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A contribution to the knowledge of nematophagous species of Verticillium

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Abstract

Nine nematophagous species and two varieties of *Verticillium* (*Verticillium* sect. *Prostrata*), occurring either as parasites of free-living nematodes or as parasites of cysts and eggs, are revised and keyed out. *V. catenulatum* is reduced to a variety of *V. chlamydosporium*. A similar fungus is distinguished as *V. suchlasporium* n. sp. (including a var. *catenatum*). *Spicaria coccospora* Drechsler is transferred to *Verticillium*. All species have been studied in pure culture. Ecological data are reviewed for each species.

Additional keywords: plant-parasitic nematodes, cyst nematodes, endoparasites, biological control, Hyphomycetes, taxonomy, distribution.

Introduction

Endoparasitic hyphomycetes are of great interest as potential biocontrol organisms of plant-pathogenic nematodes (Bursnall and Tribe, 1974; Tribe, 1977, 1979, 1980; Barron, 1977, 1982; Kerry and Crump, 1977, 1980; Kerry et al., 1982; Mankau, 1980; Morgan-Jones et al., 1981; Heijbroek, 1983; Dürschner, 1983; Cook and Baker, 1983). They comprise species that either attack free-living nematodes or colonize cysts and eggs or the young sessile females of *Heterodera* species (Kerry, 1980; Dackman and Nordbring-Hertz, 1985). Understanding the ecology of clearly defined species will hopefully open ways of an integrated control of plant-pathogenic nematodes.

The knowledge of nematode endoparasites largely goes back to work by the late Dr Charles Drechsler. Drechsler observed these fungi in mixed cultures on cornmeal agar plates. He was of the opinion that the endoparasites could hardly be isolated in pure culture. The same opinion was shared by Duddington (1955). Only since Aschner and Kohn (1958) and Barron (1969) (see also Barron, 1982; Gray, 1984) devised techniques for isolating nematode endoparasites, has the study of these fungi made much further progress. Techniques to isolate fungi from infested eggs in cysts were devised by Kerry and Crump (1977) and subsequent workers. In fact all the nematophagous *Verticillium* species grow in culture as easily as any other saprophytic species.

As all papers by Drechsler relevant to the present study were published before 1958, his descriptions are valid according to Art. 37 of the International Code of Botanical Nomenclature. Drechsler used to designate his drawings as iconotypes. In spite of the remarkable quality of Drechsler's camera lucida drawings, it is, however, not always possible to assess with certainty which fungus he had in hands. Dr A. Rossmann kindly informed me that no material of the fungi under consideration preserved by Drechsler

is available at the U. S. National Fungus Collections, Beltsville, or anywhere else. Therefore it is necessary to establish the identity of the species described by Drechsler with more recent material. When designating neotypes, the existence of living cultures of the same isolate was used as an important criterion.

The species treated here and the taxa considered as synonyms or of doubtful identity have been mentioned repeatedly in the literature. But some of the authors regrettably failed to preserve their isolates and it was impossible to get hold of cultures of all relevant taxa. Completeness of the ecological reviews for each species was therefore not attempted.

The probably related nematophagous species of *Cephalosporiopsis* and *Plesiospora* are at present unavailable in culture.

Generic concepts and morphological criteria

Simple phialidic Hyphomycetes found as nematode endoparasites have been described in the genera *Acrostalagmus*, *Cephalosporium*, *Verticillium*, *Spicaria*, *Diheterospora*, *Cephalosporiopsis* (Drechsler, 1969), *Plesiospora* (Drechsler, 1970) and *Tolypocladium*.

Among these genera, *Acrostalagmus* is undoubtedly synonymous with *Verticillium* (Gams, 1971).

The generic name *Cephalosporium* has been abandoned in favour of *Acremonium* (Gams, 1971). Only *Acremonium strictum* W. Gams was found as an egg parasite of *Heterodera schachtii* in California and the Netherlands (Nigh et al., 1980; Th. Burghouts, unpublished results), besides occasional *A. murorum* (Corda) W. Gams (Th. Burghouts and D. Hugo-Wissemann, unpublished results, L. López-Llorca, personal communication), and a single isolate of *A. camptosporum* W. Gams (M. Hashem, personal communication).

The entomogenous species described in *Cephalosporium* were reclassified in *Verticillium* sect. *Prostrata*, characterized by white or whitish cottony colonies and a strong tendency to form prostrate conidiophores, little differentiated from vegetative hyphae. This section is considered to have affinities with ascomycetes of the Clavicipitales. This group includes the species treated in the present paper. An extension of the generic definition to accommodate species with catenate conidia was introduced by Gams (1971). This extension affects the only nematophagous species described in *Spicaria*, a genus generally synonymized with *Paecilomyces*, that is transferred to *Verticillium* here.

The species of nematophagous fungi have been keyed out only once comprehensively by Cooke and Godfrey (1964), the species of *Verticillium* sect. *Prostrata* also by Gams (1971), but both treatments are no longer adequate for the nematophagous *Verticillium* species and a more comprehensive revision was long due.

While it would be highly desirable to separate the *Verticillium* anamorphs of Clavicipitales from those of Hypocreales at generic level, this distinction is so difficult in practice that it is not further considered at the moment (see also Gams and Van Zaayen, 1982).

The resting structures of some of these *Verticillium* species are very characteristic hyaline, thick-walled, multicellular, stalked bulbils, commonly called dictyochlamydospores, although they do not match Hughes' (1985) narrowed definition of chlamydospores. The development of the dictyochlamydospores was described in detail by Campbell and Griffiths (1975). After septum formation much secondary wall material

is deposited. The term dictyochlamydospores is retained also here in preference over aleuriospores, although it is not quite appropriate. The dictyochlamydospores can be very common in the aerial mycelium, or more scanty and mostly submerged in the agar. They can also merge into less differentiated, often intercalary aggregates of swollen cells.

Diheterospora, characterized by the presence of dictyochlamydospores besides verticillate phialides (Barron and Onions, 1966), was not considered generically distinct from *Verticillium* by Gams (1971), but Barron (1980, 1985) retained it and described a considerable number of rotifer parasites in it. The generic distinction between *Verticillium* and *Diheterospora* based on the presence of dictyochlamydospores is rejected here again, because these structures can occur in quite variable densities and can be completely absent in some cases, while the phialidic conidiophores of these fungi are quite indistinguishable from those of other *Verticillium* species.

Among the nematophagous species, the highest differentiation and greatest abundance of dictyochlamydospores is found in *V. chlamydosporium* with its varieties, whilst in other species they occur scantily, mostly submerged in the agar and mixed with reduced forms. In *V. suchlasporium* they may be present or almost absent. Not because of an objection against defining a genus on two distinct anamorphs, but because the criterion of dictyochlamydospores does not serve to distinguish natural groups of fungi in the present case, the genus *Diheterospora* (or *Pochonia*) is not accepted. The situation was clearly characterized by Drechsler (1942): 'It is not evident at present that in the group of zoophagous fungi here concerned the production of chlamydospores, even of very distinctive chlamydospores, can be interpreted as an indication of taxonomic separateness'.

As shown by Gams (1971), the validity of *Diheterospora* dates from Barron and Onions (1966). The name is thus predated by *Pochonia* Batista & Fonseca 1965. Other older generic names often cited in this connection are *Stemphyliopsis* A.L. Smith 1910 and *Dictyoarthrinopsis* Batista & Cif. 1957. *Stemphyliopsis* is a hyaline *Stemphylium* (Barron and Onions, 1966) and therefore not available for the dictyochlamydospores of *Verticillium*.

The genus *Dictyoarthrinopsis* Batista & Cif. 1957 has been of doubtful identity for a long time. The type material of *D. costaricensis* Bat. & Cif., Sydow's Fungi exotici exsiccati No. 635, was cited by Batista and Ciferri (1957) to be located in Pavia. It could, however, not be traced there and neither in Padova. Another specimen with that number was finally received from the Stockholm herbarium, but no fungus answering the description of *D. costaricensis* could be found on it.

A further criterion has been so far little appreciated: in the rotifer parasites the branching pattern is often irregular, short conidiogenous necks without a basal septum ('sesquiphialides') arising at the same level as phialides or below the tip of phialides, similar as in the genus *Sesquicillium* W. Gams (1968). While typical species of that genus are anamorphs of *Nectriella* in the Nectriaceae, the endoparasitic species in rotifers, together with *S. parvulum* (Jaap) W. Gams & Veenbaas-Rijks, are probably anamorphs of Clavicipitales. The occasional presence of dictyochlamydospores in some of these species points to the close relationship with other species of *Verticillium* sect. *Prostrata* and it is doubtful, whether a generic separation based on the criterion of sesquiphialides is desirable. Slides of the recently described rotifer parasites were kindly supplied by Dr G. L. Barron and this study confirmed their taxonomic distinctness from the species

described here. They require, however, further study using pure cultures, and their taxonomy is not further discussed here. In any case this group has little in common with *Tolypocladium*, although Bissett (1983) transferred *S. parvulum* (together with *V. balanoides*) to that genus.

The genera *Culicinomyces* and *Tolypocladium* are considered distinct from *Verticillium*. The mosquito parasite *Culicinomyces clavisporus* Couch et al. 1974 forms more or less appressed whorls of phialides with a conspicuously tapering neck. In this semiaquatic genus (with sporulation under water) there are now three recognized species (Sigler et al., 1987). *Tolypocladium* W. Gams 1971 (reviewed by Bissett, 1983) has more or less inflated phialides in irregular clusters borne on hardly differentiated vegetative hyphae. Its phialidic conidiogenesis clearly differentiates the genus from *Beauveria* (in spite of a statement to the contrary by Von Arx, 1986).

Methods used in this study

Conidia were streaked out on 2 % malt extract agar (MA), potato-carrot agar (PCA) and soil extract agar (SEA) (described in Gams et al., 1987). Cultures were incubated at room temperature (c. 20 °C). Direct observation of the open Petri dishes under the compound microscope is important to observe conidiophore branching patterns and the arrangement of the conidia. When dictyochlamydospores are produced scantily, they can mostly be found on SEA or PCA. In a few cases nematodes of *Panagrellus redivivus* were added to a fungus on water agar to observe the development of parasitization.

Key to the nematophagous species of *Verticillium* sect. *Prostrata*

1. Conidia isodiametric and polygonal ..... *V. gonioides*
1*. Conidia not polygonal 2

2. Conidia at least partly with truncate and thick-walled upper end, where they are adhesive ..... *V. balanoides*
2*. Conidia without truncate, thick-walled apices 3

3. Dictyochlamydospores abundant in the aerial mycelium, very thick-walled, yellowish 4
3*. Dictyochlamydospores absent or present, submerged in the agar, more thin-walled, hyaline, often appearing roughened 5

4. Phialoconidia at least partly forming chains ..... *V. chlamydosporium* var. *catenulatum*
4*. Phialoconidia not catenate .... *V. chlamydosporium* var. *chlamydosporium*

5. Phialoconidia acicular or fusiform; dictyochlamydospores consistently absent 6
5*. Phialoconidia globose or ellipsoidal or falcate; dictyochlamydospores sometimes present 7

6. Conidia 4.3-5.0 × 0.7-1.0 μm, in long chains ..... *V. leptobactrum*
6*. Conidia 3-10 × 0.8-1.2 μm, in slimy heads ..... *V. lamellicola*

7. Conidia at least partly asymmetrical along the longitudinal axis, slightly falcate 8
7*. Conidia symmetrical along the longitudinal axis, subglobose to ellipsoid . 9

8. Dictyochlamydospores commonly produced, of ± irregular shape, often reduced to swollen hyphal cells; fusiform or falcate conidia usually not exceeding 6 μm in length, with rather blunt ends ..... *V. bulbillosum*
8*. Dictyochlamydospores absent; falcate conidia up to 9.5 μm long, sharply pointed ..... *V. psalliotae*

9. Conidiophores mostly erect, rather thick-walled; colonies 3-4 mm deep; submerged dictyochlamydospores generally present 10
9*. Conidiophores commonly prostrate, not thick-walled; colonies not more than 2 mm deep; conidia in dry chains; dictyochlamydospores generally absent .... *V. coccosporum*

10. Conidia cohering in dry heads ..... *V. suchlasporium* var. *suchlasporium*
10*. Conidia cohering in chains ..... *V. suchlasporium* var. *catenatum*

The nematophagous species of *Verticillium*

Verticillium balanoides (Drechsler) Dowsett et al. – Figs 1-3.

≡ *Acrostalagmus balanoides* Drechsler, Phytopathology 31: 786. 1941.
≡ *Acremonium balanoides* (Drechsler) Subram., Kavaka 5: 98. 1978 ('1977').
≡ *Verticillium balanoides* (Drechsler) Dowsett et al., Mycologia 74: 690. 1982.
≡ *Tolypocladium balanoides* (Drechsler) Bissett, Can. J. Bot. 61: 1313. 1983.
= *Acrostalagmus zeosporus* Drechsler, Phytopathology 36: 216. 1946.
= ?*Acrostalagmus obovatus* Drechsler, Phytopathology 31: 784. 1941.
≡ *Verticillium obovatum* (Drechsler) Subram., Kavaka 5: 98. 1978 ('1977').
= ?*Acrostalagmus bactrosporus* Drechsler, Phytopathology 31: 782. 1941.
≡ *Verticillium bactrosporum* (Drechsler) Subram., Kavaka 5: 98. 1978 ('1977').
= *Verticillium sphaerosporum* J. B. Goodey, Trans. Br. mycol. Soc. 34: 272. 1951.
= ?*Verticillium sphaerosporum* var. *bispora* Watanabe, Ann. phytopath. Soc. Japan 46: 600. 1980.

Colonies slow-growing, reaching 6-10 mm diam in 20 days, whitish, with thin aerial mycelium, reverse ochraceous-grey. Vegetative hyphae often swollen, thick-walled and somewhat roughened. Conidiophores more or less erect, bearing phialides singly or 2-4 in whorls. Phialides when growing on nematodes, swollen in the lower part, 5-10 (-15) μm long, tapering from 2-2.5 μm to 0.5-1 μm, when grown on agar media more regularly subulate and more densely verticillate, 6-18(-25) μm long. Conidia acorn-shaped (*'balanoides'*), at least partly truncate and thick-walled at the tip, 2.5-3.5(-9) × 1.5-2.0(-2.5) μm (on water agar with nematodes the smallest sizes in this range are observed). Dictyochlamydospores rarely fully developed, mostly irregularly formed from lateral branches bearing a series of swollen and curling cells. In addition, intercalary swollen hyphal cells commonly occur.

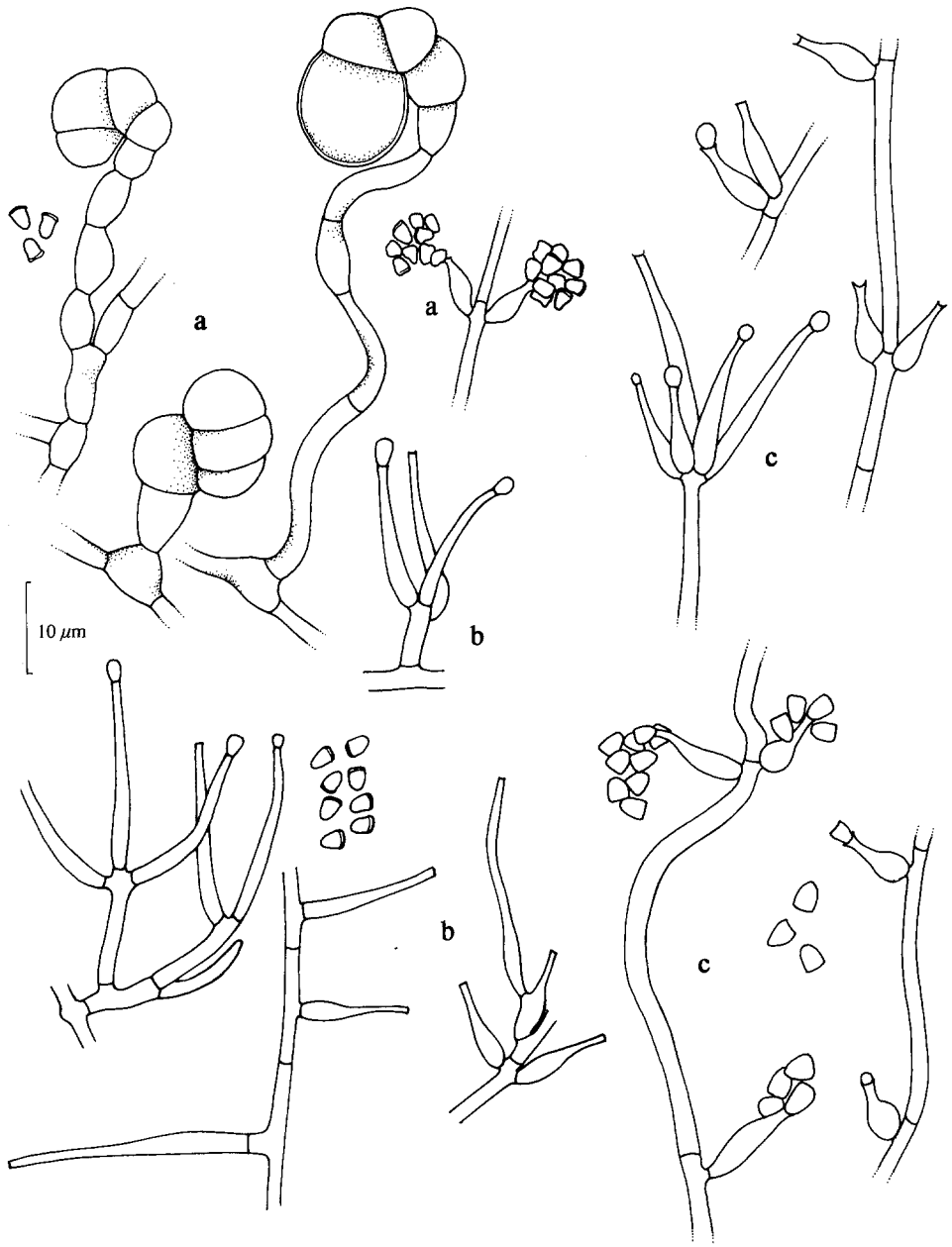

Fig. 1. *Verticillium balanoides*. a) and b) CBS 522.80; a) on water agar with nematodes, b) on cornmeal agar after 25 days. c) CBS 257.83, on soil extract agar after 9 days.

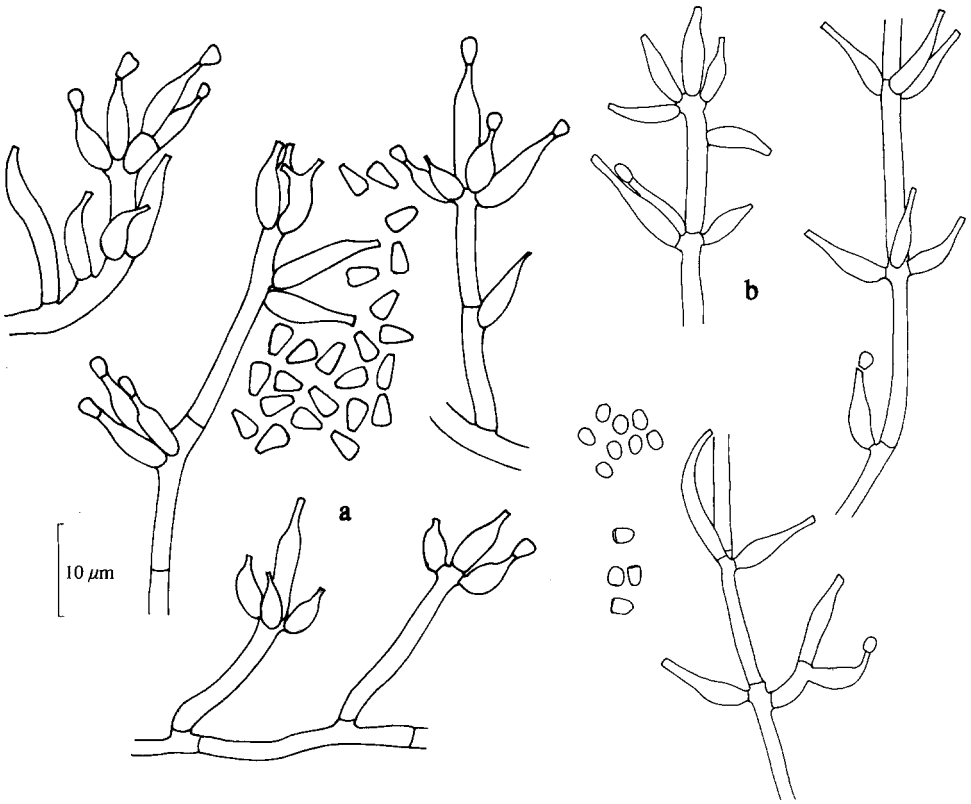

Fig. 2. *Verticillium balanoides.* a) CBS 335.80, on malt agar; b) conidiophores and conidia from the type slide of *Verticillium sphaerosporum.*

Material examined:

Two slides of *V. sphaerosporum*, **holotype** material, on *Ditylenchus dipsaci* in *Calceolaria*, Scotland, H. F. Dovaston, 30-9-1949, preserved at Rothamsted Experimental Station, Nematology Department, comm. D. Hooper.

CBS 335.80 = IMI 239515, ex nematodes, Iraq, isol. I. S. Damirdagh, comm. B. L. Brady.

CBS 522.80, endoparasitic on *Ditylenchus triformis*, ex compost, Münster i.W., F. R. G., comm. H. Nirenberg.

CBS 250.82, **neotype** of *V. balanoides*, sent by J. Reid, Winnipeg, see Dowsett et al. (1982).

CBS 614.82, ex agricultural soil, Sweden, S. Olsson, Lund, see Jansson (1982).

CBS 257.83, isol. ex nematodes by Mrs. Fritsch, Berlin, F. R. G., comm. G. Lysek.

CBS 381.84, ex nematodes, California, R. Mankau.

CBS 889.85, parasitic on *Panagrellus redivivus*, Münster i.W., F. R. G., comm. M. Hashem, Kiel.

An isolate was also obtained from J. Landmann, who had isolated the species repeatedly from agricultural, meadow and forest soils as well as from moss, leaf litter and compost in the F. R. G. (J. Landmann, unpublished results).

Discussion. Contrary to the remaining species treated in this paper, this species was originally described in *Cephalosporium*, as it bears often solitary and swollen phialides when feeding on nematodes. When grown on media like oatmeal agar or PCA, which

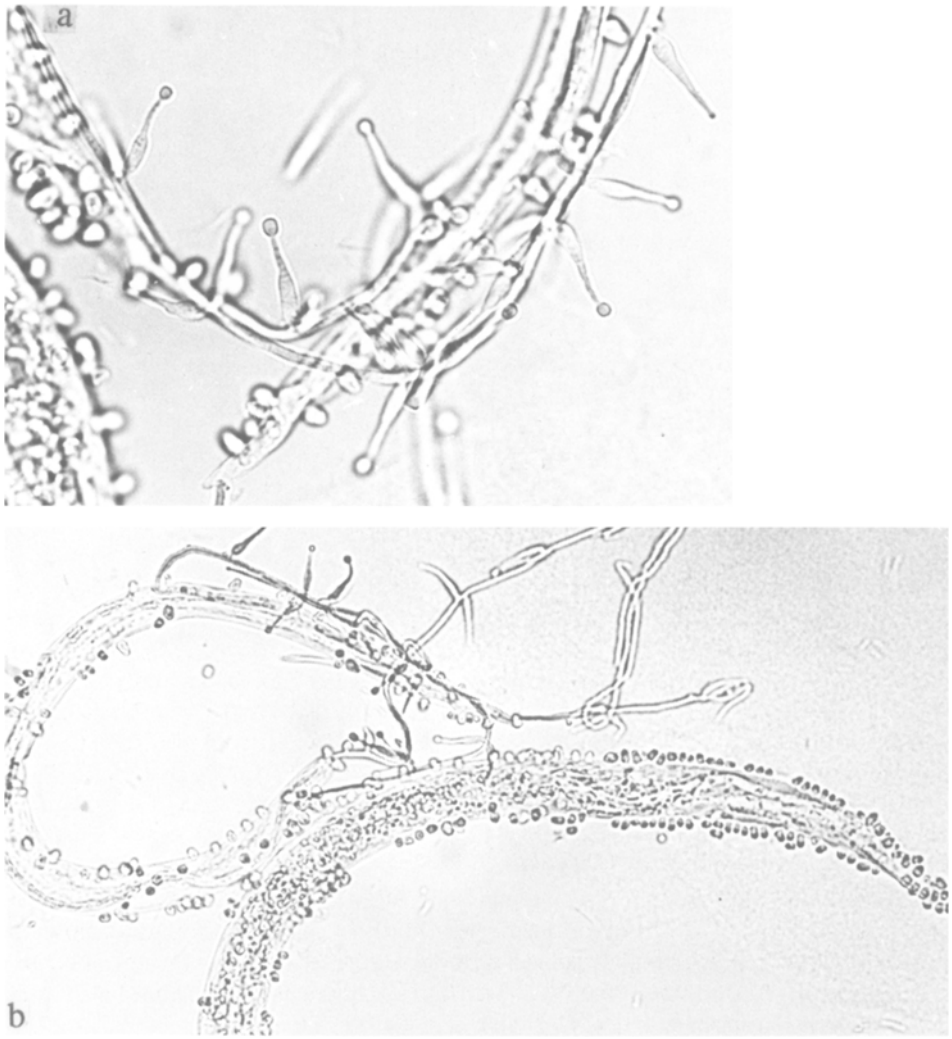

Fig. 3. *Verticillium balanoides*. CBS 522.80, on *Ditylenchus triformis*. a) Conidiophores arising from the nematode (× 1000), b) two attacked nematodes with numerous conidia attached to the cuticle, and conidiophores arising from one of them (× 500). Phot. H. Nirenberg.

allow the most differentiated development in vitro, the same isolate, however, forms repeatedly branched verticillate conidiophores with slender phialides. The same range of variation was observed by Dowsett et al. (1982), who gave a good description and also illustrated the conidia with SEM. Thus the species is a typical member of *Verticillium* sect. *Prostrata*, and not of *Tolypocladium* (Bissett, 1983).

The label of the slides of *Verticillium sphaerosporum* agrees in date and origin with that of the protologue, hence indicating the value of a holotype; the slides show the typical truncate shape of the conidia with thickened apex (Fig. 2b); many conidia were

seen to stick to the nematode. The phialides are distinctly verticillate, so that Goodey (1951) did not think of comparing the fungus to *C. balanoides*, and Duddington (in Goodey, 1951) considered it closer to *A. obovatus*.

CBS 335.80 and 250.82 would fit *A. zeosporus* Drechsler by having more elongate conidia with a less conspicuous apical wall thickening and a stronger tendency to form polyphialides (Fig. 2a). CBS 381.84 has mostly rounded conidia and relatively few conidia with truncate apex; it might fit *A. obovatus* Drechsler. All strains studied here have a certain tendency to form polyphialides. The presence of at least some conidia with truncate, thick-walled apices is considered as the most differentiated form allowing the specific distinction. Therefore these taxa are united here, although Gray (1983 b) still tried to distinguish them. The criteria used by him, viz. conidiophore length, length of the phialides and their number in the whorl, are very variable as shown here for the isolate CBS 522.80. It is unlikely that the features mentioned would be more consistent when the fungus is grown on nematodes than on a range of agar media.

According to the present scheme, this is the only recognized nematophagous species of *Verticillium* with conspicuously terminally adhesive conidia. It is also the only species that efficiently attacked *Panagrellus redivivus* on water agar within 5 days, although CBS 335.82 and 250.82 showed less activity.

Among the species listed in the nomenclator, Drechsler explicitly described conidia sticking to the nematode surface only for *C. balanoides* on *Plectus parvus* and *Acrobeloides buetschlii* (conidia 2.4-2.8 × 2.3 μm) and *A. bactrosporus* on *Plectus parvus* (conidia 2-3 × 1.3-1.6 μm). For *A. obovatus* (on *Plectus parvus*, conidia 3 × 2 μm) and *A. zeosporus* (on *Panagrolaimus subelongatus*, conidia 3.5-4.6 × 1.7-2.1 μm) no indication about adhesiveness of the conidia was given, while in the latter species the common occurrence of what are now called polyphialides was noticed. Drechsler (1942) even emphasized the absence of dictyochlamydospores in the first three of these species. For *A. zeosporus* he did not mention them either (Drechsler, 1946). Gray (1983b) listed all these species as having adhesive conidia.

No culture of *V. sphaerosporum* var. *bisporum* Watanabe (1980) could be obtained for study. According to the description, it is unlikely that this fungus is close to *V. balanoides*, forming both globose and cylindrical conidia, apparently without truncate apices. It was described as parasitizing *Aphelenchoides*, *Cephalobus* and *Panagrolaimus* species.

V. balanoides was reported as an endoparasite of *Rhabditis terricola* from various soils in Ontario (Barron, 1978), from moss in birchwood in England (Duddington, 1951) and from deciduous and coniferous leaf litter, old dung and coastal vegetation in Ireland (Gray and Duff, 1982; Gray, 1983c). The species occurred in 50 % of soil samples taken from agricultural soils in Westfalen, F.R.G. (Dürschner, 1983). It was also commonly encountered in the maritime Antarctic (Gray et al., 1982; Gray and Lewis Smith, 1984). The host range included all species of the Rhabditida, Aphelenchida and Tylenchida tested but not the Dorylaimida (Dürschner, 1983). Next to *Drechmeria coniospora* (Drechsler) W. Gams & Jansson, this is the most active endoparasite of free-living nematodes.

The temperature minimum for growth for CBS 522.80 was found to be about 15 °C (Th. Burghouts, unpublished results). The adhesive conidia were found to attract nematodes in vitro (Jansson, 1982).

Verticillium bulbillosum W. Gams & Malla in W. Gams, *Cephalosporium*-artige Schimmelpilze, p. 189. 1971.

= *V. cephalosporum* W. Gams, ibid. p. 180. 1971.

Description in Gams (1971).

Material examined:
CBS 145.70, **type isolate**, ex root of *Picea abies*, Denmark, D. Malla, 1970.
CBS 247.68, **type isolate** of *V. cephalosporum*, ex agricultural soil, Kiel-Kitzeberg, F.R.G., W. Gams, 1964.
CBS 571.78 = VKM-F 454, received as *Verticillium microspermum* Sacc., mycophilic, see Rudakov (1978).
PD 87/248, isolated from cysts of *Heterodera* sp. in the Netherlands, J.W. Veenbaas-Rijks.
And many other isolates from different origins.

Discussion. *V. cephalosporum* W. Gams was originally distinguished from *V. chlamydosporium* by the complete absence of dictyochlamydospores. When the strains used by Gams (1971) were reexamined, it became apparent that they comprised a mixture of different taxa: the type isolate, CBS 247.68, produced very rarely dictyochlamydospores and had very thin-walled, occasionally asymmetrical conidia, not quite typical of *V. bulbillosum*; most of the remaining isolates had to be reclassified in *V. suchlasporium* var. *suchlasporium*, though some of the isolates never produced dictyochlamydospores. *V. bulbillosum* has rarely been recorded as a parasite of cyst nematodes (Dackman and Nordbring-Hertz, 1985). Isolates of the species from Afghanistan and Pakistan were also listed as ovicidal to eggs of *Ascaris lumbricoides* (Fassatiová and Lýsek, 1982), penetrating the eggs and destroying the embryos.

Verticillium chlamydosporium Goddard var. **chlamydosporium** – Fig. 4.

Verticillium chlamydosporium Goddard, Bot. Gazette 56: 275. 1913.
≡ *Diheterospora chlamydosporia* (Goddard) Barron & Onions, Can. J. Bot. 44: 866. 1966.
= *Stemphyliopsis ovorum* Petch, Trans. Br. mycol. Soc. 23: 146. 1939.
= *Diheterospora heterospora* Kamyschko, Botan. Mater. 15: 138. 1962 (nom. inval., Art. 37).
= *Pochonia humicola* Batista & Fonseca, Publ. Inst. Micol. Recife 462: 4-10. 1965.
= *Dictyoarthrinopsis kelleyi* Dominik & Majchrowicz, Mycopath. Mycol. appl. 28: 210. 1966.

Colonies on MA after 15 days about 15 mm diam, white to cream-coloured or pale ochraceous due to dictyochlamydospores, reverse yellow to ochraceous. Aerial mycelium usually rather thin. Phialides arising singly or in whorls of 2-3 from prostrate hyphae, also in terminal whorls of 4-5. Phialides slender subulate, 15-26 × 1.0-1.5 μm, tapering distally to 0.4-0.6 μm. Conidia subglobose to ovoid or ellipsoidal, (2.5-)3-4.5(-5.5) × 1.5-2.2(-3) μm, the base somewhat apiculate, rather thin- and smooth-walled. Dictyochlamydospores abundantly produced in the aerial mycelium, stalked, 20-25 μm diam, at maturity thick-walled (2-3 μm), smooth, appearing yellow to orange when mounted in lactic acid with aniline blue (immature cyanophilic), occasionally with wart-like excrescences.

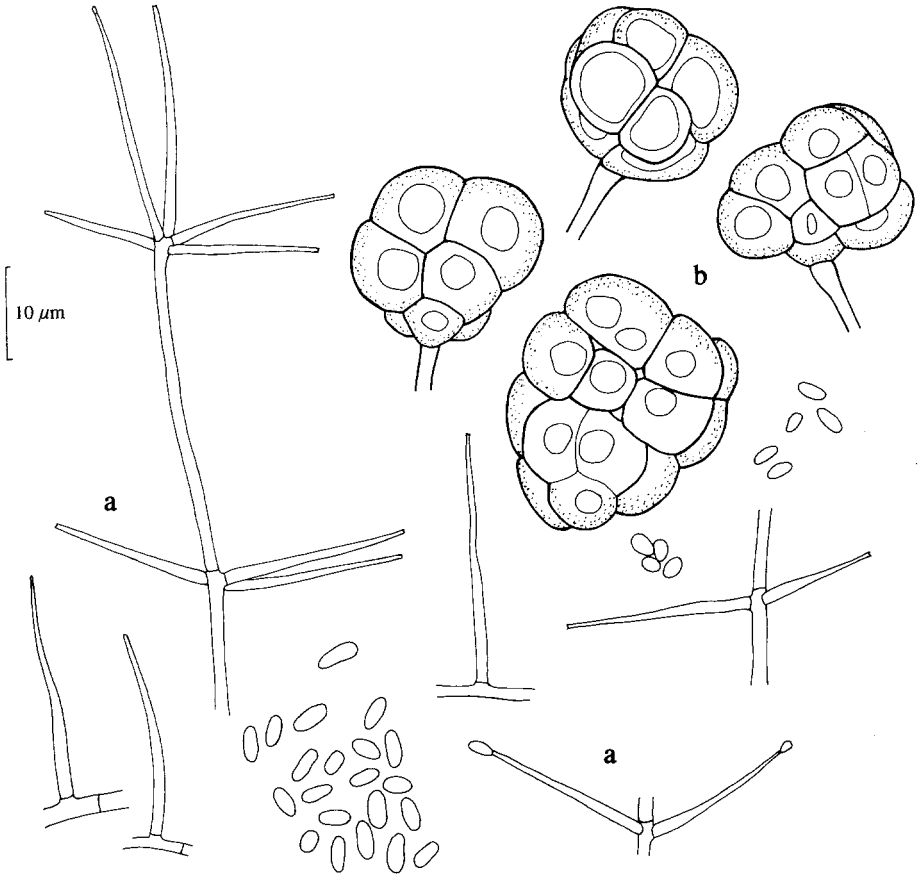

Fig. 4. *Verticillium chlamydosporium* var. *chlamydosporium*. CBS 361.64, on potato-carrot agar. a) Verticillate and simple conidiophores and conidia, b) dictyochlamydospores.

Material examined:
CBS 468.59 = IMI 76105, ex soil, St. Chély du Tarn, France, comm. A.P. Struyk.
CBS 361.64, isol. J.H. van Emden ex potato rhizosphere, Wageningen, Netherlands, 1964.
CBS 429.64 = IMUR 1972, ex soil, Ceará-Mirim, Rio Grande do Norte, Brazil, J. Oliveira da Silva, 1964, **type isolate** of *Pochonia humicola*.
CBS 594.66, ex soil, Conakry, Guinea, Africa, T. Dominik and I. Majchrowicz, type of *Dictyoarthrinopsis kelleyi*. This isolate was noticed to be highly keratinolytic.
CBS 103.65 = ATCC 16289, ex agricultural soil under rape seed, Kiel-Kitzeberg, F.R.G., W. Gams, designated here as **neotype** of *V. chlamydosporium*.
And many further isolates not preserved (some more listed in Gams, 1971).

Discussion. Cultures of fresh isolates are yellowish and appear finely granular due to abundant dictyochlamydospores produced in greater abundance than the phialoconidia. After repeated subcultures the proneness to form dictyochlamydospores declines.

V. chlamydosporium was regarded as a species aggregate (Bursnall and Tribe, 1974)

and the fungus described here as *V. suchlasporium* var. *suchlasporium* has probably often been confused with it. That species is distinct because of its taller, mostly erect and more densely verticillate conidiophores and its dictyochlamydospores mostly buried in the agar.

The synonymy of *Pochonia humicola* and *Dictyoarthrinopsis kelleyi* with *V. chlamydosporium* is established beyond doubt by the descriptions and the available type cultures. A further similar species is *A. tagenophorus* Drechsler, described as a parasite of rotifers. This species, however, was described as having flattened dictyochlamydospores with cells in 2-dimensional arrangement. The justification of this unusual criterion is confirmed by Barron's slide # 247 of this species and # 10834 of *Diheterospora cylindrospora* Barron, both of which also show some sesquiphialides.

Amongst the nematophagous *Verticillium* species this species is, besides *V. bulbillosum*, most commonly recorded as a saprophyte in soil fungal analyses. Goddard (1913) already isolated the species from a rich clay garden soil in Ann Arbor, Michigan, using dilution plates (many more references in Domsch et al., 1980). It is also the species most frequently reported as a major endoparasite of *Heterodera* species, but only exceptionally from *Globodera* (Bursnall and Tribe, 1974; Tribe, 1977, 1979, 1980; Kerry and Crump, 1977; Kerry et al., 1980, 1982). The fungus is easily isolated from infested eggs obtained after crushing attacked cysts. The species has been reported as a cyst and egg parasite of i.a. *Heterodera glycines* (Gintis et al., 1983), but also of eggs of *Meloidogyne arenaria* (Godoy et al., 1982; Morgan-Jones et al., 1983). More data on its distribution were given by Dackman and Nordbring-Hertz (1985). Gintis et al. (1983) observed strong chitinase activity. The species has also been listed as ovicidal to eggs of *Ascaris lumbricoides* (Fassatiová and Lýsek, 1982), penetrating the eggs and destroying the embryo, and also from snail eggs (Gams, 1971).

When intact cysts of *Globodera rostochiensis* were scattered over a culture of *V. chlamydosporium* growing on oatmeal agar and left there for two weeks, hyphae penetrated the cyst wall at many places and grew further to penetrate the eggs (D. Hugo-Wissemann, unpublished results); penetration of cysts was also observed by Kerry et al. (1976, cited in Tribe, 1980).

The temperature minimum for growth is near 10 °C, and no growth occurs at 6 °C (Th. Burghouts, unpublished results; Dackman and Nordbring-Hertz, 1985).

Verticillium chlamydosporium (Kamyschko ex Barron & Onions) W. Gams var. **catenulatum** (Kamyschko ex Onions & Barron) W. Gams **comb. nov.** – Fig. 5.

Diheterospora catenulata Kamyschko, Botan. Mater. 15: 138. 1962, nom. inval. Art. 37.
≡ *Diheterospora catenulata* Kamyschko ex Barron & Onions, Can. J. Bot. 44: 868. 1966.
≡ *Verticillium catenulatum* (Kamyschko ex Barron & Onions) W. Gams, *Cephalosporium*-artige Schimmelpilze, p. 190. 1971.

Colonies as in *V. chlamydosporium* var. *chlamydosporium*. Conidia subglobose to dacryoid, 2-3.5(-4) × 1.7-2.5 μm, the base (and sometimes the tip) slightly apiculate, mostly cohering in chains, partly also in heads. Dictyochlamydospores as in var. *chlamydosporium*, exceptionally also with wart-like escrescences (CBS 250.83A).

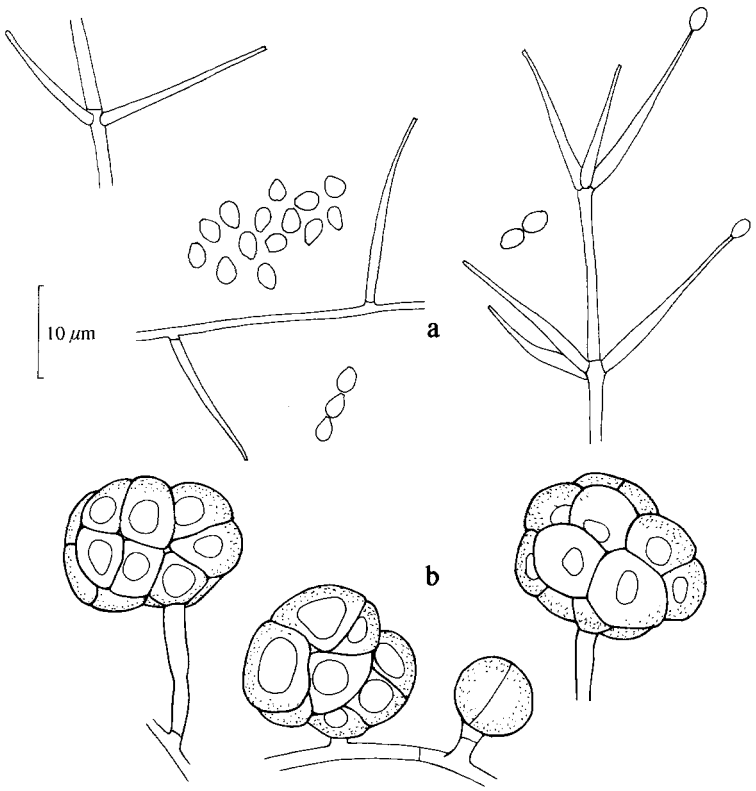

Fig. 5. *Verticillium chlamydosporium* var. *catenulatum*. CBS 551.69, on potato-carrot agar. a) Verticillate and simple conidiophores and conidia, b) dictyochlamydospores.

Material examined:

CBS 504.66 = IMI 113164 = ATCC 16683 = O.A.C. 10250, ex soil in mixed wood, Guelph, Ont., Canada, G.L. Barron. Designated here as **lectotype** of *V. chlamydosporium* var. *catenulatum* selected from among the numerous material cited by Barron and Onions (1966).

CBS 397.69 = O.A.C. 10474, isol. G. L. Barron, ex soil, Ontario, Canada, comm. G. C. Bhatt.

CBS 250.83A, ex egg *Heterodera avenae*, Sweden, C. Dackman.

CBS 250.83B, ex egg *Heterodera avenae*, Denmark, M. Juhl.

CBS 749.83 = CCM-F 04982, ex soil in mixed forest, Slovenskí Raj, Slovakia, comm. L. Marvanová.

Discussion. Compared with the other available morphological criteria considered here, the distinction between conidial chains and heads has limited weight and does not even allow a sharp delimitation between the isolates. Hence the two taxa, *chlamydosporium* and *catenulatum*, are considered only varieties of one species.

The interpretation of *V. catenulatum* by Gams (1971) also included some isolates now classified in *V. suchlasporium* var. *catenatum*. The localization of the dictyochlamydospores is, however, quite different in the two. Here more importance is attributed to the localization of the dictyochlamydospores than to the arrangement of the conidia in chains or in heads.

V. chlamydosporium in both its varieties is the commonest species of this group occurring in general soil fungal analyses. It can be assumed that it is least dependent on nematodes for its development.

The minimum temperature for growth was found to be near 10 °C (Th. Burghouts, unpublished results).

Verticillium coccosporum (Drechsler) W. Gams, **comb. nov.** – Fig. 6a.

≡ *Spicaria coccospora* Drechsler, Phytopathology 31: 787. 1941.
≡ *Paecilomyces coccosporus* (Drechsler) A. H. S. Brown & G. Smith, Trans. Br. mycol. Soc. 40: 74. 1957.

Drechsler (1941) described the fungus as parasitizing *Plectus parvus*, forming globose conidia 1.3-1.7 μm diam, without stating anything about conidial attachment to the nematode or about formation of dictyochlamydospores (in 1942 he even emphasized their absence). Gray and Duff (1982) and Gray (1983c) reported similar fungi with conidia 1.4 μm diam sticking to free-living nematodes.

Unfortunately no living culture fitting these criteria is available at the moment. The fungus obviously does not belong to *Paecilomyces*, as its phialides are too slender and not aggregated in penicillate conidiophores. For specific delineation see below under *V. suchlasporium* var. *catenulatum*.

The following isolates are tentatively assigned to this species, but the conidia are larger, ovoid to subglobose, 3.0-3.5 × 1.8-2.0(-2.5) μm; the colonies are lower and not tough, the conidiophores prostrate, up to 1.5(-2.0) μm wide and not thick-walled. In CBS 691.86 a few exceptional dictyochlamydospores were seen.

Material examined:
CBS 789.85 and CBS 691.86, ex egg masses of *Lymantria dispar* (gipsy moth), G. C. Carroll, Eugene, Oregon (see Carroll, 1987).

Verticillium suchlasporium W. Gams & Dackman, **sp. nov.** var. **suchlasporium** – Figs 7 a and b.

≡ *Verticillium* sp. 1 of Dackman and Nordbring-Hertz (1985).

Coloniae fere celeriter crescentes, lanosae, ad 4 mm elevatae, albidae vel cremeae vel flavae. Conidiophora erecta vel prostrata, ad 200 μm alta et vulgo ter verticillata. Phialides aculeatae, 15-30 × 1.2-2 μm, ad 0.8-1.0 μm angustatae. Conidia capitulis siccis cohaerentia, subglobosa vel dacryoidea, 3-4.5(-6) × (1.5-)2.0-2.5(-3) μm, firmitunicata et nonnumquam modice asperulata. Dictyochlamydosporae vulgo paucae, in agaro submersae, stipitatae, rotundatae, 20-30 μm diam., strato mucido circumdatae, maturae vulgo asperulatae.

Holotypus vivus et exsiccatus CBS 251.83, isolatus ex ovis *Heteroderae avenae* in Suecia, C. Dackman No. 10, 1983.

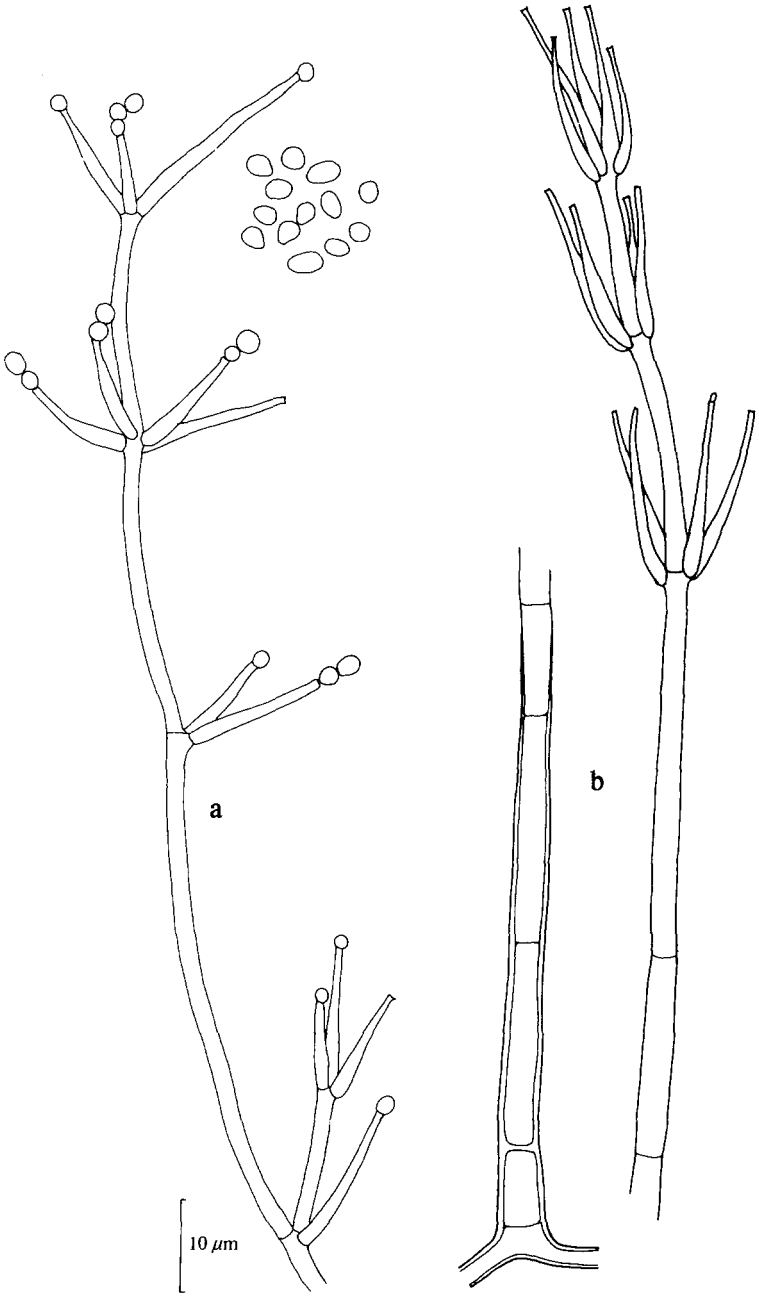

Fig. 6. a) *Verticillium coccosporum*. Conidiophores of CBS 876.85. b) *Verticillium suchlasporium* var. *catenatum*, an erect, strongly verticillate conidiophore of CBS 248.83.

Fig. 7. *Verticillium suchlasporium* var. *suchlasporium*. a) Verticillate conidiophores and conidia. b) Submerged sporulation with elongate conidia. CBS 228.82C (and other isolates).

Colonies on MA and SEA rather fast growing, reaching 23-30 mm diam in 15 days, white to yellow, deeply cottony (3-4 mm); reverse cream-coloured or yellow. Submerged mycelium very tough when grown on MA. Conidiophores mostly erect, but also prostrate, about 200 μm high, at the base moderately thick-walled (0.5 μm) and up to 4-5 μm wide, repeatedly septate and tapering apically to 1.5-2.5 μm, bearing often 3 whorls of 3-4 phialides each. Phialides 15-30 × 1.2-2 μm, tapering apically to 0.8-1.0 μm, sometimes swollen near the base to 2.5 μm. Conidia in dry heads, subglobose to dacryoid, 3-4.5(-6) × (1.5-)2.0-2.5(-3) μm, rather firm-walled, smooth-walled or slightly roughened, the contents but not the wall of mature conidia staining with aniline blue. Submerged in the agar another form of sporulation is sometimes observed, when little differentiated phialides give rise to a few elongate conidia, about 5-12 × 1.5-2 μm (Fig. 7 b). Dictyochlamydospores usually scanty, submerged in the agar, rarely near the surface, size (20-30 μm diam) and shape as in *V. chlamydosporium*, surrounded by a slimy, (meta-)cyanophilic layer, 1-1.5 μm thick that may cause a roughening when it dries up.

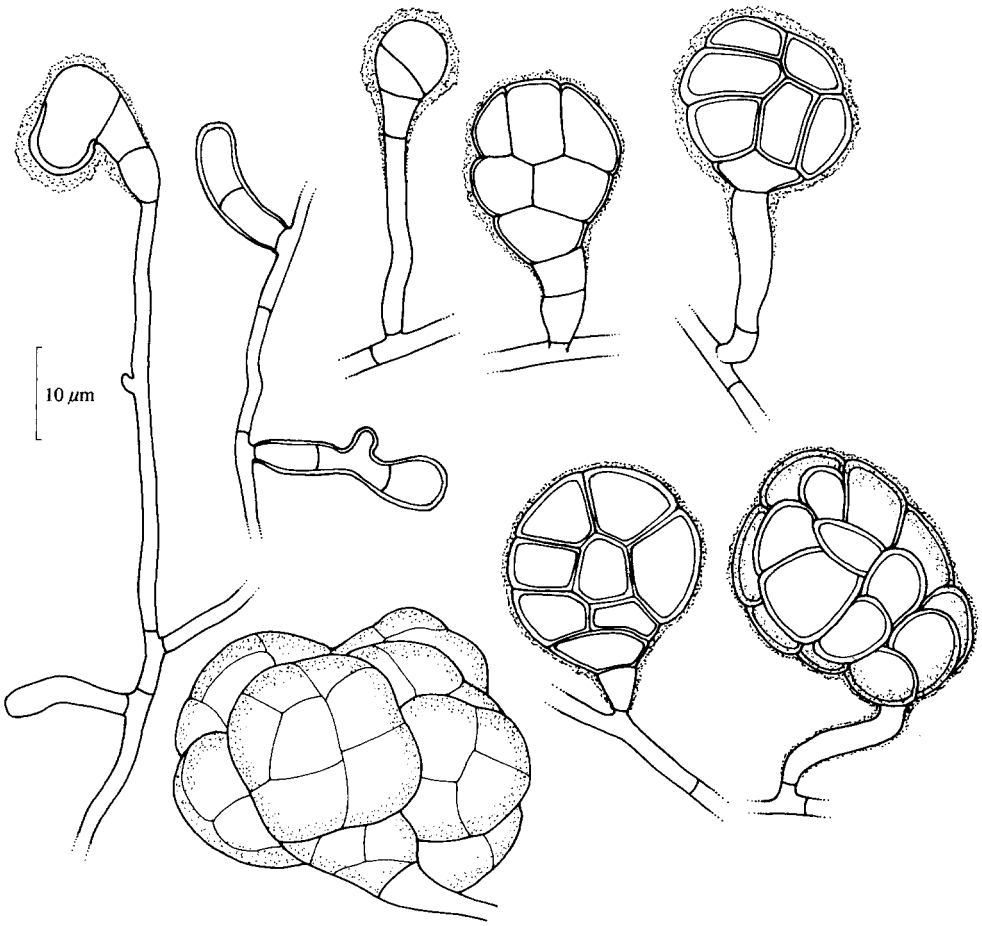

Fig. 7c. *Verticillium suchlasporium* var. *suchlasporium*. Various stages of dictyochlamydospore development. CBS 228.82 B and C.

Vegetative hyphae sometimes swollen and thick-walled, cyanophilic and forming appressorium-like branches.

Material examined:
CBS 352.70, ex *Thuja-Abies* bog, Wisconsin, W. F. Whittingham (3558), 1967.
CBS 405.70, ex agricultural soil, Wageningen, J. W. Veenbaas-Rijks, 1968.
CBS 207.72, ex agricultural soil, Wageningen, J. H. van Emden, 1972.
CBS 184.78A, and 184.78 B, ex sand dune soil, Katwijk a. Z., Netherlands, W. Gams, 1978.
CBS 425.80 A-C ex cysts of *Heterodera schachtii*, comm. G. J. Bollen, 1980.
CBS 432.80 = AP 2323b, ex soil, U.S.A., comm. C. J. K. Wang, Syracuse, New York.
CBS 228.82 A-D, ex eggs of *Heterodera schachtii*, Bergen op Zoom, Netherlands, F. Zoon, 1982.
CBS 251.83, **type isolate**, 813.83 and 814.83, ex eggs of *Heterodera avenae*, Sweden, C. Dackman, 1983.
CBS 815.83 and 816.83, ex eggs of *Heterodera avenae*, Denmark, M. Juhl.
CBS 307.85 and 308.85, ex cysts of *Globodera* sp., Netherlands, J. de Haan.
And many more isolates not preserved.

Discussion. Undoubtedly *V. suchlasporium* belongs to the species with affinity to the Clavicipitales, although the often erect, thick-walled conidiophores conflict with the definition of *Verticillium* sect. *Prostrata*. Only the whitish, lanose colonies point to this affinity, besides the dictyochlamydospores.

In *V. suchlasporium* like in *V. chlamydosporium* two varieties can be distinguished with conidial chains or heads. While the difference in conidial shape may be slightly greater in the two varieties of *V. suchlasporium*, the rare occurrence of submerged roughened dictyochlamydospores, more complex and higher conidiophores and dry, slightly roughened conidia are common features of both varieties. In the strains CBS 352.70, 405.70, 307.85 and 308.85 dictyochlamydospores were never observed.

It was tempting to call the new species *V. 'subchlamydosporium'* because it has fewer and submerged dictyochlamydospores. The name proposed here is just an abbreviation to facilitate pronunciation.

This is the commonest taxon isolated from cysts of *Heterodera*, particularly *H. avenae* in southern Sweden (Dackman and Nordbring-Hertz, 1985) and Denmark (Juhl, 1982, but referred to as *V. chlamydosporium*), but found very rarely in *Globodera* (D. Hugo-Wissemann, unpublished results). According to my experience, it is rather rarely isolated in soil fungal analyses. The species has a strong chitinase activity (Dackman et al., unpublished results).

The temperature minimum for growth is considerably lower than in *V. chlamydosporium*, growth being possible below 6 °C (Th. Burghouts, unpublished results; Dackman and Nordbring-Hertz, 1985). At 20 °C *V. suchlasporium* grows faster than *V. chlamydosporium*, but at 25 °C this relation is reversed, because *V. chlamydosporium* then reaches about 40 mm diam in 15 days and *V. suchlasporium* does not grow faster than at 20 °C.

Addition of *Panagrellus redivivus* to cultures of the fungus did not promote sporulation and only a few worms became moribund in 6 days with CBS 228.82A, and none with 352.70 or 425.80B.

Verticillium suchlasporium var. **catenatum** W. Gams & Dackman, var. nov. – Figs 6b and 8.

= ?*Spicaria simplex* Petch, Naturalist, Lond. 1936: 59.
≡ *Paecilomyces simplex* (Petch) A. H. S. Brown & G. Smith, Trans. Br. mycol. Soc. 40: 76. 1957.

A varietate *suchlasporio* differt conidiis vulgo catenis cohaerentibus.

Holotypus vivus et exsiccatus CBS 248.83, isolatus ex ovis *Heteroderae avenae* in Suecia, C. Dackman No. 17, 1983.

Colonies as in var. *suchlasporium*. Conidiophores commonly erect, sometimes also prostrate, about 200 μm tall, at the base up to 0.7 μm thick-walled, tapering from 4.5 μm to 2-3 μm in the upper part, often bearing 3 whorls of 3-4 phialides. Phialides 10-20 × 1.3-1.7(-2.5) μm, tapering to 0.5-0.8 μm. Conidia dacryoid to ovoid, 2.5-4(-6) × 1.7-2.5(-3) μm, firm-walled, with chromophilic contents, cohering in chains or partly dry heads. Dictyochlamydospores scanty, submerged in the agar.

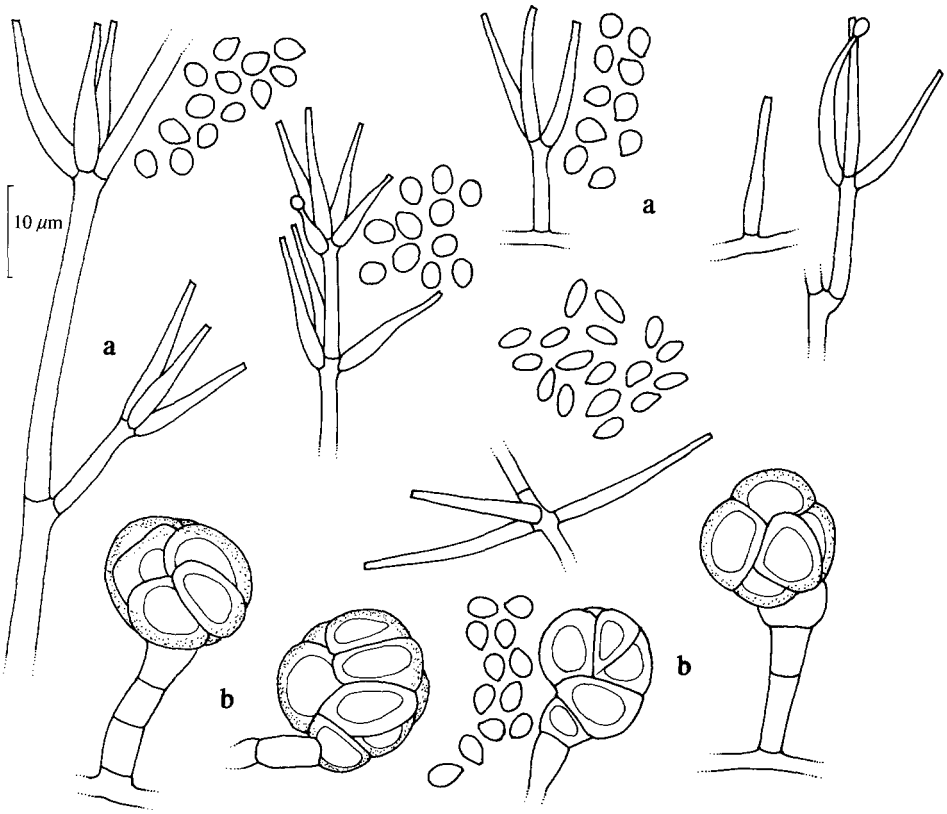

Fig. 8. *Verticillium suchlasporium* var. *catenatum*. a) Verticillate conidiophores and conidia, b) dictyochlamydospores. CBS 248.83 and other isolates.

Material examined:
CBS 756.68, ex agricultural soil, Wageningen, Netherlands, J.W. Veenbaas-Rijks.
CBS 551.69 = G.C.B. 1678, ex forest soil under *Thuja occidentalis*, Puslinch, Ont., Canada, isol. G.C. Bhatt (det. G.L. Barron as *Diheterospora catenulata*).
CBS 383.70A, ex garden soil, Baarn, Netherlands, H.A. van der Aa.
CBS 383.70B, ex agricultural soil, Wageningen, Netherlands, J.W. Veenbaas-Rijks.
CBS 383.70C, ex root of *Picea abies*, Denmark, D.S. Malla.
CBS 248.83 (**type isolate**), ex eggs of *Heterodera avenae*, Sweden, C. Dackman.
CBS 817.83, ex eggs of *Heterodera avenae*, Denmark, M. Juhl.

Discussion. The degree of difference between the two varieties of *V. suchlasporium* is comparable to that in *V. chlamydosporium*. The form with conidial heads is designated as type variety as it is apparently more common than the catenate form.

It is unlikely that *V. suchlasporium* var. *catenatum* is identical with *Spicaria coccospora* Drechsler. Besides the absence of dictyochlamydospores, the most important difference with the original description appears to be the conidial size, 1.3-1.7 µm diam in *V. coccosporum*, 1.7-2.5 µm in the present fungus. Moreover, Gray (1983c) noticed a fungus responding to *V. coccosporum* with such tiny and adhesive conidia, which

would obviously not fit *V. suchlasporium* var. *catenatum*. Therefore it was decided to describe the present fungus as a new taxon.

A similar fungus of uncertain identity is *Spicaria simplex* Petch, described as parasitizing myxomycetes, having conidia 2.5-3.2 × 1.8-2.2 μm (Brown and Smith, 1957). It might fit the present taxon better than *V. chlamydosporium* var. *catenulatum* as suggested by Gams (1971). But collections from myxomycetes have to be examined before taking a decision.

The temperature minimum for growth was found to be near 6 °C (Th. Burghouts, unpublished results; Dackman & Nordbring-Hertz, 1985). On water agar with *Panagrellus redivivus* a few worms were moribund with CBS 756.68 or 248.83 after 6 days.

Verticillium psalliotae Treschow, Dansk bot. Ark. 11(1): 7. 1941.

= *Verticillium epiphytum* Hansford, Proc. Linn. Soc. Lond. 155: 41. 1943.

Description in Gams (1971).

This species commonly occurs on various fungi, but was found only once in a population of cysts of *Globodera rostochiensis* by D. Hugo-Wissemann (unpublished results).

Verticillium lamellicola (F.E.V. Smith) W. Gams, *Cephalosporium*-artige Schimmelpilze, p. 183. 1971.

≡ *Cephalosporium lamellicola* F.E.V. Smith, Trans. Br. mycol. Soc. 10: 93. 1924.
= ?*Oospora pucciniophila* Sydow, Annls mycol. 15: 263. 1917.

Description in Gams (1971).

This species was rarely found as a parasite of *Heterodera glycines* cysts in Alabama (Godoy et al., 1982); it can also parasitize eggs of *Meloidogyne arenaria* and has a high chitinase activity.

Verticillium leptobactrum W. Gams, *Cephalosporium*-artige Schimmelpilze, p. 194. 1971.

Description in Gams (1971).

The species is remarkable because of the predominantly solitary phialides. Thus it is intermediate between *Verticillium* sect. *Prostrata* and *Acremonium* sect. *Albolanosa* Morgan-Jones & W. Gams (1982).

Material examined:
CBS 774.69, **type isolate**, ex decaying wood, Starożyn near Augustów, Poland, W. Gams, 1966.
CBS 523.80, infecting nematode eggs and embryos, Utrecht, comm. M. Muitelaar.
CBS 251.81, ex cysts of *Heterodera glycines*, Alabama, comm. G. Morgan-Jones.
CBS 249.83, ex *Heterodera* sp., H. Deitermann, Bonn.
Many other isolates of this species have become available, mainly isolated from various forest soils.

Discussion. This species is rarely found as a parasite of nematodes. It was reported from cysts of *Heterodera glycines* in Alabama (Morgan-Jones & Rodríguez-Kábana, 1981; Godoy et al., 1982), it can also parasitize eggs of *Meloidogyne arenaria* and has a high chitinase activity.

The temperature minimum for growth was found to be below 10 °C (Th. Burghouts, unpublished results).

Verticillium gonioides (Drechsler) W. Gams & Stalpers **comb. nov.** – Fig. 9.

≡ *Acrostalagmus gonioides* Drechsler, J. Wash. Acad. Sci. 32: 347. 1942.

Colonies reaching 14-16 mm diam in 10 days, white, cottony. Phialides arising mostly in whorls of 2-5 on prostrate hyphae. Phialides 13-30 × 1.5-2(-2.5) μm, tapering distally to 0.5 μm. Conidia isodiametric, 2-2.5 μm diam, with irregularly polyhedric outline, some elongate, with smooth outline, up to 5 × 2.5 μm. Dictyochlamydospores irregular, mostly submerged, formed as lateral branches with swollen cells, wall about 1 μm thick; in addition monilioid intercalary hyphae are commonly present.

Material examined:
CBS 891.72, designated **neotype** of the species, ex *Pulcherricium coeruleum*, Teutoburger Wald, F.R.G., 1972. isol. J.A. Stalpers.
CBS 241.80 = AP-2609, ex forest litter, Adirondack Mts, New York, C.J.K. Wang.

Discussion. No culture of this species isolated from nematodes is available. Drechsler (1941) described the fungus on *Bunonema* sp. without stating anything about conidial adhesion to the nematode. He also mentioned irregular dictyochlamydospores, 12-30 × 6-15 μm, consisting of 8-18 cells; the conidia were given as 1.3-2.1 μm diam. Hence there is little doubt about the identification of the present isolates. Gray (1983a) reported the conidia to adhere to the nematodes.

Tuberculispora jamaicensis Deighton & Pirozynski (1972) might be a related fungus with mostly solitary phialides, a strong tendency to form polyphialides and much more pronounced conidial papillae.

The two isolates studied here have, however, been shown to possess the ability to attack cysts and eggs of *Heterodera* spp. (G. Hänßler, personal communication). Upon adding *Panagrellus redivivus* to a culture of the fungus on water agar, a few nematodes became infected by both available isolates after 8-10 days.

The species was reported as an endoparasite of *Rhabditis terricola* in Ontario soils (Barron, 1978), as occurring on nematodes in peatland in Ireland (Gray, 1983c), and in the maritime Antarctic (Gray and Lewis Smith, 1984).

General discussion

The nematophagous *Verticillium* species can be grouped ecologically into species that become attached to the surface of free-living nematodes whence they penetrate their host, and the species infecting nematode cysts and eggs. Conidial ingestion by nematodes as in *Harposporium*, followed by internal penetration, apparently does not

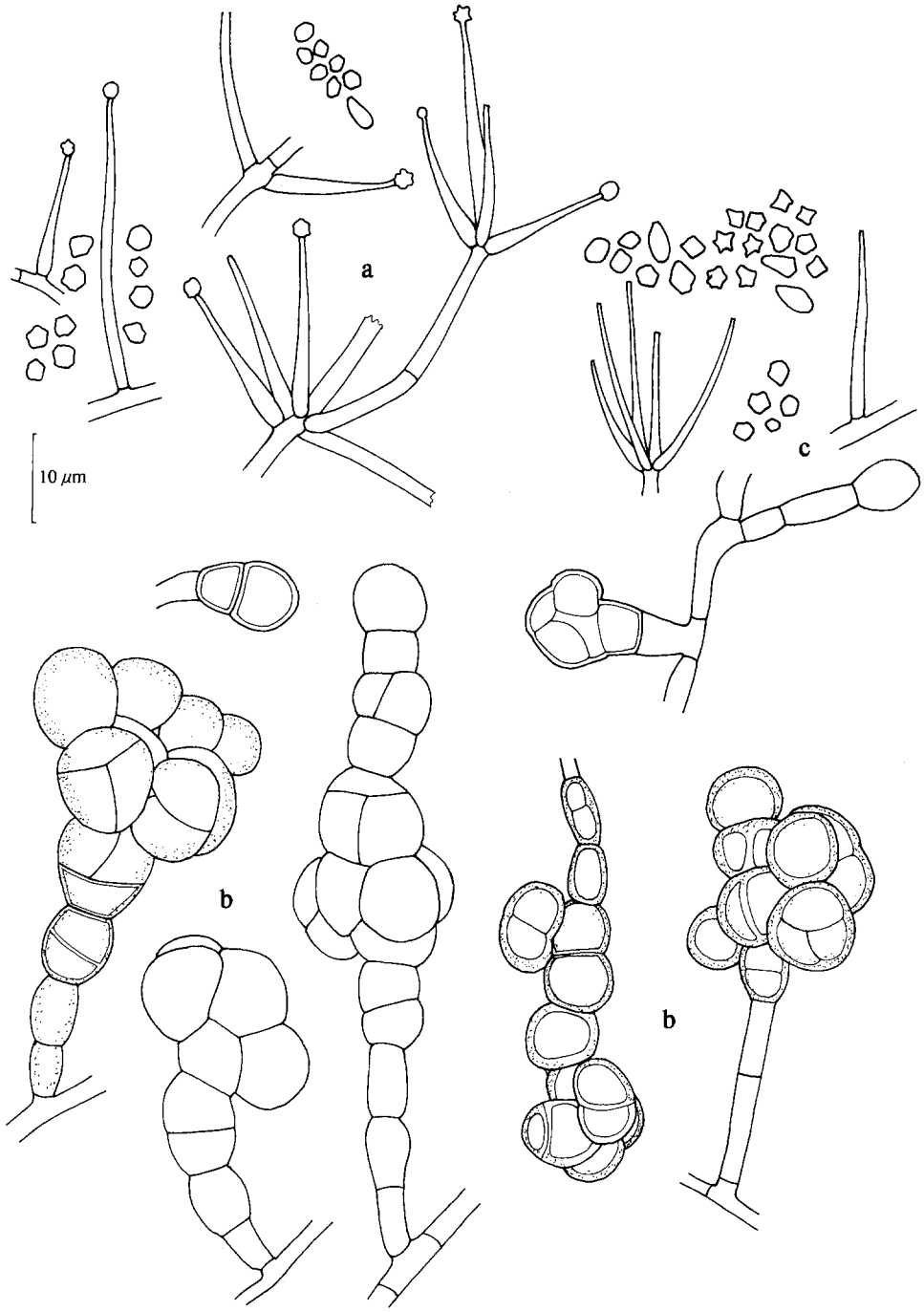

Fig. 9. *Verticillium gonioides*. a) Verticillate and simple conidiophores and conidia, b) various stages of dictyochlamydospore formation in CBS 891.72, c) the same in CBS 241.80.

occur with nematophagous *Verticillium* species. *V. balanoides* (sensu lato) and probably *V. gonioides* and *V. coccosporum* fall into the first group, the remaining taxa belong to the second group.

Among *Verticillium* sect. *Prostrata*, the species mentioned here do not form a homogeneous group, comprising species with many, few or no dictyochlamydospores, with strongly elongate to globose conidia, with abundantly branched or predominantly simple conidiophores. On the other hand, the parasites of rotifers, briefly mentioned above, seem to form a natural group because of their tendency to form sesquiphialides.

It is remarkable that the commonest species of the section *Prostrata*, *V. lecanii* (Zimm.) Viégas, is not found among the nematode parasites and *V. psalliotae* Treschow only exceptionally, while other common, apparently saprophytic species, such as *V. chlamydosporium* and *V. bulbillosum* are more or less potent parasites of nematode eggs. *V. lecanii* was apparently found only once as a parasite of cysts of *Heterodera glycines* in Alabama (Gintis et al., 1983).

Gams (1971) adopted a rather broad species concept in *Verticillium* sect. *Prostrata*. With few exceptions this concept has so far stood the test of time, even for *V. lecanii* (Jackson and Heale, 1985). The classification along similar lines proposed here for the nematophagous species will have to be vindicated by more advanced techniques.

Acknowledgements

I am greatly indebted to Drs A.Y. Rossman and L.R. Batra, U.S. National Fungus Collections, Beltsville, for their efforts to locate Drechsler's material. Several curators of herbaria listed tried to trace material of *Dictyoarthrinopsis costaricensis*. Dr G.L. Barron kindly supplied slides of his species of *Diheterospora*. Mr D. Hooper, Rothamsted Experimental Station, located type material of *V. sphaerosporum* preserved by J.B. Goodey. This study would not have been possible without the help of the numerous contributors mentioned in the text, who supplied cultures and data on the origin. I also thank Drs B. Nordbring-Hertz and M.A.J. Williams and Mr G.J. Bollen for critical reading of the manuscript. Mrs F. Claus-Stibbe inked most of the drawings. Finally I wish to thank my students Theo Burghouts, Amsterdam, and Doris Hugo-Wissemann, Aachen, for supplying some ecological data reported here.

Samenvatting

Een bijdrage tot de kennis van nematofage soorten van Verticillium

Negen nematofage soorten en twee variëteiten van *Verticillium* (*Verticillium* sectie *Prostrata*), die óf als parasieten van vrijlevende aaltjes óf als parasieten van cysten en eieren optreden, worden gereviseerd en er wordt een determinatiesleutel van gepresenteerd. *V. catenulatum* wordt gereduceerd tot een variëteit van *V. chlamydosporium*. Een hierop lijkende schimmel wordt onderscheiden als *V. suchlasporium* n.sp. (incl. een variëteit *catenatum*). *Spicaria coccospora* Drechsler wordt naar *Verticillium* overgebracht. Alle soorten werden in reincultuur onderzocht. Voor iedere soort worden oecologische gegevens vermeld.

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