *Agaricus bisporus*, cv. Les Miz 60, mushroom farm in Mühlendorf near Geilenkirchen, F.R.G., July 1981. – CBS 300.70A, isolated from soil in rain forest near Brisbane, Australia, J.H. Warcup; this isolate also caused brown spots in *A. bitorquis* after artificial inoculation; it was segregated into a yellow and a white strain (CBS 270.79A and B) by T. Yokoyama (pers. comm., 1979).

Like in var. *fungicola*, the conidia are very variable in size and shape. The only consistent difference between the varieties is the temperature maximum. We therefore refrain from describing the brown-spot pathogen as a new species.

This fungus shows an unusual reaction to benomyl: Whilst the ED_{50} is less than $1 \mu\text{g ml}^{-1}$, all higher concentrations of the fungicide applied ($1, 10, 100 \mu\text{g ml}^{-1}$) reduced growth to the same amount (8 vs. 55 mm diam in 9 days at 22°C). This fact may explain why this pathogen cannot be controlled with benzimidazole fungicides. Its pathogenicity will be reported in a subsequent paper (Van Zaayen and Gams, 1982).

3. *Verticillium fungicola* var. *flavidum* W. Gams & Van Zaayen, var. nov. — Fig. 4.

Coloniae albae ad dilute sulfureae, floccosae. Odor vulgo fortis pungens. Conidiophora erecta, multos verticillos phialidum ferentia. Phialides $16-30 \mu\text{m}$ longae, e $1.7-2.5 \mu\text{m}$ ad $0.7-1.2 \mu\text{m}$ paulatim angustatae. Conidia oblonga ad fere cylindrica, saepe utrinque angustata et paulo rotundata, recta vel nonnumquam curvata, levia, magnitudine irregularia, $4-10 \times 1.2-2.5 \mu\text{m}$, $2.5-4 \times$ longiora quam lata. Chlamydosporae absentes. Sclerotia $300-600$

Fig. 4. *Verticillium fungicola* var. *flavidum*. a. CBS 290.80, b. CBS 342.80.

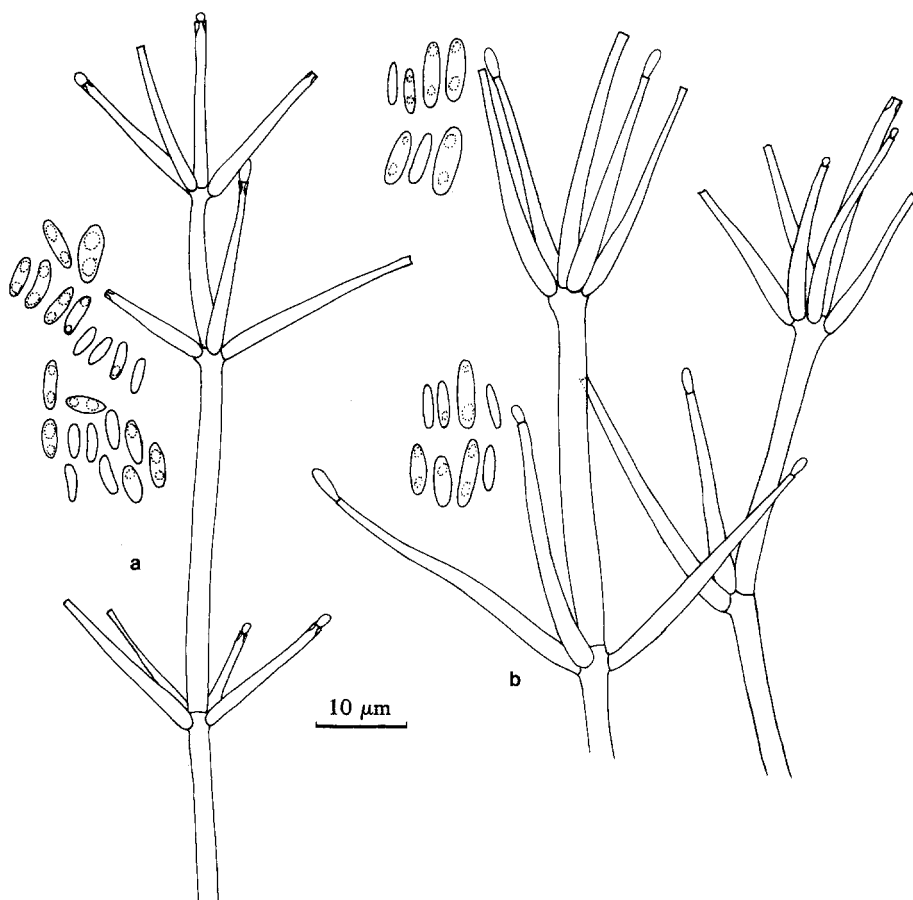


Fig. 4. *Verticillium fungicola* var. *flavidum*. a. CBS 290.80, b. CBS 342.80.

μm diam., hyphis irregulariter intertextis obiecta, pallide ochracea in coloniis vetustis inveniuntur. Teleomorphosis ignota. Typus CBS 342.80, isolatus ex acubus putrescentibus *Abietis albae* in Gallia, a F. Gourbière (No. A 111), 1979.

Colonies on MEA reaching 2–3 cm diam in 10 days at about 20 °C, white to pale sulphur yellow, thinly floccose to rather deeply cottony, particularly in the centre and near the margin. Reverse colourless. Odour in most transfers pungent (especially when freshly isolated), resembling burnt celluloid. Prismatic and octahedral crystals rare. Vegetative hyphae 0.7–3.5 μm wide. Sporulation abundant, with conidiophores usually arising from submerged hyphae; conidiophores erect, 300–over 500 μm tall, to 4 μm wide at the base, bearing several to many whorls of 2–8 phialides. Phialides 16–30 μm long, from 1.7–2.5 μm gradually tapering to 0.7–1.2 μm . Conidia adhering sometimes transversely in parallel bundles or mostly in globose heads, long ellipsoidal to almost cylindrical, but often with conically tapering ultimately rounded tips, with equal ends, straight or slightly curved, smooth-walled, of very irregular shape and size, 4–10 \times 1.2–2.5 μm , length/width ratio 2.5–4, moderately chromophilic, with two or more inconspicuous guttules. Chlamydospores absent. Sclerotia found in old cultures, subglobose, whitish to pale ochraceous, 300–600 μm diam, covered with irregularly radiating hyphae. Teleomorph unknown.

Temperature optimum at or below 20 °C, no growth occurring at 27 °C (Fig. 1).

Material examined: CBS 342.80, type, from decaying needles of *Abies alba*, France, F. Gourbière (no. A 111), 1979. – CBS 290.80, from decaying fruit-body of *Russula nigricans*, Moss near Gerolstein, Eifel, F.R.G., W. Gams, 1979. – CBS 300.70D, from *Coltricia perennis*, near Sistranser Alm, Tyrol, Austria, W. Gams, Oct. 1965. – CBS 879.73, from decaying agaric, 'De Utrecht' estate, Esbeek, N-Brabant, H.A. van der Aa, Aug. 1973. – CBS 238.80, from forest litter, Adirondack Mts., N.Y., C.J.K. Wang (AP-2412), 1980. – CBS 530.71, from *Laccaria proxima*, near Malmédy, Belgium, W. Gams, Sept. 1981.

This variety mainly differs from var. *fungicola* in its lower temperature optimum, presence of sclerotia, yellowish colonies and pungent odour. As all these distinctive characters (apart from the temperature relationships) are variable (the variability increasing in the above order) and tend to disappear with prolonged subculturing, we refrain from describing this fungus as a new species. It is non-pathogenic to *Agaricus* species (Van Zaaen and Gams, 1982). It thus seems that isolates from wild agarics mainly represent the variety *flavidum*, while var. *fungicola* is hardly known from fungi other than the cultivated *A. bisporus*.

Mating experiments with these isolates and the other varieties of *V. fungicola* and incubation at various temperatures with and without near-UV light did not yield any perithecia.

This fungus showed the same high sensitivity to benomyl with an ED_{50} of less than 1 $\mu\text{g ml}^{-1}$ as *V. fungicola* var. *fungicola*. However, increasing concentrations of the fungicide showed a corresponding inhibition as in other sensitive fungi.

4. *Verticillium biguttatum* W. Gams, *spec. nov.* – Fig. 5.

Coloniae albae, tenuiter velutinae. Odor aromaticus. Conidiophora copiosa ex hyphis submersis oriunda, erecta, 150–280 μm alta, prope basim 3.5–4.5 μm lata, multos verticillos phialidum ferentia. Phialides 18–30 μm longae, e 2.0–2.5 μm paulatim ad 1.2–1.5 μm *Neth. J. Pl. Path.* 88 (1982)

Fig. 5. *Verticillium biguttatum*. a. CBS 228.80, b. CBS 288.79.

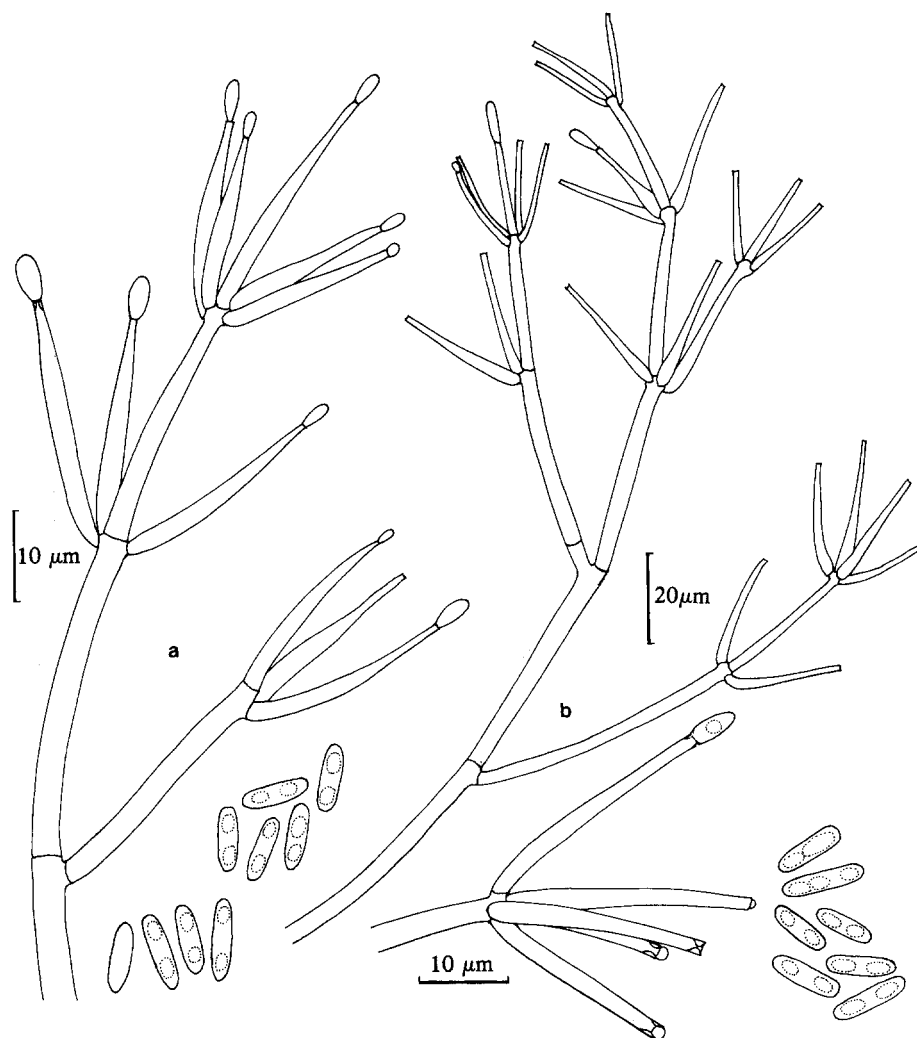


Fig. 5. *Verticillium biguttatum*. a. CBS. 228.80, b. CBS 288.79.

angustatae. Conidia cylindrica, magnitudine regularia, basi truncata, $5.5-9.5 \times 1.5-2.2$ µm, duabus guttulis repleta. Typus CBS 288.79, vivus et exsiccatus, isolatus e sclerotiis *Rhizoctoniae solani* in Neerlandia a G. Jager, 1979.

Colonies on MEA reaching 2.0–3.0 cm diam in 10 days at about 20 °C, white, very thinly velvety. Reverse colourless to cream-coloured. Odour aromatic at first, later resembling decaying agarics. Crystals absent. Vegetative hyphae 1.0–3.5 µm wide. Sporulation abundant; conidiophores arising from submerged hyphae, erect, 150–280 µm tall, 3.5–4.5 µm wide at the base, with 1–2(–4) septa and no branches in the lower part, above which several whorls of 3–5 phialides or branches which in

turn may bear whorls of phialides; conidiophores appearing roughened when observed directly, but smooth-walled when mounted in water or lactic acid. Phialides 18–30 μm long, from 2.0–2.5 μm gradually tapering to 1.2–1.5 μm . Conidia regularly cylindrical with slightly tapering and truncate base, straight, smooth-walled, with little variation in size and shape, 5.5–9.5 \times 1.5–2.2 μm , length/width ratio 2.7–4.5, strongly chromophilic, showing two conspicuous guttules. Chlamydo-spores absent. Teleomorph unknown.

Temperature optimum 24–27 °C, maximum 30 °C (Fig. 1).

Material examined: CBS 847.70 and 848.70, from agricultural soils, Wageningen, J.W. Veenbaas-Rijks, 1970. – CBS 288.79 (type culture), 353.77 A-C, 360.77, 228.80 (= M73), from sclerotia of *Rhizoctonia solani* on potato, Haren (Gr.), comm. G. Jager, 1977–1980.

This species is distinct by its regularly cylindrical conidia; the two guttules are conspicuous because of the chromophilic behaviour of the plasm.

This species is an efficient hyperparasite of *Rhizoctonia solani* and, together with *Gliocladium* species, may be an important biological control agent of the black scurf disease of potato (Jager et al., 1979).

5. *Nectriopsis tubariicola* W. Gams, *spec. nov.* – Fig. 6.

Anamorph *Verticillium* sp.

Perithecia fere tota in mycelio albo immersa, albida, sicca ochracea, lageniformia, e basi paulatim in papillam transeuntia, 270–300 \times 140–225 μm , pariete levi, transparente, circa 20 μm crasso. Asci cylindrici, in apice haud inspissati, 100–150 \times 4.5–6 μm . Ascosporae oblique uniseriatae, fusiformes, utrinque paulo rotundatae vel truncatae, hyalinae, verrucosae, apices versus rugosiores, 12–16 \times 3.0–4.0 μm ; partim singulae vi expulsaе, partim in massa mucida circum ostiolum aggregatae.

Coloniae albae, floccosae-coactae. Reversum hyalinum. Odor aromaticus. Crystalli absentes. Hyphae vegetativae 1.0–2.5(–3.5) μm latae. Conidiophora *Verticillii* copiosa, erecta ex hyphis aeriis oriunda, ad 220 μm vel ultra longa, ad 4 μm lata prope basim, 1–3 verticillos 3–4(–7) phialidum ferentia. Phialides 22–35(–45) μm longae, e 1.7–2.7 μm paulatim ad 0.8–1.3(–1.7) μm angustatae. Conidia in capitulis globosis aggregata, obovoidea, basi modice truncata, levia, magnitudine regularia, 6.0–9.0 \times 3.0–3.7 μm , modice chromophila, una vel duabus guttulis repleta. Chlamydosporae in coloniis vetustis parcae formatae.

Holotypus CBS 998, in *Tubaria* sp., Larser Bos, Oostelijk Flevoland Polder, W. Gams, 11 Nov. 1978.

Perithecia almost completely immersed in a white mycelial weft, whitish, ochraceous when dry, flask-shaped, the body gradually merging into the papilla, 270–300 \times 140–225 μm , wall smooth, transparent, about 20 μm thick. Asci cylindrical, without any apical wall thickening, 100–150 \times 4.5–6 μm . Ascospores obliquely uniseriate, fusiform with slightly rounded or truncate ends, hyaline, with fine, chromophilic warts which are larger at the ends, 12–16 \times 3.0–4.0 μm ; ascospores partly forcibly discharged singly, partly collecting in slimy masses around the ostiole.

Colonies on MEA reaching 1.6–3.0 cm diam in 10 days at about 20 °C, white, floccose-felty. Reverse colourless. Odour aromatic, sweetish. Crystals absent. Vegetative hyphae 1.0–2.5(–3.5) μm wide. Sporulation abundant; conidiophores usually arising from felty aerial hyphae, erect, up to over 220 μm tall to 4 μm wide at the base, bearing 1–3 whorls of 3–4(–7) phialides. Phialides 22–35(–45) μm long, from 1.7–2.7 μm gradually tapering to 0.8–1.3(–1.7) μm . Conidia forming glo-

Fig. 6. *Nectriopsis tubariicola*. a. asci and ascospores, b. two perithecia, c. detail of papilla, CBS 998. – d. conidiophore and conidia, CBS 116.79.

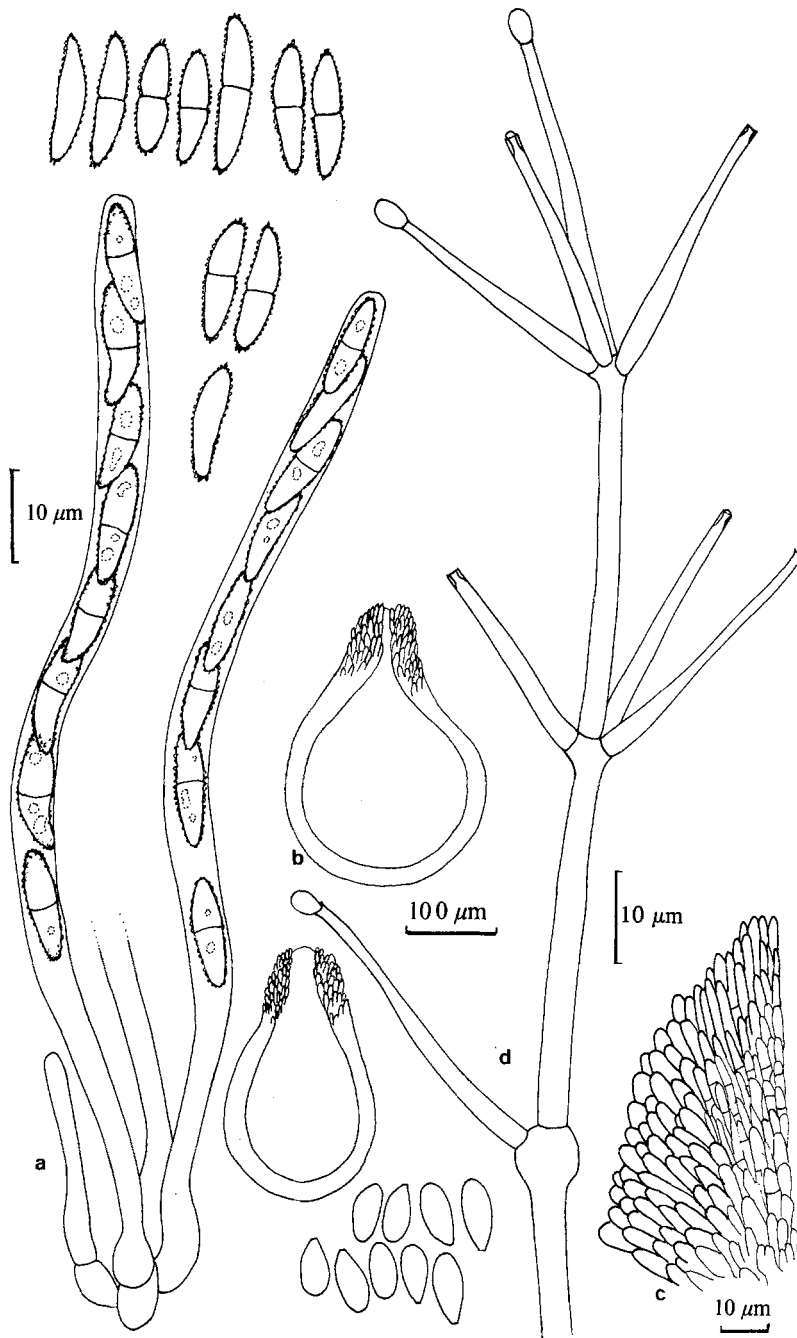


Fig. 6. *Nectriopsis tubariicola*. a. asci en ascosporen, b. twee peritheciën, c. detail van papil, CBS 998. – d. conidiofoor en conidiën, CBS 116.79.

bose heads, obovoid, with slightly truncate base, smooth-walled, of regular size, $6.0-9.0 \times 3.0-3.7 \mu\text{m}$, length/width ratio 2.0–2.8, moderately chromophilic, with 1 or 2 conspicuous guttules. Chlamydospores scanty in old cultures, single or in short chains, globose, hyaline, $7.5-12 \mu\text{m}$ diam. No perithecia were obtained in cultures of mass ascospore isolates.

Temperature optimum 20°C , no growth occurring at 27°C .

Material examined: CBS 386.73, conidial isolate, from *Tubaria furfuracea*, Baarn, H.A. van der Aa, 1973. — CBS 115.79, from CBS 998, and 116.79, from CBS 997, mass ascospore isolates, from *Tubaria* sp., Larser Bos, Oostelijk Flevoland Polder, W. Gams, 11 Nov. 1978. — CBS 524.81, conidial isolate, from *Tubaria furfuracea*, Maarssen, H.A. van der Aa, Oct. 1981.

To date this fungus is only known from *Tubaria* species in the Netherlands. It was at first identified as *Hypomyces tremellicola* (see below) according to the description by Samuels (1976), but differences were noticed in growth speed, colony pigmentation, conidial measurements and absence of the teleomorph *in vitro*.

We consider *Nectriopsis* the most appropriate genus for this fungus, as will be discussed under *N. tremellicola*. No epithet is assigned to the *Verticillium* anamorph until further revision.

6. *Nectriopsis tremellicola* (Ell. & Everh.) W. Gams, *comb. nov.* — Fig. 7.

≡ *Hypocrea tremellicola* Ell. & Everh., N.Am. Pyrenom. p. 85. 1892.

≡ *Hypocreopsis tremellicola* (Ell. & Everh.) Seaver, Mycologia 2: 83. 1910.

≡ *Hypomyces tremellicola* (Ell. & Everh.) Rogerson apud Samuels, Mem. N.Y. Gdn 26(3): 20. 1976.

Anamorph *Verticillium* sp.

Perithecia sitting almost superficially on or embedded to various extent in a white mycelial mat, broadly flask-shaped, $210-280(-350) \times 160-200(-275) \mu\text{m}$, with a sharply delimited slender papilla which is surrounded by a collar of hyaline ampulliform cells, pale reddish brown when dry, wall of textura epidermoidea, $10-15 \mu\text{m}$ thick, transparent. Asci densely filling the cavity, cylindrical, $85-100 \times 3.5-4.5 \mu\text{m}$, with a flattened and rounded apex often showing an indistinct thickened plate before spores are visible, but generally unthickened when mature. Ascospores strictly uniseriate in the ascus, often in end-to-end position, ellipsoidal to sole-shaped or somewhat clavate, 2-celled with broader and sometimes longer upper and narrower lower cell, hyaline, beset with fine to coarse chromophilic warts, $7.5-10(-12) \times 3-3.5(-4) \mu\text{m}$, at maturity collecting in slimy balls at the mouth of the perithecium.

Colonies on MEA reaching 3.6–5 cm diam in 10 days at about 20°C , thinly floccose and whitish above; reverse with pale or intense livid-vinaceous diffusing pigment. Odour slight and indistinct. Crystals absent. Vegetative hyphae $0.6-3(-4) \mu\text{m}$ wide. Sporulation abundant; conidiophores arising from submerged or aerial hyphae, ascendent, often only in the upper part erect, up to $800 \mu\text{m}$ long, $2.8-4.2(-5) \mu\text{m}$ wide and thin-walled at the base, with several septa and no branches in the lower part, above with 1–3 whorls of (1–)3–7 phialides or rarely an additional branch which in turn may bear 1–2 whorls of phialides; conidiophores appearing slightly roughened when observed directly in the Petri dish, but smooth-walled when mounted in water or lactic acid. Phialides $18-40 \mu\text{m}$ long, $1.7-2.2$

Fig. 7. *Nectriopsis tremellicola*. a, b. conidiophores, a. CBS 438.81, 6-day-old, b. CBS 440.81, 1-month-old, on oatmeal agar. — c. two perithecia, d. detail of papilla, e. asci and ascospores, C.T.R. 80-143, e' from holotype.

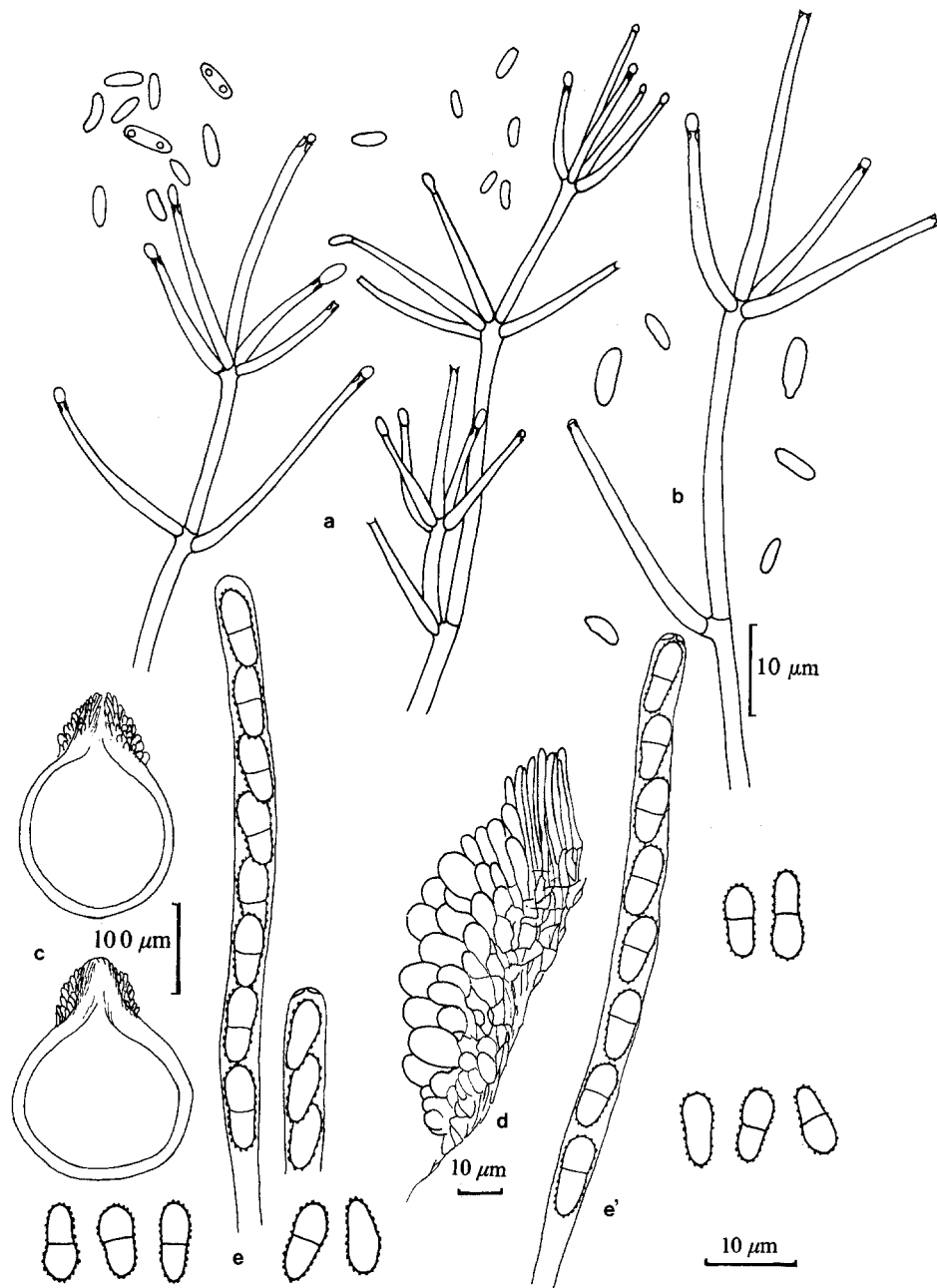


Fig. 7. *Nectriopsis tremellicola*. a, b. conidioforen, a. CBS 438.81, 6 dagen oud, b. CBS 440.81, 1 maand oud op haverhout agar. — c. twee peritheciën, d. detail van papil, e. asci en ascosporen; C.T.R. 80-143, e' van de type collectie.

μm wide at the base. Conidia forming globose heads, cylindrical to allantoid with slightly truncate base, smooth-walled, with rather little variation in size, $3.5-6(-10.5) \times 1.4-2.2 \mu\text{m}$, length/width ratio $2.7-3.2(-4.0)$, moderately chromophilic, non-guttulate or with 1-3 inconspicuous guttules, in older cultures more commonly ellipsoidal. Chlamydospores absent.

Perithecia were reported to be formed between compatible single-spore isolates (Samuels, 1976) but could not be obtained in the cultures examined under a range of conditions.

Temperature optimum 27°C , maximum 33°C .

Material examined:

a) Herbarium specimens: *Hypocrea tremellicola*, holotype, on *Tremella albida* (probably on a *Crepidotus* sp. fide C.T. Rogerson), Ohio, U.S.A., Morgan 894. — C.T.R. 69-107, on *Crepidotus* sp., vicinity of Lake Sherman, Warren Co., New York, S.J. Smith No. 44584, 14 Aug. 1969. — C.T.R. 78-153, on *Crepidotus* sp., Frost Valley, along West Branch of Neversink Creek, Catskill Mountains, Ulster Co., New York, C.T. Rogerson, 16 Sept. 1978. — C.T.R. 80-143, on *Crepidotus* sp., woods in Longwood Gardens, near Kennett Square, Chester Co., Pennsylvania, C.T. Rogerson, 19 Oct. 1980 (all in NY).

b) Living cultures: CBS 438.81 A-C, several single-spore isolates from C.T.R. 69-107 above. CBS 439.81, from C.T.R. 78-153. CBS 440.81, from C.T.R. 80-143.

Samuels (1973) argued in favour of the synonymy of *Nectriopsis* Maire with *Nectria*. In 1976 and 1979 (Samuels and Rossman) he described the *Nectria candicans* group and characterized it by "non-stromatic, globose, thin-walled, white to brownish perithecia, producing spinulose hyphae or hairs"; most of the former *Nectriopsis* species fit in this group. However, he placed this and two other species with rounded ascospore ends in *Hypomyces*, viz. *H. aureo-nitens* Tul. and *H. berkeleyanus* Plowr. & Cooke, apparently because the asci show a minute apical thickening and the beaked perithecia sit on or in a mycelial weft. Müller and Von Arx (1962, and subsequent publications) restricted *Hypomyces* to species with strictly fusiform and apiculate ascospores and asci with a pronounced cap-like apical thickening perforated by a canal, thus teleomorphs of *Cladobotryum*, *Pseudohansfordia*, *Sibirina*, *Sepedonium* and *Mycogone*.

Perithecia sitting on or in a mycelial weft on basidiomycete fruit-bodies or myxomycetes with pale, transparent walls composed of flattened thin-walled cells characterize *Nectriopsis*; in addition the species treated here show an outer wall differentiation in the papillar region. The hairs seem to have secondary importance. The generic distinction of *Nectriopsis* from *Hypomyces* is correlated with the occurrence of *Acremonium*, *Verticillium* and *Gliocladium* anamorphs which are absent in *Hypomyces* sensu stricto. Admittedly the delimitation of *Nectriopsis* from *Nectria* may cause problems, but it seems preferable to retain this genus rather than to either extend the scope of *Nectria* still further, so that it becomes a collection of very discordant elements, or to describe a new genus for the species with beaked perithecia.

Samuels (1976) listed many more collections of *H. tremellicola* (but only from America) and gave generally wider ranges for all microscopic measurements. He included more collections from other substrates of which two were found to deviate, after examination of dried specimens and living cultures (C.T.R. 76-34 and C.T.R. 71-214). It is thus likely that collections listed from other hosts than *Crepidotus* do not belong to *N. tremellicola*.

Fig. 8. *Nectriopsis broomeana*. a, b. conidiophores and conidia of CBS 247.70 and CBS 278.80A, respectively. – c-e. perithecia, ascogonia, ascospores of CBS 416.80.

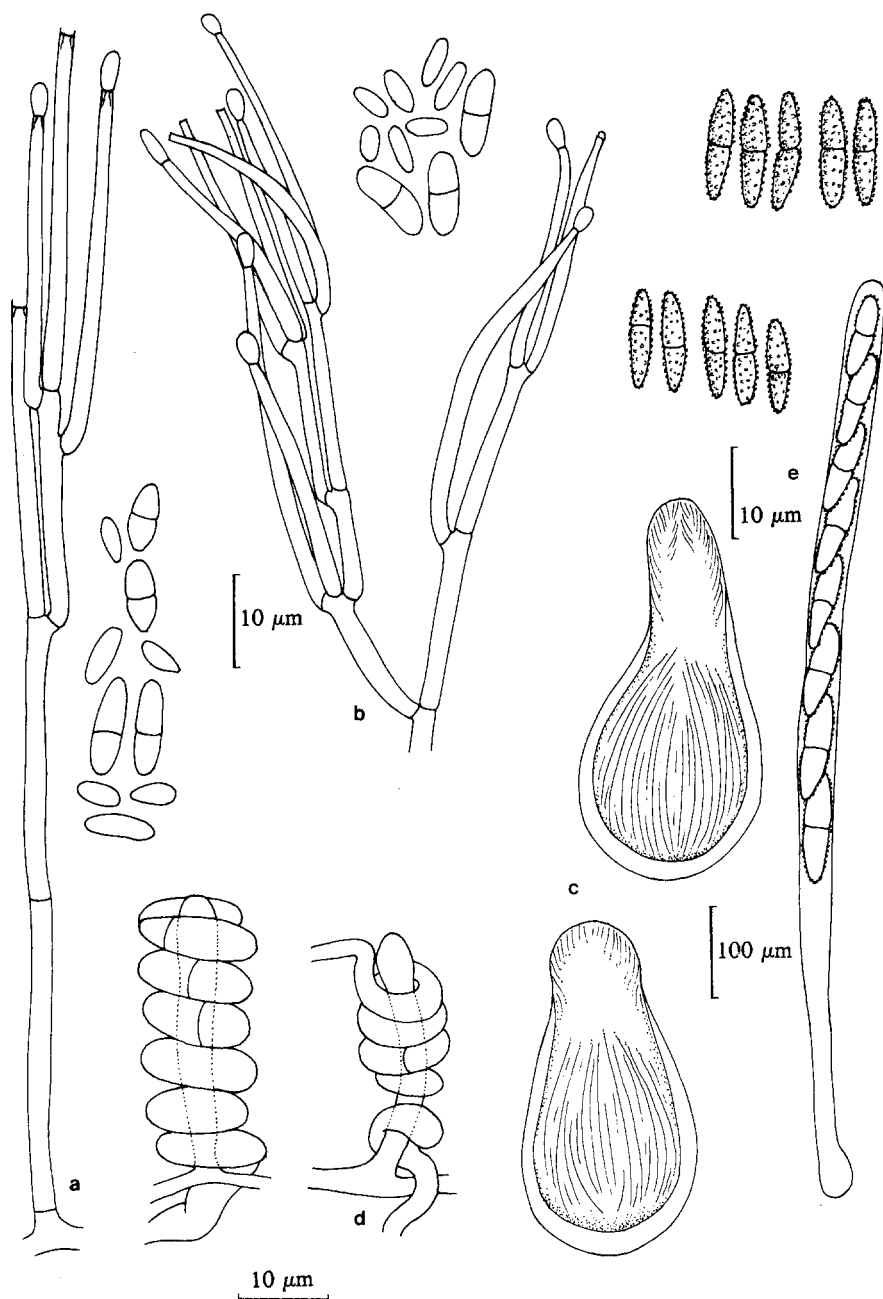


Fig. 8. *Nectriopsis broomeana*. a, b. conidioforen en conidiën van respectievelijk CBS 247.70 en CBS 278.80A. – c-e. peritheciën, ascogonia, ascosporen van CBS 416.80.

7. **Nectriopsis broomeana** (Tul.) W. Gams, *comb. nov.* — Fig. 8.

≡ *Hypomyces broomeanus* Tul., Sel. Fung. Carpol. 3: 108. 1865 (basonym).

Anamorph **Gliocladium microspermum** (Sacc.) W. Gams, *comb. nov.*

≡ *Verticillium microspermum* Sacc., Syll. Fung. 4: 153. 1886.

= *Gliocladium strictum* Petch, Trans. Br. mycol. Soc. 21: 274. 1938.

Colonies on MEA reaching 2.5–3 cm diam in 10 days at about 20 °C, white, loosely floccose; reverse colourless or pale yellow. Odour indistinct. Crystals absent. Vegetative hyphae 1.0–4.5 µm wide. Sporulation abundant, conidiophores arising from single or slightly fasciculate aerial hyphae, rarely from submerged hyphae, erect, 125–225 µm tall, 2.5–4.5 µm wide at the base, smooth or minutely roughened, bearing several ramifications with 1(–2) phialides at each level or branches which in turn may bear phialides, thus forming rather appressed penicilli. Phialides 30–42 µm long, from 2.0–2.5 µm tapering gradually to 0.8–1.7 µm at the tips. Conidia long-ellipsoidal to cylindrical, rarely somewhat curved, with indistinctly truncate base, smooth-walled, of variable size, one-celled, 4.5–7.0 × 2.0–2.7 µm, but commonly becoming 2-celled (rarely 3-celled) and 7.0–9.5(–15) × 2.6–3.2 µm, non-guttulate. Chlamydospores present in 1-month-old colonies, hyaline, forming intercalary chains, cells 5–8.5 µm diam, finely roughened.

Temperature optimum 24–27 °C, maximum 30 °C.

Material examined (all from *Heterobasidion annosum*): CBS 422.64, Holzdorf near Weimar, G.D.R., G. Arnold, Aug. 1962. — CBS 439.65, conidial isolate, Westensee, Kr. Rendsburg, F.R.G., W. Niesel, 1965. — CBS 287.80 A and B, 288.80, 289.80, single-ascospore isolates, CBS 416.80 = 287.80A × 288.80, all from C.T.R. 79-315, collected 2 km north of Bebenhausen near Tübingen, F.R.G., R.J. Bandoni, Aug. 1979, isol. C.T. Rogerson; and some further conidial isolates.

This species is highly specialized as a colonizer of old carpophores of *Heterobasidion annosum* (Fr.) Bref. Perithecia were seen in 6-week-old cultures on oatmeal agar after mating of compatible single-spore isolates (CBS 287.80A or 289.80 with CBS 288.80). The teleomorph was also described by Arnold (1970); it is congeneric with *Nectriopsis tubariicola* and not a good *Hypomyces*. The anamorph does not quite fit *Verticillium* because of the appressed penicillate branches, nor is it a typical *Gliocladium*, as the branching is rather scanty and arises at irregular levels. Therefore and because of its specific mycophilic habit, this species is included in the present study. The distinction between *Verticillium* with divergent and *Gliocladium* with appressed phialides is somewhat artificial and both genera in their present circumscription are heterogeneous, comprising the anamorphs of different Hypocreaceous genera.

8. **Verticillium rexianum** (Sacc.) Sacc., the anamorph of

Nectriopsis exigua (Pat.) W. Gams, *comb. nov.*

≡ *Hypomyces exiguus* Pat., Bull. Soc. mycol. Fr. 18: 180. 1902 (basonym)

≡ *Nectria myxomyceticola* Samuels, Mycologia 65: 409. 1973 [non *N. exigua* Hino & Katumoto]

and

9. **Verticillium lindauianum** Bubák, both growing commonly on Myxomycetes, have been extensively described by Gams (1971, p. 172 and 226) and Samuels (1973).

V. rexianum has its temperature optimum at 24 °C and the maximum at 30 °C, *V. lindauianum* the optimum at 20 °C and the maximum at 27 °C.

Key to the species

1. Growing on myxomycetes 2
 Growing on other fungi 3
2. Conidia subglobose, moderately chromophilic, 2.0–3.0 µm diam (to 4.5 µm long) 9. *V. lindauianum*
 Conidia ellipsoidal, strongly chromophilic, 4.0–6.0 × 2.0–2.7 µm 8. *V. rexianum*
3. Conidia all straight, cylindrical, with slightly truncate base, regularly biguttulate, of very constant size, 5.5–9.5 × 1.5–2.2 µm 4. *V. biguttatum*
 Conidia at least partly curved if cylindrical, or else obovoid to ellipsoidal or fusiform 4
4. Conidia always obovoid to ellipsoidal, straight, length/width ratio not exceeding 2.8 5
 Conidia cylindrical or fusiform, sometimes slightly curved, in old cultures sometimes also obovoid to ellipsoidal 6
5. Conidiophores arising from fasciculate aerial hyphae 5. *Verticillium* anamorph of *Nectriopsis tubariicola*
 Conidiophores arising from submerged hyphae Some unsettled taxa
6. Conidiophores usually with few, appressed branches or phialides, giving a penicillate aspect; conidia often 2-celled, ellipsoidal to cylindrical 7. *Gliocladium microspermum* anamorph of *N. broomeana*
 Conidiophores usually with three or more divergent phialides in a whorl; conidia consistently 1-celled 7
7. Conidia in young cultures on MEA cylindrical to allantoid, of rather constant size, 3.5–6 × 1.4–2.2 µm, in old cultures and on OA larger and ellipsoidal; colony reverse livid-vinaceous 6. *Verticillium* anamorph of *N. tremellicola*
 Conidia fusiform to ellipsoidal, often slightly curved, of very unequal size; colony reverse uncoloured to yellowish 8
8. Colonies white or often yellowish; sclerotium-like structures formed after 3 weeks; pungent odour commonly present; growth at 24 °C much slower than at 20 °C 3. *V. fungicola* var. *flavidum*
 Colonies white to pale cream-coloured; sclerotium-like structures absent; odour indistinct; growth at 24 °C faster than at 20 °C 9
9. Good growth possible at 27 °C 2. *V. fungicola* var. *aleophilum*
 No growth possible at 27 °C 1. *V. fungicola* var. *fungicola*

Discussion

Before new species can be described in *Verticillium*, all previously published taxa have to be revised. This work is in progress and sufficiently advanced to allow the following conclusions: White species with cylindrical to fusiform conidia have often been mentioned as *Verticillium (Acrostalagmus) album* auct., but all applications of this epithet are doubtful. Similarly the epithet *niveum* is no longer available as both *Verticillium niveum* Berk. and *Acrostalagmus niveus* Delacr. were insufficiently described, and type material is no longer available in either Herb. K or PC. From type material in Herb. K, the probable identity of *Verticillium niveum* Petch (Ann. R. bot. Gdns Peradeniya 7: 317. 1922), an illegitimate homonym, was seen to be *Verticillium lecanii* (Zimm.) Viégas. Petch had often identified this variable fungus as various species of *Cephalosporium*, when it was growing on insects; in this case the fungus overgrew some dematiaceous hyphomycetes.

In addition, the genera *Acrostalagmus* Corda, *Acrocylindrium* Bonorden, *Cylindrophora* Bonorden and *Cylindrodendrum* Bonorden, which are now regarded as facultative synonyms of *Verticillium*, as well as the illegitimate genus *Monosporium* Bonorden, are most likely to have contained comparable fungi. But either there is no type material preserved and the identity of the fungi in question remains doubtful, or the type specimen was found to contain a demonstrably different fungus. A documentation of the whole revision has to be deferred to a later date.

The distinction of the sections *Prostrata* and *Albo-erecta* seems to reflect natural affinities, the former comprising anamorphs of *Cordyceps* and *Torrubiella* (Clavicipitaceae), the latter *Nectriopsis* (Hypocreaceae); the distinction may, however, cause practical difficulties. The progressively procumbent and little-differentiated conidiophores of the former can easily be seen by observing undisturbed colonies growing on poor media, like soil extract of potato-carrot agars, in Petri dishes directly under the compound microscope. *V. fungicola* (and its varieties) and the very variable *V. psalliotae* (sect. *Prostrata*), which both have fusiform and more or less curved conidia, are easily confused, for which reason Gams (1971) wrongly assigned an isolate from mushroom to *V. fungicola* instead of to *V. psalliotae* (CBS 504.48). As the temperature relationships are very different in these two species (except *V. fungicola* var. *aleophilum*) (Fig. 1), the distinction is now much more obvious. This fact also explains why *V. psalliotae* which is generally of little importance in mushroom cultures, can equally attack *A. bisporus* and *A. bitorquis* (Upstone and Carter, 1979); its thermal death point is 42 °C (Van Zaayen en Rutjens, 1981). Another comparable species aggregate in Sect. *Prostrata* is *V. lamellicola* (F.E.V. Smith) W. Gams, which has its maximum growth temperature at 27 °C.

In this study not all fungicolous *Verticillium* species have been included, as some taxa of less common occurrence are not yet sufficiently delimited and others, e.g. a common mycoparasite on *Laccaria* species, fall beyond the scope of section *Albo-erecta*. Three further taxa claimed to have *Verticillium* anamorphs can be excluded from this section: the anamorph of *Hypomyces petchii* Arnold (Z. Pilzk. 37: 187. 1971) is not a *Verticillium*; the type culture, CBS 148.78, is now sterile and produces chlamydospores typical of *Hypomyces* s. str.; the anamorph might be placed in *Cladobotryum*. *Hypocrea avellanea* Rogerson & Carey in Carey and Rogerson (1976), growing on deformed basidiomata of *Marasmius subnudus*, and other

Hypocrea species with white colonies and scattered *Verticillium* conidiophores can be excluded from sect. *Albo-erecta* because of their broadly and thinly spreading colonies.

Hypomyces berkeleyanus Plowr. & Cooke, anamorph *Verticillium berkeleyanum* Karsten, Meded. Soc. Fauna Fl. fenn. **18**: 64. 1891, known from *Stereum* spp. and described by Samuels (1976) next to *Hypomyces tremellicola*, is a typical *Nectria* (*Nectria berkeleyana* (Plowr. & Cooke) Dingley, Trans. R. Soc. N.Z. **79**: 183. 1951), the anamorph of which is identical with *Acremonium butyri* (van Beyma) W. Gams (1971) (type of anamorph in Herb. H): ***Acremonium berkeleyanum* (Karst.) W. Gams comb. nov.** This conclusion is confirmed by the study in culture of CBS 501.81, isolated from identical material on *Stereum hirsutum* collected in the Abbert Forest, O-Flevoland Polder, 29 July 1981. Further studies will show whether other known teleomorphs of *A. berkeleyanum*, viz. *Nectria vilior* Starb. (Samuels and Rossman, 1979) and *N. viridescens* C. Booth, are conspecific with *N. berkeleyana*.

Acknowledgements

We wish to thank Dr. C.T. Rogerson, New York Botanical Garden, for supplying specimens and interfertile isolates of *Nectriopsis tremellicola* and *N. broomeana* and helpful suggestions on the manuscript. Mr G.J. Bollen, Wageningen, tested the sensitivity to benomyl in two of our isolates. Dr C.A.N. van Oorschot corrected the text and Miss I. ten Hoedt inked the drawings.

Samenvatting

Een bijdrage aan de taxonomie en pathogeniteit van met schimmels geassocieerde Verticilliumsoorten. I. Taxonomie

Het geslacht *Verticillium* wordt onderverdeeld in vier secties (waaronder twee nieuwe) en een restgroep. De nieuwe sectie *Nigrescentia* bevat onder meer de bekende ziekteverwekkende soorten met donkere ruststructuren. De nieuwe sectie *Albo-erecta* wordt gekarakteriseerd door witte (of geelachtige) kolonies en rechtopstaande conidioforen en bevat hoofdzakelijk op andere fungi groeiende soorten. Zeven soorten (waaronder twee nieuwe) en twee nieuwe variëteiten worden beschreven en in een sleutel verwerkt. Drie andere soorten bezitten perfecte vormen van *Nectriopsis* (waaronder één nieuwe en twee nieuwe combinaties). Dit geslacht werd door Samuels met *Nectria* samengevoegd, maar kan gehandhaafd worden en lijkt beter geschikt om de hier beschreven ascomyceten onder te brengen dan *Hypomyces*.

Verticillium fungicola var. *fungicola*, de algemene veroorzaker van droge mollen bij de champignon (*Agaricus bisporus*), wordt beschreven en met zijn temperatuurmaximum beneden 27 °C nauwkeuriger gedefiniëerd dan in een vroegere studie (Gams, 1971). Een vergelijkbare schimmel met een temperatuurmaximum van ongeveer 33 °C, die bij *A. bitorquis* bruine vlekken veroorzaakt, wordt beschreven als *V. fungicola* var. *aleophilum*. Isolaten van wilde paddestoelen met een optimum duidelijk beneden 24 °C en een maximum beneden 27 °C, geelachtig mycelium en opvallende sclerotiën, worden beschreven als *V. fungicola* var. *flavidum*. *V. biguttatum* W. Gams, sp. nov., met cilindrische, biguttate conidiën, is een algemene

grondschimmel en hyperparasiet van *Rhizoctonia solani*. *Gliocladium microspermum* (Sacc.) W. Gams, comb. nov., de imperfecte vorm van *Nectriopsis broomeana* (Tul.) W. Gams, comb. nov., een tussenvorm tussen *Gliocladium* en *Verticillium*, wordt opgenomen wegens zijn voorkomen op vruchtlichamen van de dennemoorder.

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