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A revision of *Verticillium* section *Prostrata*. V. The genus *Pochonia*, with notes on *Rotiferophthora*°)

by

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With 19 figures

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Abstract: A part of the species formerly classified in *Verticillium* sect. *Prostrata* is unrelated to the majority subsumed in *Lecanicillium* on molecular grounds. Most species of this clade have conspicuous dictyochlamydospores (formerly assembled in *Diheterospora*), while others are distinct only by the tendency to form swollen vegetative hyphae, chromophilic, relatively short conidia, and the lack of crystals. The genus *Pochonia* which predates *Diheterospora* is used for this group. The distinctness of *P. chlamydosporia* and *P. suchlasporia*, each with two varieties, is confirmed. A teleomorph, *Cordyceps chlamydosporia*, is newly described for the former. Eight anamorph taxa are keyed out, including two new species, *P. microbactrospora* and *P. rubescens*. Two species of *Rotiferophthora* were available for investigation, and their generic distinctness was confirmed. The parasite of rust fungi *Verticillium epiphytum* and a fungicolous species with conspicuous intercalary chlamydospores, *V. incurvum*, were studied for comparison with *Pochonia*, but are not formally classified. *Verticillium epiphytum* is close to but falls outside *Pochonia*, *V. incurvum* is probably a nectriaceous anamorph. *Verticillium pseudohemipterigenum* with erect conidiophores bearing numerous flask-shaped phialides in dense whorls is also not formally reclassified.

Key words: Hyphomycetes, teleomorph, *Cordyceps*, taxonomy, key, fungicolous, nematophagous, parasites of rotifers.

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°) Part III, Gams & Zare, Nova Hedwigia 72: 329-337, 2001; Part IV, Zare & Gams, Nova Hedwigia 73: 1-50.

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Introduction

The need for a revision of the former *Verticillium* section *Prostrata* Gams (1971) stimulated a series of studies in which morphological and molecular methods were integrated in a reexamination of a large number of strains of diverse origins. Three major clades, B, C and D, were clearly distinguished based on sequences of the internal transcribed spacers (ITS, Zare et al. 2000) and further subdivided according to sequences of the large and small subunits of rDNA (LSU+SSU, Sung et al. 2001).

Based on the type species, the anamorph of *Cordyceps militaris* (L.) Link, section *Prostrata sensu stricto* is *Lecanicillium* (Gams & Zare 2001; Zare & Gams 2001a). This genus represents anamorphs of the *Cordyceps sensu stricto* clade. In contrast, a distinct *C. ophioglossoides* clade comprises a 'group C', which will be treated as *Haptocillium* (Zare & Gams 2001b). A third, heterogeneous group with three subgroups (D 1-3) takes an intermediate position (Sung et al. 2001). The present paper is mainly concerned with group D2, which was not very clearly resolved against its verticillium-like neighbours, D1 = *Verticillium epiphytum* Hansf. and D3 = *V. pseudohemipterigenum* H.C. Evans & Y. Jun. The only species of *Rotiferophthora* examined by Sung et al. (2001) has a sister position to group D3 and is thus clearly distinct. The commonest and most characteristic species of group D2, *V. chlamydosporium*, appeared somewhat remote from the remaining taxa, both according to ITS and LSU+SSU sequences of rDNA, rendering the group possibly paraphyletic. Gams & Zare (2001) classified species of group D2 under the oldest available genus name, *Pochonia* Batista & Fonseca (1965).

Goddard (1913), in the oldest description of the type species, used the generic name *Verticillium.* He was obviously aware of the fact that the phialidic anamorph gives more information about natural affinities of such fungi than the chlamydosporic synanamorph.

Barron & Onions (1966) used the name *Diheterospora* Kamyschko (Kamyschko 1962) for this group, disregarding the fact that the genus was not validly published in 1962. No generic type species was indicated in the original work (Art. 37 of the International Code of Botanical Nomenclature), only Barron & Onions (l.c.) designated it, thus validating the genus. Gams (1971) therefore concluded that *Diheterospora* dated from 1966 and is predated by *Pochonia.* Gams (1971, 1988) did not regard the distinction of this genus from *Verticillium* sect. *Prostrata* as workable, because it was based only on the presence or absence of dictyochlamydospores. The recent molecular studies clearly show the justification of a separate genus. The circumscription of this genus deviates considerably from the previous concept of *Diheterospora* and, therefore, we advocate the change to the simpler and nomenclaturally correct name, *Pochonia*, rather than proposing conservation of the name *Diheterospora* (Gams & Zare 2001). Other generic names used for representatives of this group are inappropriate: *Stemphyliopsis* A.L. Smith was based on an albino mutant of *Stemphylium. Dictyoarthrinopsis* Batista & Cif. was probably based on a fungus with little-differentiated chlamydospore masses, unrelated to the dictyochlamydospores of *Pochonia.*

The species of this genus mainly parasitize cyst nematodes (except *P. microbactrospora*, which was isolated from a rotifer), *P. chlamydosporia* var. *chlamydosporia* and its teleomorph also grow on slug eggs. Most species produce dictyochlamydospores or at least some irregularly swollen vegetative hyphae. However, dictyochlamydospores may be totally absent in some strains, while they occur also in the other discrete genera *Haptocillium* (Gams 1988, Sung et al. 2001, Gams & Zare 2001, Zare & Gams 2001b) and *Rotiferophthora* Barron (Barron 1991).

The term dictyochlamydospore is used by all authors working on these fungi to designate a unique feature with a stalked, hyaline, thick-walled, multicellular resting stage, that can be formed either in large numbers in the aerial mycelium or submerged in the agar. In the latter case, they are more or less scanty and often showing a roughened surface. But the theme of dictyochlamydospores is variable; the shape need not be subglobose or isodiametric with cells slightly bulging out. They can be more irregular in shape and less differentiated, and stalks may be absent. Many species of *Rotiferophthora* have flattened dictyochlamydospores. *Pochonia bulbillosa* has a strong tendency to form intercalary swollen hyphal cells rather than well-differentiated dictyochlamydospores. In some isolates the capacity to form dictyochlamydospores is lost due to degeneration; in some others they have never been seen at all.

Gams (1988) gave a full treatment of four species and two varieties of the genus including ecological observations, which is not repeated *in extenso* here.

Materials and methods

Morphological methods were described by Zare et al. (2000). Media recommended for identification include oatmeal agar (OA) and potato-carrot agar (PCA). Molecular methods used for sequencing were described by Zare et al. (2000) and Sung et al. (2001) and for RFLP by Zare & Gams (2001a). The strains examined are listed after each species treated and the GenBank numbers of new sequences are tabulated in our previous papers.

Taxonomic part

A reconstruction of the phylogeny of the species distinguished here is given in Fig. 1. A systematic representation of RFLP patterns is shown in Table I.

Pochonia Batista & Fonseca, Publ. Inst. Micol. Recife 462: 4, 1965.

= *Diheterospora* Kamyschko [Bot. Mater. Otd. Sporov. Rast. Bot. Inst. Komarova Akad. Nauk S.S.S.R. (Not. syst. Sect. Crypt. Inst. bot. Akad. Sci. USSR) 15: 137. 1962 (nom. inval., Art. 37.1)] ex Barron & Onions, Canad. J. Bot. 44: 861. 1966.

Type species *Pochonia humicola* Batista & Fonseca [= *P. chlamydosporia* (Goddard) Zare & W. Gams].

Teleomorph: *Cordyceps*.

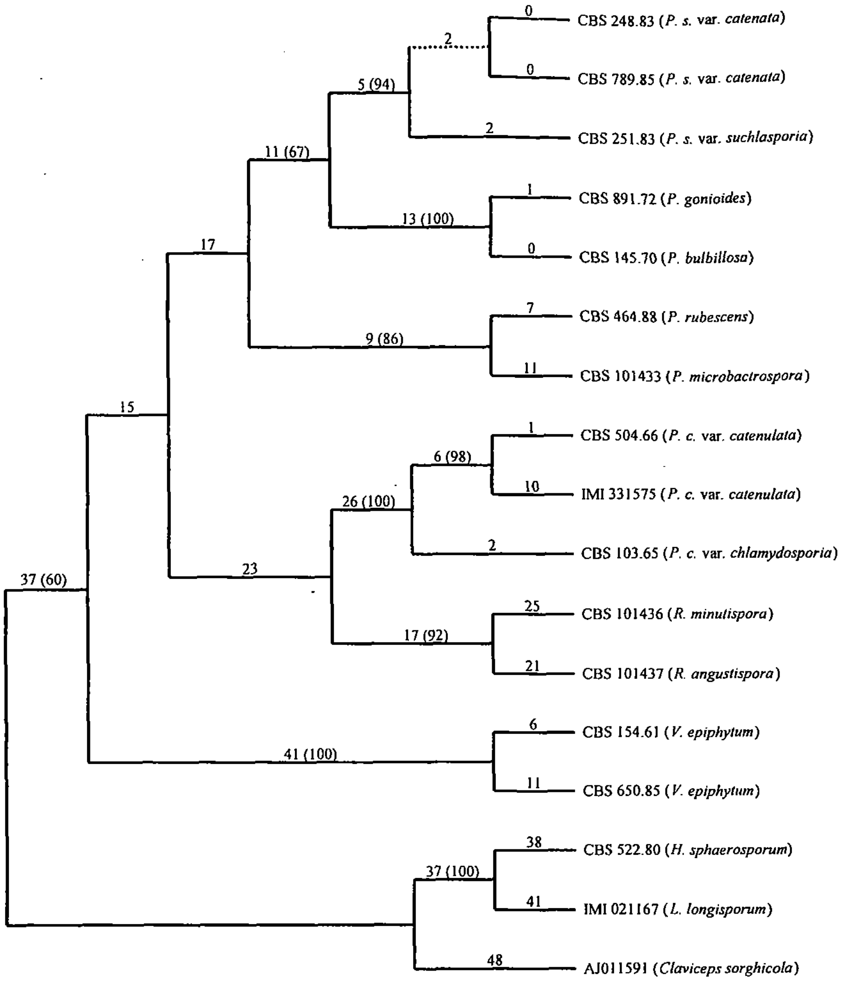

Fig. 1. One of the three equally parsimonious trees recovered using sequences of ITS region and 5.8S gene. Dashed line indicates the branch that collapsed in the strict consensus tree. Plain numbers above lines indicate branch lengths, and numbers in brackets show the Jackknife support values. CI = 0.79, HI = 0.20, RI = 0.72, RC = 0.57, tree length = 483. *L.* = *Lecanicillium*, *P.* = *Pochonia*, *R.* = *Rotiferophthora*, *V.* = *Verticillium*, *H.* = *Haptocillium.*

Colonies rather fast-growing, reaching 15-40 mm diam. in 10 days. Conidiophores usually prostrate and little differentiated from the vegetative hyphae, but sometimes erect and differentiated. Conidiogenous cells phialides, aculeate, i.e. tapering to a narrow tip, in which collarette and periclinal wall thickening are hardly visible, verticillate or solitary. Conidia adhering in globose heads or chains, subglobose, ellipsoidal to rod-shaped, isodiametric-polyhedric, or falcate with blunt ends. Dictyochlamydospores produced on the surface of the colony or submerged in the agar, three-dimensional, pluricellular, thick-walled structures, usually formed on short stalks. Crystals mostly absent.

Species accommodated in *Pochonia* mainly parasitize nematode cysts and all of them produce dictyochlamydospores or at least some irregularly swollen hyphae. The

Table I. RFLP patterns of the ITS region, mtDNA and β-tubulin gene in species of *Pochonia* (*P.*), *Rotiferophthora* (*R.*) and residual species of *Verticillium* (*V.*). Symbols for different patterns in the second column: ITS patterns = Capital letters, mtDNA = Arabic figures, β-tubulin gene = Roman figures.

Taxa and Accession codes	**Pattern**	**RFLPs of ITS region** (fragment size in bp)			**RFLPs of mtDNA** (fragment size in kbp)	**RFLPs of the β-tubulin gene** (fragment size in bp)			
		Msp I	*Hinf* I	*Hae* III	*Hae* III	*Alu* I	*Cfo* I	*Hinf*I	*Hae* III
P. chlamydosporia var. *chlamydosporia*, CBS 103.65, IMI 156157 IMI 359233, IMI 321351	**A, 1, I**	260, 220, 150	270, 220, 90, 50	330, 170, 90, 50	7.4, 5.8, 5.4, 3.2, 3	340, 120, 80	460	360, 180	240, 180, 140
P. c. var. *chlamydosporia*, IMI 331547, CBS 429.64	**A, 2, I′**	260, 220, 150	270, 220, 90, 50	330, 170, 90, 50	7.4, 4.6, 3.7, 3.2, 3, 1.6	340, 120, 80	460	540	240, 180, 140
P. c. var. *chlamydosporia*, CBS 594.66, CBS 600.88	**A, 3, I′**	260, 220, 150	270, 220, 90, 50	330, 170, 90, 50	8, 6.2, 3.9, 3.1, 3.3, 2.2	340, 120, 80	460	540	240, 180, 140
P. c. var. *chlamydosporia*, IMI 113169	**A′, 4, I**	260, 220, 150	270, 220, 90, 50	270, 170, 90, 70	9.2, 6.1 , 5.2, 3.9, 3.2, 3, 2	340, 120, 80	460	360, 180	240, 180, 140
P. cf. *c. chlamydosporia*, CBS 292.95	**A, 5, I″**	260, 220, 150	270, 220, 90, 50	330, 170, 90, 50	7.6, 6.2, 4.3, 2.8, 1.7	340, 120, 80	320, 160	540	360, 180
P. c. var. *catenulata*, IMI 080556	**A, 6, I″**	260, 220, 150	270, 180, 90, 50	330, 170, 90, 50	5.2, 5, 4, 3.5, 2.8, 2.4, 2.2, 1.6	340, 120, 80	320, 160	540	360, 180
P. c. var. *catenulata*, CBS 504.66	**A, 7, I″**	260, 220, 150	270, 180, 90, 50	330, 170, 90, 50	6.5, 4.5, 3.9, 3, 2.4, 1.6	340, 120, 80	320, 160	540	360, 180
P. c. var. *catenulata*, CBS 397.69, IMI 076422	**A, 8, I′**	260, 220, 150	270, 220, 90, 50	330, 170, 90, 50	7.4, 4.6, 3.7, 3.2, 3, 1.6	340, 120, 80	460	540	240, 180, 140
P. c. var. *catenulata*, IMI 113172	**A, 9, I**	260, 220, 150	270, 220, 90, 50	330, 170, 90, 50	7.2, 5.8, 5.4, 3, 3	340, 120, 80	460	360, 180	240, 180, 140
P. c. var. *catenulata*, (*Cordyceps* sp.) IMI 338017, IMI 331575	**A, 10, I″**	260, 220, 150	270, 220, 90, 50	330, 170, 90, 50	7.4, 4.3, 3.7, 3.4, 3, 2.5, 1.6	340, 120, 80	320, 160	540	360, 180
P. c. var. *catenulata*. IMI 080555, CBS 496.96	**A, 11, I**	260, 220, 150	270, 220, 90, 50	330, 170, 90, 50	8.4, 7.4, 3, 2.4, 1.6	340, 120, 80	460	540	240, 180, 140
P. suchlasporia var. *suchlasporia*, CBS 251.83	**B, 12, II**	260, 190, 150	320, 240, 90	300, 150, 90, 50	9.2, 7, 5, 4.6, 3.8, 2.8	340, 120, 80	280, 200	320, 220	240, 180, 140
P. s. var. *suchlasporia*, CBS 816.83	**B, 13, II**	260, 190, 150	320, 240, 90	300, 150, 90, 50	8, 6, 4.4, 4, 3.4, 2.8	340, 120, 80	280, 200	320, 220	240, 180, 140
P. s. var. *catenata*, IMI 113078	**B, 14, II**	260, 190, 150	320, 240, 90	300, 150, 90, 50	7, 6, 4.3, 2.8	340, 120, 80	280, 200	320, 220	240, 180, 140
P. s. var. *catenata*, CBS 383.70a, CBS 416.95	**B, 15, II**	260, 190, 150	320, 240, 90	300, 150, 90, 50	8.8, 7, 4.6, 2.8	340, 120, 80	280, 200	320, 220	240, 180, 140
P. s. var. *catenata*, CBS 789.85, CBS 495.90	**B, 16, II**	260, 190, 150	320, 240, 90	300, 150, 90, 50	8, 6.5, 4.4, 2.8	340, 120, 80	280, 200	320, 220	240, 180, 140

Taxa and Accession codes	Pattern	RFLPs of ITS region (fragment size in bp)			RFLPs of mtDNA (fragment size in kbp)	RFLPs of the β-tubulin gene (fragment size in bp)			
		Msp I	*Hinf* I	*Hae* III	*Hae* III	*Alu* I	*Cfo* I	*Hinf* I	*Hae* III
P. suchlasperia var. *catenata*, CBS 248.83, CBS 817.83	**B, 17, II**	260, 190, 150	320, 240, 90	300, 150, 90, 50	9, 6.2, 4.4, 3.4, 2.8	340, 120, 80	280, 200	320, 220	240, 180, 140
P. rubescens, CBS 425.80a, CBS 352.70	**C, 23, II**	260, 220, 150	300, 160, 90, 80	330, 150, 90, 50	9, 7, 5.7, 4.6, 2.8, 2.6	340, 120, 80	280, 200	320, 220	240, 180, 140
P. rubescens, CBS 464.88	**C, 24, II**	260, 220, 150	300, 160, 90, 80	330, 150, 90, 50	9, 7, 5, 4.6, 2.8	340, 120, 80	280, 200	320, 220	240, 180, 140
P. rubescens, CBS 405.70	**C, 25, II**	260, 220, 150	300, 160, 90, 80	330, 150, 90, 50	8, 7, 4.6, 2.8	340, 120, 80	280, 200	320, 220	240, 180, 140
P. rubescens, IMI 293909	**C, 26, II**	260, 220, 150	300, 160, 90, 80	330, 150, 90, 50	12.5, 7, 4.6, 4.2, 2.8, 2.6	340, 120, 80	280, 200	320, 220	240, 180, 140
P. gonioides, CBS 891.72	**D, 18, III**	260, 190, 150	320, 240, 90	280, 150, 90, 80	7.5, 4.3, 4.1, 4, 3.8, 2.6, 1.5	340, 120, 80	280, 200	540	240, 180, 140
P. gonioides, CBS 611.89	**D, 19, III**	260, 190, 150	320, 240, 90	280, 150, 90, 80	10.5, 7.5, 6, 5.5, 4.1, 4, 2.6	340, 120, 80	280, 200	540	240, 180, 140
P. bulbillosa, CBS 145.70, CBS 578.78, CBS 426.81	**D, 20, III**	260, 190, 150	320, 240, 90	280, 150, 90, 80	8, 6.5, 4.2, 2.8	340, 120, 80	280, 200	540	240, 180, 140
P. bulbillosa, CBS 247.68	**D′, 21, II**	260, 190, 150	320, 240, 90	370, 150, 90	7.1, 6.3, 5, 4.4, 2.85, 1.5, 1.4	340, 120, 80	280, 200	320, 220	240, 180, 140
P. microbactrospora, CBS 101433	**E, 22, -**	240, 200, 150	310, 150, 80, 70	340, 150, 100	7.5, 4, 3.2, 3, 2.7, 1.8				
R. angustispora, CBS 101437	**F, 27, IV**	270, 230, 150, 60	280, 270, 90, 60	270, 150, 120, 90	9.5, 8.2, 6.4, 6, 1.8	500	280, 200	380, 120	
R. minutispora, CBS 101436	**G, 28, V**	250, 200, 150, 50	260, 250, 90, 60	270, 150, 90, 60	8.2, 7, 4.5, 4.2, 4.1, 3.9, 2.6, 2.5, 1.5, 1.4	540	280, 200	540	240, 160, 140
V. incurvum, CBS 460.88	**H, 29, -**	270, 190, 140	290, 220, 90	430, 90, 80	4.3, 4.1, 3.9, 2.5, 2.7, 1.4, 1.2	540			
V. epiphytum, CBS 384.81	**I, 30, VI**	480, 150	250, 250, 90, 50	550, 90	8.5, 4.8, 4.2, 3.5, 2.4	420, 120	300, 200	350, 190	360, 180
V. epiphytum, CBS 154.61, IMI 346243, IMI 286186	**I, 31, VII**	480, 150	250, 250, 90, 50	550, 90	8, 6.2, 4.2, 2.9, 2.6, 2.6	420, 120	300, 200	540	400, 140
V. epiphytum, CBS 650.85	**I, 32, VII**	480, 150	250, 250, 90, 50	550, 90	8, 7, 4.4, 2.6	420, 120	300, 200	540	400, 140
V. epiphytum, IMI 338015	**I, 33, VII**	480, 150	250, 250, 90, 50	550, 90	8.6, 5, 4.4, 4.2, 3.6, 3.4	420, 120	300, 200	540	400, 140

species can be rather easily distinguished from each other on the basis of conidial shape and the position and abundance of dictyochlamydospores. The relative affinity of the taxa distinguished by Gams (1988) is confirmed here by molecular studies.

Key to the species of *Pochonia*

1. At least part of the conidia crescent-shaped or falcate .... 7. *P. bulbillosa*
[If chlamydospores 1-celled and moderately thick-walled, parasites of epiphyllous fungi in the tropics, see *V. epiphytum* at the end of this paper]
1'. Conidia not crescent-shaped or falcate 2

2. Conidia isodiametric-polyhedric; dictyochlamydospores present, usually on the agar surface .... 6. *P. gonioides*
2'. Conidia rod-shaped, smooth, with truncate ends, 2.0-2.5 × 0.8-1.0 µm; dictyochlamydospores sparse, submerged in the agar .... 8. *P. microbactrospora*
2''. Conidia of other shapes, oval, subglobose to subcylindrical, smooth; dictyochlamydospores above, on, or in the agar 3

3. Dictyochlamydospores, at least in fresh isolates, abundant, particularly in the aerial mycelium; conidiophores typically prostrate 4
3'. Dictyochlamydospores, if present, mostly submerged in the agar; conidiophores prostrate or erect 5

4. Conidia only in heads, never in chains .... 1. *P. chlamydosporia* var. *chlamydosporia*
4'. Conidia mostly in chains; some heads may be present .... 2. *P. chlamydosporia* var. *catenulata*

5. Colony reverse developing red shades on PDA; conidiophores prostrate, verticillate; dictyochlamydospores scanty or absent .... 5. *P. rubescens*
5'. Colony reverse yellow to cream (not red) on PDA; conidiophores partly erect, richly verticillate; dictyochlamydospores partly submerged in the agar 6

6. Conidia only in heads, never in chains .... 3. *P. suchlasporia* var. *suchlasporia*
6'. Conidia mostly in chains, some heads may be present .... 4. *P. suchlasporia* var. *catenata*

1. **Pochonia chlamydosporia** (Goddard) Zare & W. Gams, Nova Hedwigia 72: 52, 2001) var. **chlamydosporia** Figs 3-5, 6a, b

≡ *Verticillium chlamydosporium* Goddard, Bot. Gazette 56: 275, 1913 (basionym).

≡ *Diheterospora chlamydosporia* (Goddard) Barron & Onions, Canad. J. Bot. 44: 866, 1966.

= *Stemphyliopsis ovorum* Petch, Trans. Brit. Mycol. Soc. 23: 146, 1939.

= *Diheterospora heterospora* Kamyschko, Bot. Mater. Otd. Sporov. Rast. Bot. Inst. Komarova Akad. Nauk S.S.S.R. (Not. Syst. Sect. Crypt. Inst. Bot. Acad. Sci. USSR) 15: 138, 1962 (generic nom. inval., Art. 37.1).

= *Pochonia humicola* Batista & Fonseca, Publ. Inst. Micol. Recife 462: 5, 1965.

= *Dictyoarthrinopsis kelleyi* Dominik & Majchrowicz, Mycopathol. Mycol. Appl. 28: 210, 1966.

Teleomorph: *Cordyceps chlamydosporia* H.C. Evans (see below)

Colonies reaching 20-38 mm diam. in 10 days, white, later becoming cream-coloured, appearing powdery with age due to the production of dictyochlamydospores; in fresh isolates appearing finely granular due to abundant dictyochlamydospores produced on the surface of the colony; reverse cream-coloured, pale yellow to orange. Conidiophores prostrate aerial hyphae, producing solitary phialides or 2-3 phialides per node along the conidiophore or terminal whorls of 4-5 phialides. Phialides slender subulate, 12-26 × 1.0-1.5 µm. Conidia formed in globose heads, subglobose to ovoid or ellipsoidal, smooth-walled, (1.8-)2.5-4.5 × (1.0-)1.2-2.2 µm. Dictyochlamydospores produced in the aerial mycelium, stalked, measuring (10.5-)15-25 (-30) × 14-25 µm, becoming thick-walled with age. Young dictyochlamydospores staining blue when mounted in lactic acid-cotton blue, later often turning reddish or remaining unstained. Crystals absent. Temperature optimum: 24-27(-30)°C (23-40 mm diam., depending on the strain). No growth at 33°C. Gams (1988) reported a minimum temperature for growth of both varieties near 10°C.

STRAINS EXAMINED:

CBS 429.64 = MUCL 9880, ex soil, Brazil, 1964, Oliveira da Silva, ex-type of *P. humicola*.

CBS 103.65 = ATCC 16289, ex soil under *Brassica napus* (rape seed), Germany, 1965, W.Gams, **ex-neotype** (designated by Gams 1988).

IMI 113169, ex soil, Canada, 1965, J.W. Carmichael.

CBS 594.66, ex soil, Africa, T. Dominik & I. Majchrowicz, ex-type of *Dictyoarthrinopsis kelleyi*.

IMI 156157, ex root of *Piper betle*, India, 1971, P.D. Wangikar.

CBS 600.88, ex *Heterodera avenae*, Sweden, 1982, C. Dackman.

IMI 321351, ex cyst nematode on *Solanum tuberosum*, 1988, D.H. Crump.

IMI 359233, ex gall of *Meloidogyne*, Chile, 1993, B.A. Latorne.

CBS 292.95, ex soil under *Araucaria*, São Paulo, Brazil, 1995, L. Pfenning, deviating by absence of dictyochlamydospores.

Gams (1988) subsumed the former species *Verticillium catenulatum* (Kamyschko ex Barron & Onions) W. Gams as a variety of this species, creating var. *chlamydosporium* for the type variety. The varietal ranking of similar taxa differing only in conidial arrangement seems to be supported by our molecular observations (Fig. 1). RFLP patterns of the ITS region were identical, those of mtDNA were variable and those of the β-tubulin gene were less variable; but these variations were not correlated with the varieties distinguished.

Strain CBS 292.95, though it failed to produce any dictyochlamydospores, had identical ITS and almost identical β-tubulin RFLP patterns to the rest of the strains placed under this taxon.

Some authors considered *V. chlamydosporium* to be a complex showing continuous variation in morphology and physiology (Irving & Kerry 1986; Kerry et al. 1986), but with the segregation of *V. suchlasporium* by Gams (1988) the species was rendered more homogeneous. Arora et al. (1996) found some variation in RFLP patterns generated with ITS and IGS amplicons and in ERIC RAPD patterns among 28 isolates identified as *V. chlamydosporium*. Unfortunately, except that of *P. rubescens* (# 88), no ex-type strains or other comparable isolates of the taxa presented here were included in that study.

The varieties of *Pochonia suchlasporia* are distinguished by their taller, mainly erect and more densely verticillate conidiophores and scanty dictyochlamydospores which are mostly buried in the agar.

Biochemical and molecular studies by Carder et al. (1993) did not confirm the distinction between *P. suchlasporia* and *P. chlamydosporia* and their varieties. These authors partly examined the same strains as those used in this study. Our results do not support their conclusions but rather confirm the classification proposed by Gams (1988).

Teleomorph: **Cordyceps chlamydosporia** H.C. Evans, sp. nov. Figs 2, 4, 5

Mycelium albidum vel dilute flavum hospitem dense obtegens. Stromata singula simplicia, albida vel pallide aurantiaca, anguste cylindrica, 12-16 × 0.5-1.25 mm, sursum expansa. Pars fertilis terminalis, 2.0-3.5 mm longa, albida vel dilute aurantiaca. Perithecia gregaria, erumpentia, superficialia, laevia, dilute flava interdum aurantiascentia vel brunnescentia, late lageniformia, (500-)600-650 × 250-300 µm; ostiola prominentia, collis longis, 150-200 × 80-120 µm, periphysibus repletis. Asci 8-spori, cylindrici, (160-)200-550 × (2-)3-4(-4.5) µm, galero inspissato terminati. Ascosporae hyalinae, filiformes, irregulariter fasciculatae, indistincte septatae, haud secedentes in cellulas, 150-350 × 1.0 µm.

Holotypus IMI 380125, ad ova mollusci, in sylva Pichilingue lectus, Provincia Los Ríos, in Aequatoria, Apr. 1974, H.C. Evans (herb. IMI).

Mycelium white to pale yellow, densely covering the egg mass. Stromata single, unbranched, white to pale orange, narrow cylindrical, 12-16 × 0.5-1.25 mm, widening towards the tip. Fertile area terminal, 2.0-3.5 mm in length, white to pale orange. Perithecia crowded, initially immersed in the mycelium, becoming erumpent and superficial; smooth, pale yellow, occasionally brownish orange, broadly flask-shaped, (500-)600-650 × 250-300 µm, with a prominent ostiole and a long neck region, 150-200 × 80-120 µm, lined with periphyses. Asci 8-spored, cylindrical, (160-)200-500 × (2-)3-4(-4.5) µm, with a prominent cap. Ascospores hyaline, filiform, two fascicles of four somewhat distended in the ascus, septa indistinct, not fragmenting into part-spores, 150-350 × 1.0 µm.

Holotype IMI 380125, on mollusc eggs in forest litter, Pichilingue, Los Ríos Province, Ecuador, Apr. 1974, H.C. Evans (herb. IMI).

MATERIAL EXAMINED (paratypes):

IMI 380126, on mollusc eggs in forest soil, Pichilingue, Los Ríos Province, Ecuador, May 1974, H.C. Evans.

IMI 380127 (380128), on mollusc eggs in forest log, Guamá, Pará State, Brazil, Sep. 1977 (Jan. 1980), H.C. Evans.

IMI 380129, on mollusc eggs in forest soil, Ouro Preto do Oeste, Rondonia State, Brazil, May 1985, H.C. Evans (culture deposited as IMI 331547 = CBS 101244).

IMI 380130, on mollusc eggs in forest soil, Rio Napo, Napo Province, Ecuador, July 1987, T. Læssøe.

The type specimen comprises three egg clutches, up to 7.0 × 4.5 mm, two bearing *Cordyceps* stromata and the other producing five branched synnemata, 14-18 × 0.5-0.8 mm, white to pale tan, compact at the base, becoming broader towards the tip due to a loose mass of aerial hyphae bearing phialides and pale yellow dictyochlamydospores, imparting a yellow powdery appearance to the synnemata. The holotype, with abundant dictyochlamydospores, not only on the egg masses but also on well-defined synnemata, provided circumstantial evidence of the teleomorph-

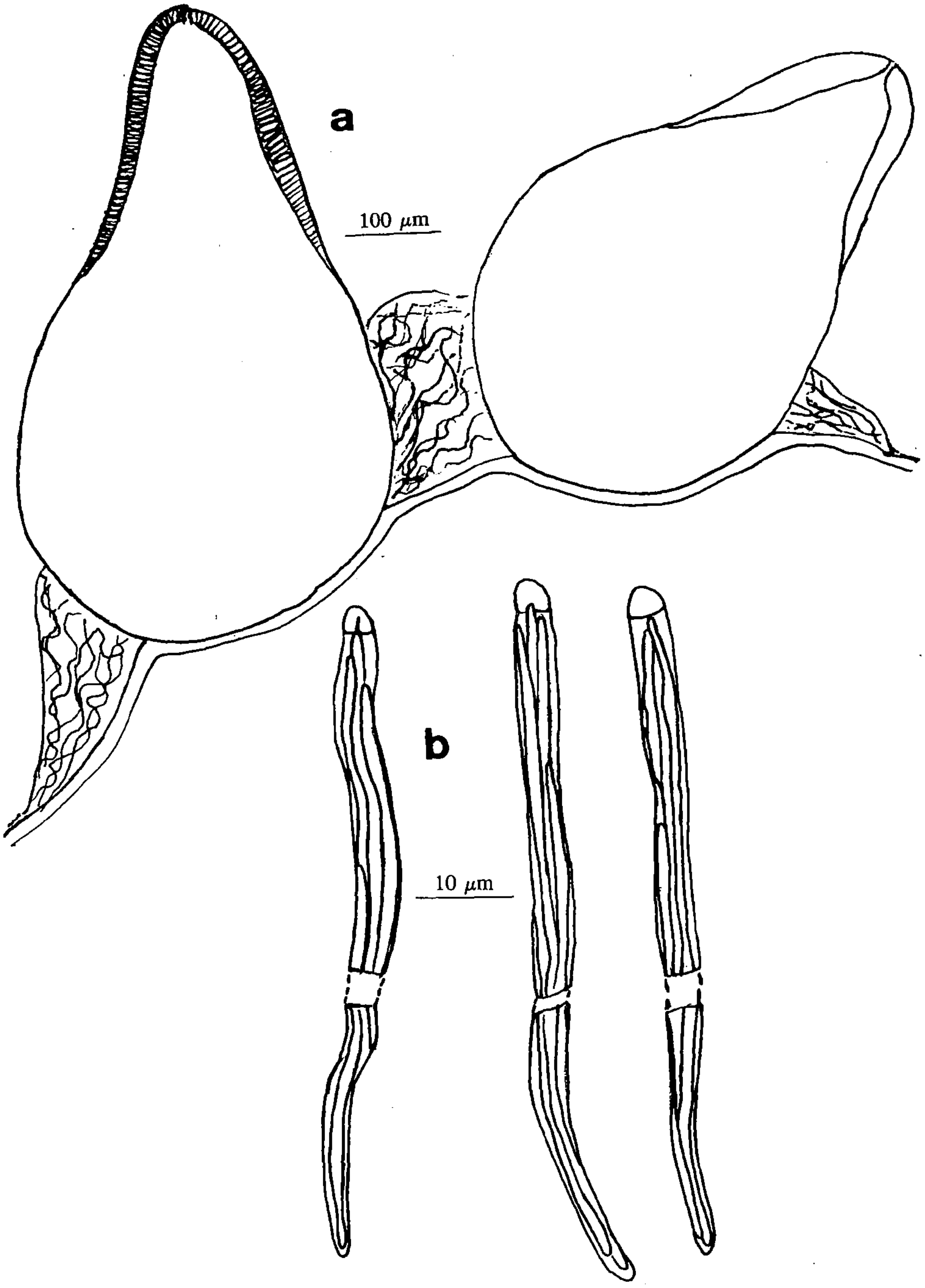

Fig. 2. *Cordyceps chlamydosporia*, holotype IMI 380125. a. Perithecia on stroma; b. Asci and ascospores.

anamorph connection. However, it was not until typical cultures were obtained from the ascospores of a specimen from Brazil (IMI 331547 = CBS 101244) that the association was confirmed.

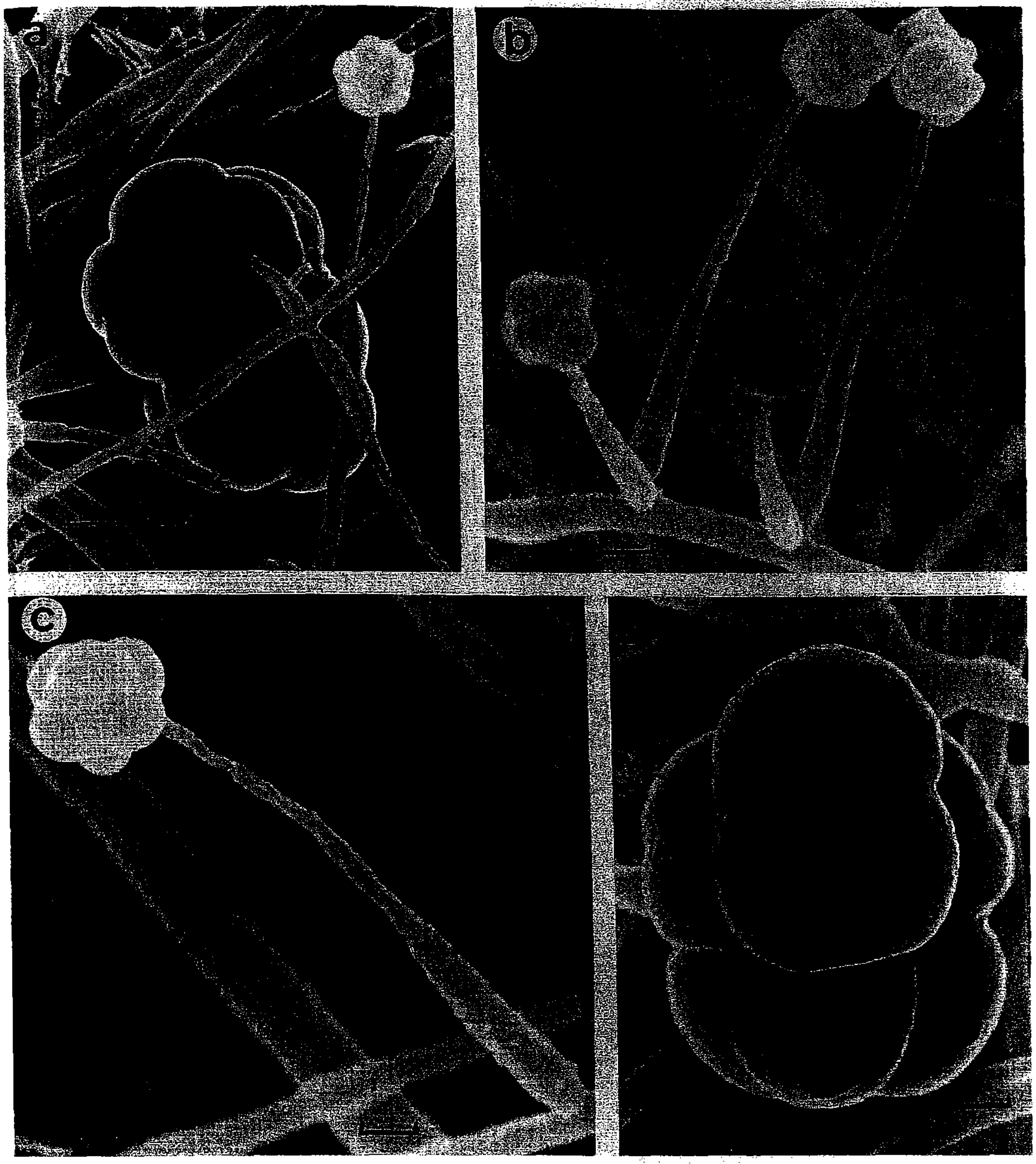

Fig. 3. *Pochonia chlamydosporia* var. *chlamydosporia*, IMI 331547, SEM of spore structures, 10 days on PCA. a. Phialides and dictyochlamydospore, bar = 3 µm; b. Phialides and conidial heads, bar = 2 µm; c. Details of solitary phialide and conidial head, bar = 1.5 µm; d, Dictyochlamdospore, bar = 2 µm.

The perithecia of *C. chlamydosporia* are buried initially but become semi-erumpent and later superficial as they mature, possibly due to the transition from the anamorph (synnemata) to the teleomorph (stromata). The latter in IMI 380127 and 380130 are well developed, with little evidence of the anamorph remaining, and up to 4 cm in length. The holotype and several paratypes possess perithecia with a

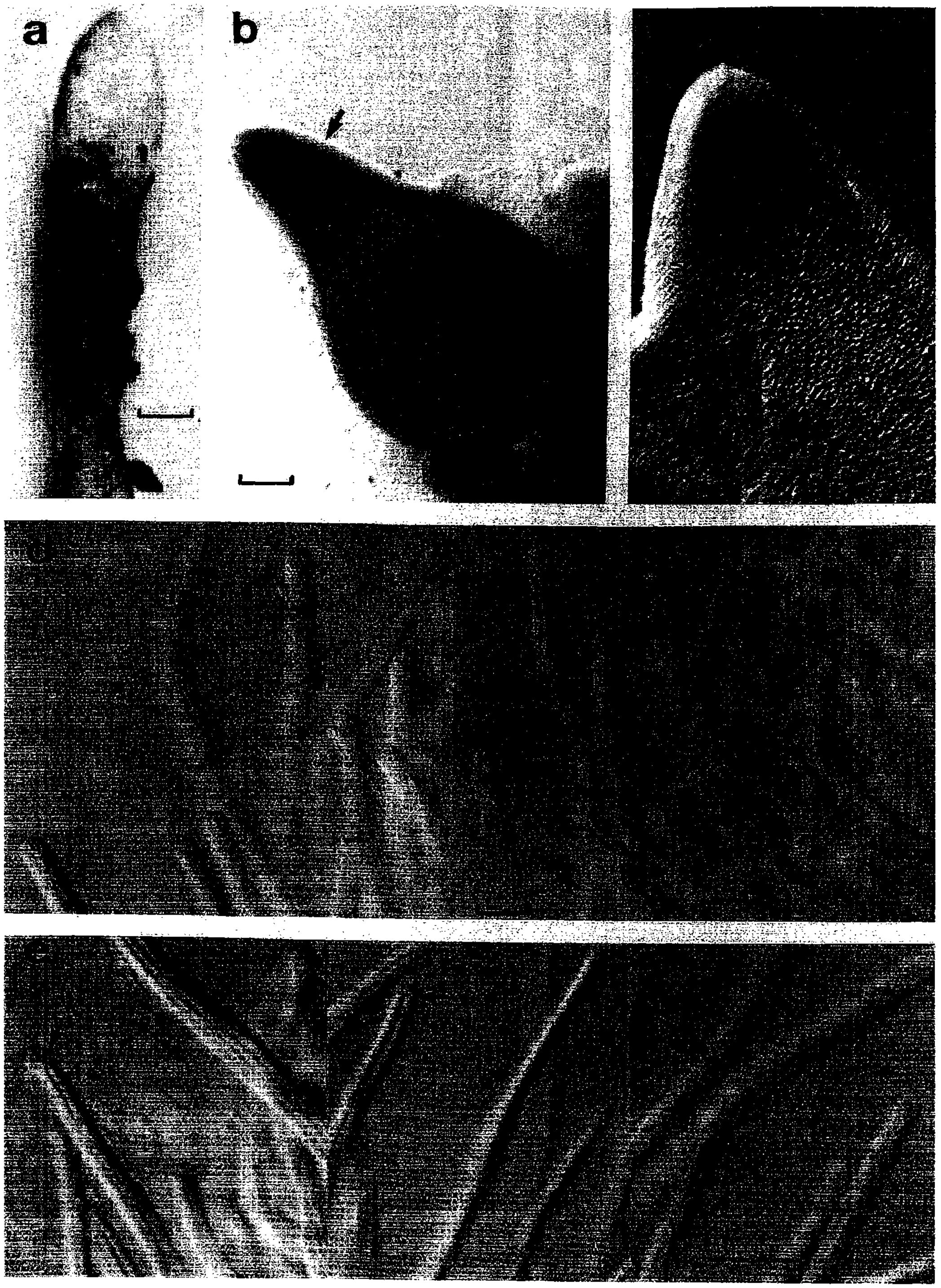

Fig. 4. *Cordyceps chlamydosporia*, holotype IMI 380125. a. Apical region of stroma with mature, erumpent perithecia, bar = 1 mm; b. Perithecium superficially embedded in stromatal tissue, showing palisade of cylindrical cells in neck region (arrow), bar = 60 µm; c. Perithecial neck, showing palisade layer (short arrow) and asci emerging from ostiole (long arrow), bar = 120 µm; d. Immature asci with prominent caps; e. Mature asci showing ascospores pushing into the cap region (arrow), bar = 7 µm for d and e.

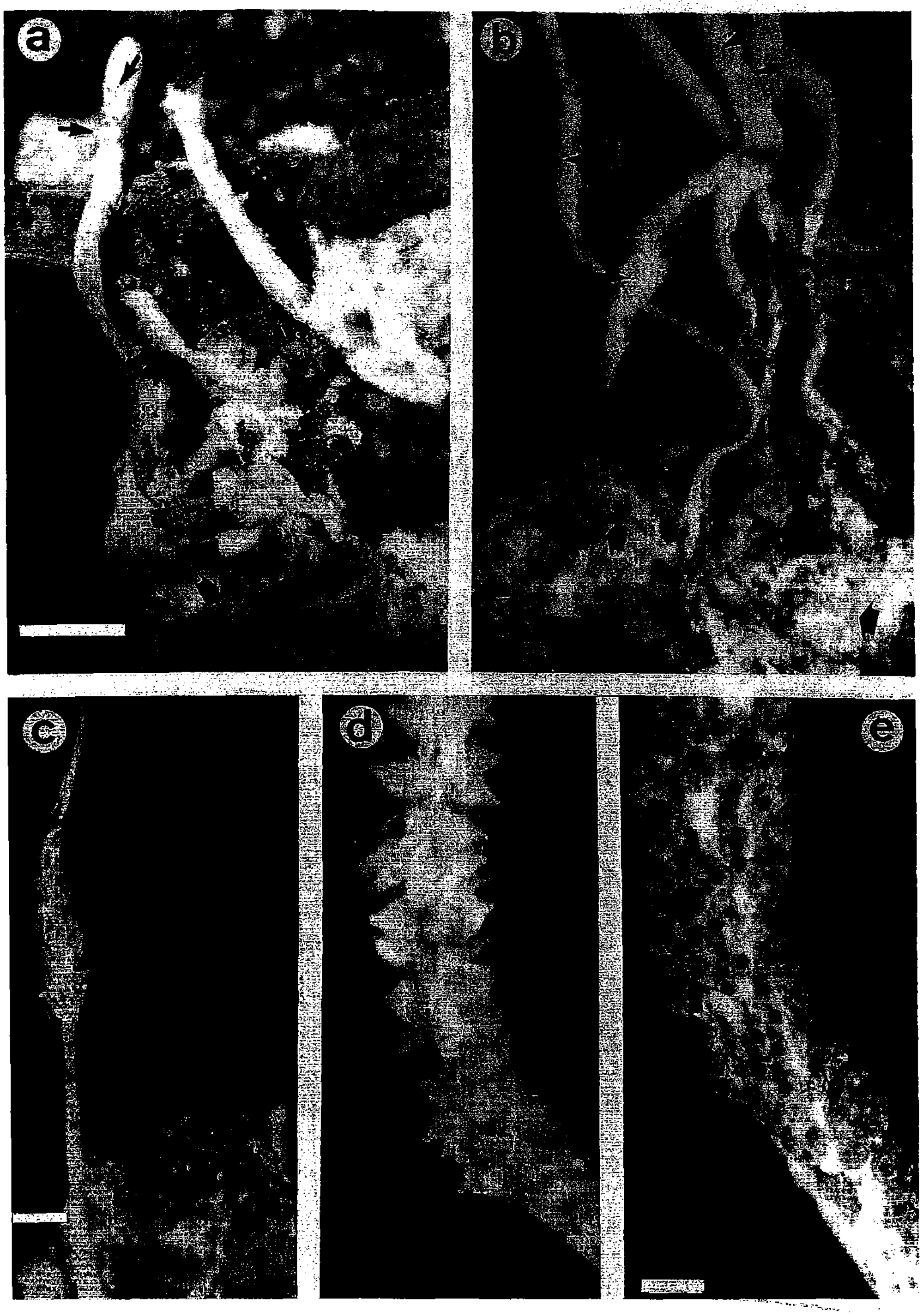

Fig. 5. *Cordyceps chlamydosporia*, macromorphology. a. Holotype, IMI 380125 *in situ*, showing young stroma with semi-erumpent perithecia (small arrows), arising from mollusc egg sac (large arrow), bar = 3 mm for a and b; b. Holotype *in situ*, showing synnemata arising from two mollusc egg sacs (large arrows), the upper region is surrounded by a loose mycelial covering producing phialides and powdery dictychamydospores (small arrows); c. Upper region of mature stroma with pale (yellow) perithecia, bar = 1.5 mm; d. IMI 380127, showing erumpent, pale (yellow) perithecia on mature stroma; e. IMI 380126, showing dark (reddish brown) perithecia on old stroma, bar = 0.5 mm for d and e.

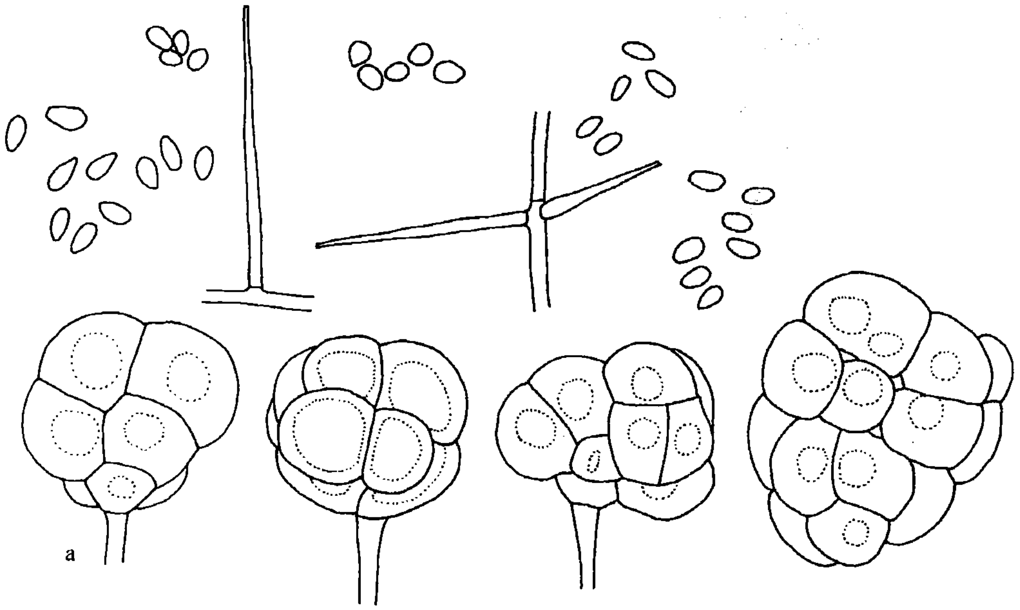

Fig. 6 a. *Pochonia chlamydosporia* var. *chlamydosporia*. a. Phialides and conidia of various strains, b. dictyochlamydospores of CBS 361.64 on PCA.

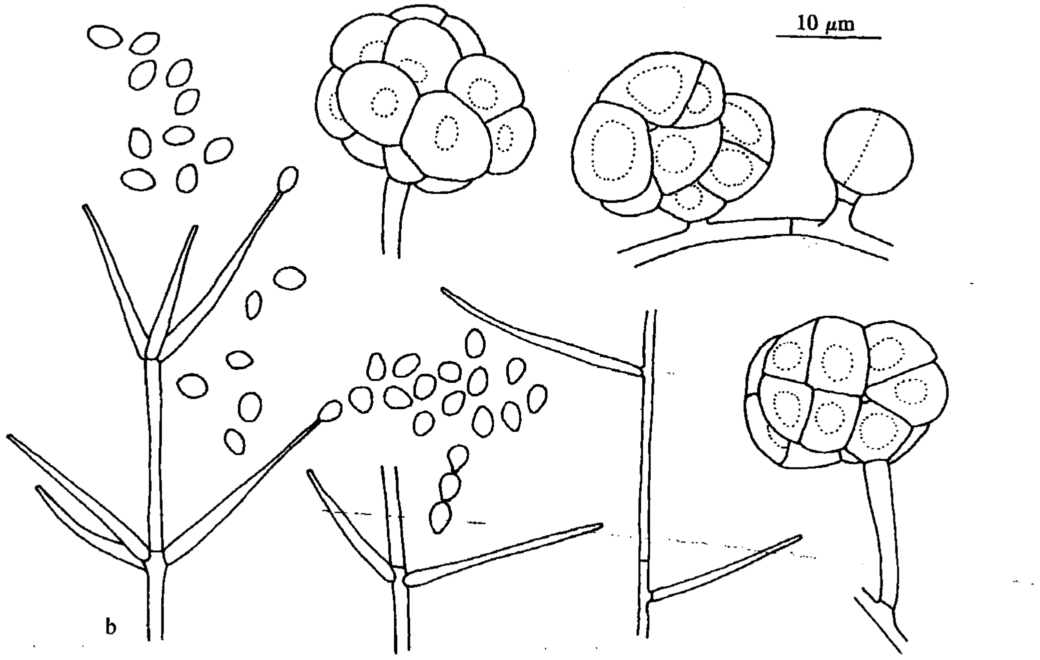

Fig. 6 b. *Pochonia chlamydosporia* var. *catenulata*, phialides and dictyochlamydospores of CBS 504.66 on PCA.

distinct palisade of cylindrical cells composing the outer layer of the perithecial neck, whilst this is ill-defined in others. In IMI 380126, the old stromata bear yellow to reddish brown perithecia. Nevertheless, this variation is considered to be acceptable within such geographically-separated populations, stretching from coastal Ecuador to the lower Amazon in Brazil.

The last major revision of the genus *Cordyceps* was undertaken by Mains (1958), for North American species only, in which he recognized four subgenera, based primarily on the presence or absence of an apical cap in the ascus and the degree of immersion of the perithecia on the stroma. Those species with superficial or free perithecia were assigned to the subgenus *Racemella*, and all six described species possess filiform ascospores which either do not form part-spores or separate only tardily. *Cordyceps chlamydosporia* falls readily into this grouping, together with *C. atewensis* Samson, Evans & Hoekstra, described on an homopteran insect from Ghana (Samson et al. 1982). The germinating ascospores of this species were reported to produce a *Hirsutella* stage, and a remnant palisade of *Hirsutella*-like conidiogenous cells occurs on the stromata of both IMI 380128 and 380130. It is possible that several synanamorphs exist in the life-cycle and that the strategy in a forest habitat with dispersed host populations would be for local spread by rain-splashed slime-spores, with long-distance dispersal being provided by the forcibly-discharged, aerial ascospores, and the dictyochlamydospores serving for long-term survival. Their abundant production on well-defined synnemata, particularly in the type, suggests that they are also actively-dispersed propagules.

Thus, many of the records of this fungus are from soil, but there is no doubt that *P. chlamydosporia* is a primary pathogen of mollusc eggs, as well as of cyst nematodes (Kerry 1995). Whether or not distinct ecotypes or pathotypes of this extremely wide-ranging species exist, remains to be proven. However, given the increasing importance of mollusc pests in agriculture, especially of alien or non-indigenous species (Cowie 2001), the potential of *P. chlamydosporia* as a biocontrol agent warrants further investigation. Petch (1939) reported this fungus (as *Stemphyliopsis ovorum*) as a problem in breeding units of the giant African snail (*Achatina fulica* Bouw., Achatinidae) in Sri Lanka in the 1920s, which was then being spread around the tropics as a potential food source. Ironically, this snail has since become a major pest wherever it was introduced, and unfortunately, ill-conceived, non-scientific and, therefore, ecologically disastrous attempts have been made to control it through the importation of predatory snails (Cowie 2001).

Pochonia chlamydosporia has been reported as a parasite of cysts and eggs of *Heterodera* (but only exceptionally of *Globodera*) species (Willcox & Tribe 1974, Bursnall & Tribe 1974, Kerry & Crump 1977, Tribe 1977, Morgan-Jones et al. 1981, Gintis et al. 1983) and occasionally of *Meloidogyne* species (Godoy et al. 1982, Morgan-Jones et al. 1983). It is a potential biocontrol agent of *Heterodera* cyst nematodes (de Leij & Kerry 1991, de Leij 1992). The species is also listed as ovicidal to eggs of *Ascaris lumbricoides*, penetrating the eggs and destroying the embryo (Fassatiová & Lysek 1982); it was also reported previously from snail eggs (Gams 1971). More data on the distribution of the species are given by Dackman & Nordbring-Hertz (1985).

2. **Pochonia chlamydosporia** var. **catenulata** (Kamyschko ex Barron & Onions) Zare & W. Gams (Nova Hedwigia 72: 52, 2001) Fig. 6b, 7

≡ *Diheterospora catenulata* Kamyschko, [Bot. Mater. Otd. Sporov. Rast. Bot. Inst. Komarova Akad. Nauk S.S.S.R. (Not. Syst. Sect. Crypt. Inst. Bot. Acad. Sci. USSR) 15: 140, 1962, nom. gener. inval., Art. 37.1] ex Barron & Onions, Canad. J. Bot. 44: 868, 1966 (basionym).

≡ *Verticillium catenulatum* (Kamyschko ex Barron & Onions) W. Gams, *Cephalosporium*-artige Schimmelpilze, p. 190, 1971.

≡ *Verticillium chlamydosporium* var. *catenulatum* (Kamyschko ex Barron & Onions) W. Gams, Netherlands J. Pl. Pathol. 94: 134, 1988.

Teleomorph: *Cordyceps* sp., similar to *C. chlamydosporia*. It differs from *C. chlamydosporia* by perithecia which are never erumpent but always buried in a more organized stroma. Because of insufficient material, we cannot yet formally describe this new species.

Colonies similar to *P. chlamydosporia* var. *chlamydosporia*, reaching 22-40 mm diam. in 10 days. Phialides arising from prostrate hyphae, solitary or up to 5 per node. Conidia produced in chains, partly also in heads, globose to subglobose, with slightly apiculate base, measuring (1.5-)2.0-3.5 × 1.5-3.0 µm. Dictyochlamydospores as in *P. c.* var. *chlamydosporia*. Crystals absent. Temperature optimum: 24-27°C (27-36 mm diam.). Very little growth at 33°C.

STRAINS EXAMINED:

IMI 113172, ex hair bait buried in garden soil, UK, 1956, P.M. Stockdale.

IMI 076422, ex soil, Trinidad, 1959, I.D. Firman.

IMI 080555, ex soil, Australia, 1960, J.W. Carmichael & G.L. Barron.

IMI 080556, ex soil, Australia, 1960, Durie & Frey.

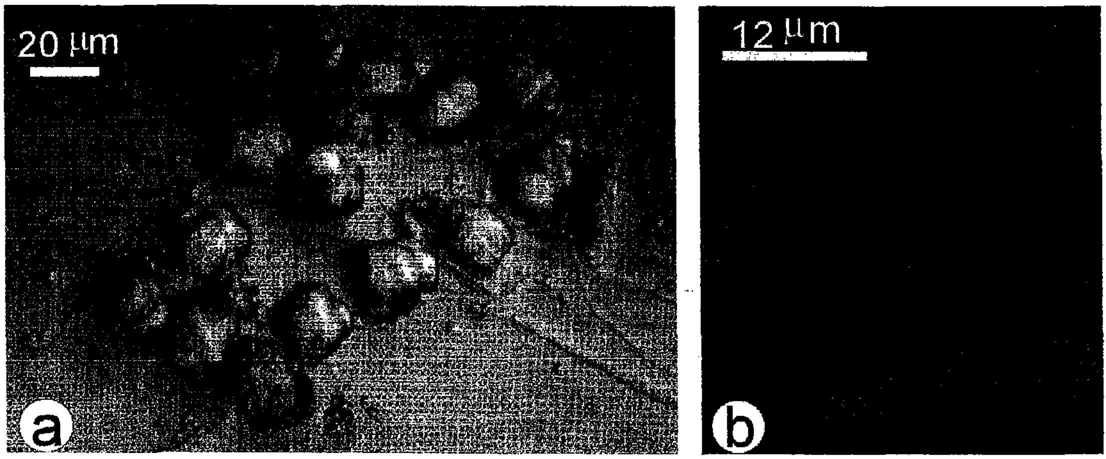

Fig. 7. *Pochonia chlamydosporia* var. *catenulata*. a. Dictyochlamydospores, b. conidial chains. a. IMI 331575, b. IMI 338017., a. DIC, b. SEM.

CBS 504.66 = IMI 113164, ATCC 16683, OAC 10250, ex soil, Canada, 1963, G.L. Barron, **ex-type**.

CBS 397.69 = MUCL 15018, ex soil, Canada, 1969, G.C. Bhatt.

IMI 331575 and 338017, ex beetle larva (Coleoptera), Ecuador, 1974, H.C. Evans, single-ascospore isolates of the *Cordyceps* teleomorph.

CBS 496.96, ex leaf litter, Cuba, 1996, R.F. Castañeda.

Dictyochlamydospores are indistinguishable in the two varieties. Strain IMI 080556 consistently produced smaller dictyochlamydospores, 14.5 × 10.5 µm. Strains IMI 331575 and IMI 338017, single-ascospore isolates of a *Cordyceps* sp., are indistinguishable from other strains studied under this taxon.

The difference in arrangement of the conidia in chains or heads is again found to be of limited significance, and strains showing either of the arrangements are therefore only distinguished at varietal rank. Conidia in *P. c.* var. *catenulata* are generally more globose to subglobose, while those of var. *chlamydosporia* are more ellipsoidal. RFLPs of ITS region, β-tubulin gene and mtDNA do not consistently separate the two varieties, but parsimony analysis using sequences from ITS regions distinguished them (Fig. 1, also Zare et al. 2000).

3. **Pochonia suchlasporia** (W. Gams & Dackman) Zare & W. Gams, comb. nov., var. **suchlasporia** Fig. 8

≡ *Verticillium suchlasporium* W. Gams & Dackman, Netherlands J. Pl. Pathol. 94: 136, 1988 (basionym).

Colonies reaching 10-12 mm diam. in 10 days, high, woolly, white to yellow, reverse yellow to brownish cream, rather slow-growing. Conidiophores mostly erect but also prostrate, rather thick-walled, up to 4-5 µm wide at the base, tapering apically to 1.5-2.5 µm, bearing up to 3 whorls of 3-4 phialides. Phialides 15-30 × 1.2-2.0 µm, sometimes swollen near the base to 2.5 µm. Conidia in dry heads, subglobose, chromophilic, measuring 2.3-4 × 1.5-2.5 µm. Dictyochlamydospores usually scanty, submerged in the agar, rarely near the surface, surrounded by a slimy layer, 15-25 × 10-20 µm. Crystals absent. Temperature optimum: 18-21°C (17-18 mm diam.). No growth at 27°C.

STRAINS EXAMINED:

CBS 251.83, ex eggs of *Heterodera avenae*, Sweden, 1983, C. Dackman, **ex-type**.

CBS 816.83, ex eggs of *H. avenae*, Denmark, 1983, M. Juhl. More strains documented in Gams (1988).

Gams (1988) noticed another, uncommon form of sporulation in which phialides give rise to a few elongate conidia measuring 5-12 × 1.5-2 µm (Fig. 8c).

Pochonia suchlasporia is rather widely separated from *P. chlamydosporia* in molecular analyses (Zare et al. 2000; Sung et al. 2001), but it forms a tight cluster with the remaining species of the genus in its LSU + SSU sequences, with 98% bootstrap support (Sung et al. 2001). The RFLP patterns of the ITS region and the β-tubulin gene are identical in all isolates of both varieties of either species but different between the species.

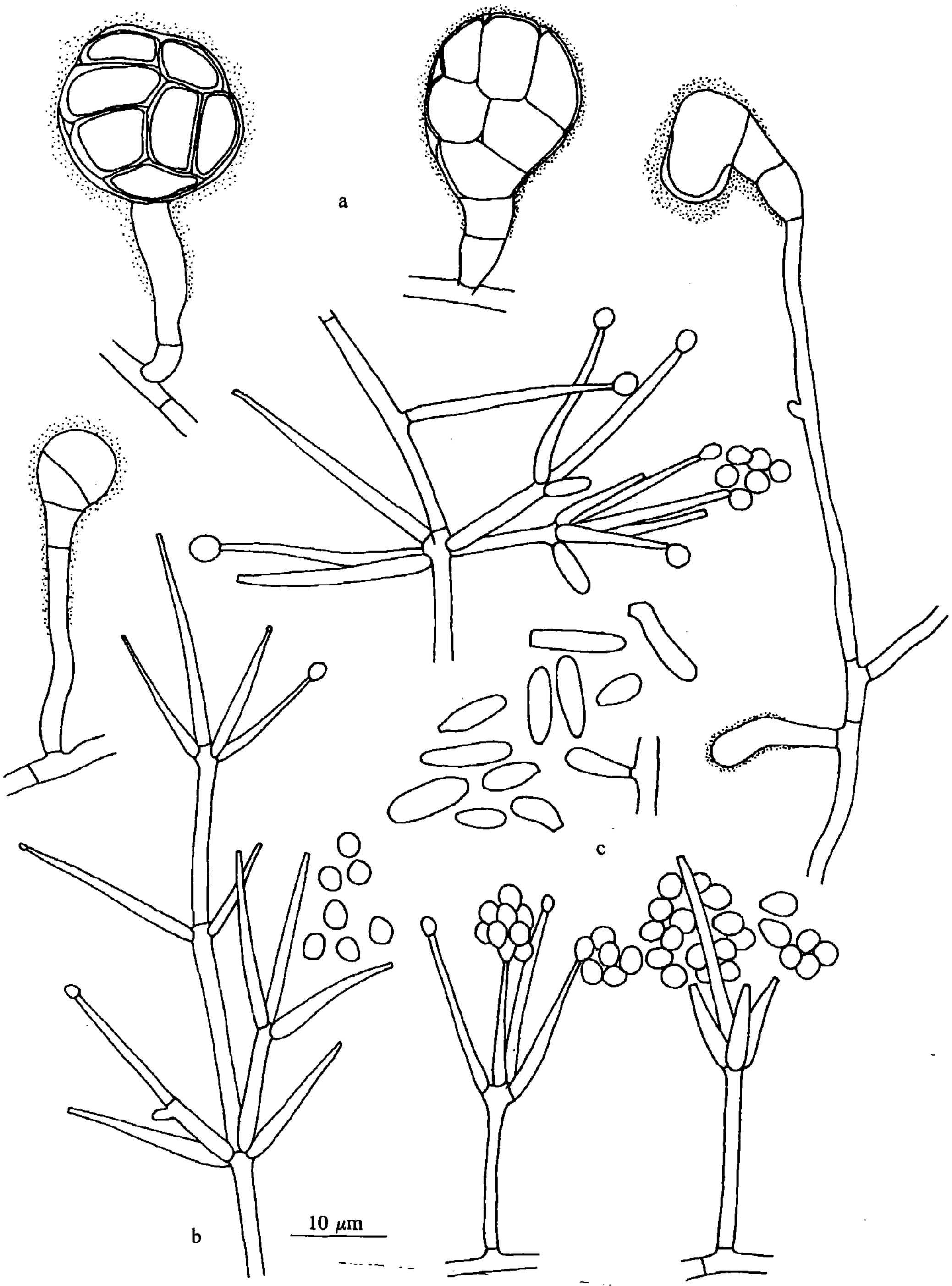

Fig. 8. *Pochonia suchlasporia* var. *suchlasporia*. a. Dictyochlamydospores of CBS 228.82B on SEA, b. conidiophore and conidia of CBS 228.82C on OA, c. conidiophore, conidia and elongate submerged conidia of CBS 228.82B on PCA.

Like in *P. chlamydosporia*, both varieties of *P. suchlasporia* had identical RFLP patterns of the ITS region and the β-tubulin gene; the more variable patterns of mtDNA did not consistently separate the two varieties; but parsimony analysis using sequences from the ITS regions distinguished them (Fig. 1, and Fig. 1 in Zare et al. 2000).

The two varieties of *P. suchlasporia* form a significant portion of egg and cyst parasites of *Heterodera* species in Sweden (Dackman & Nordbring-Hertz 1985), Denmark (Juhl 1982) and the Netherlands (G.J. Bollen & F. Zoon, pers. comm.). They are at an ecological advantage over *P. chlamydosporia* because of the lower cardinal temperatures (Gams 1988).

4. **Pochonia suchlasporia** var. **catenata** (W. Gams & Dackman) Zare & W. Gams, comb. nov. Fig. 9

≡ *Verticillium suchlasporium* var. *catenatum* W. Gams & Dackman, Netherlands J. Pl. Pathol. 94: 140, 1988 (basionym).

Colonies, conidiophores and phialides as in *P. s.* var. *suchlasporia*. Conidia subglobose to ovoid, chromophilic, measuring 2-3.7 × 1.7-2.3 µm, cohering in chains or partly in dry heads. Dictyochlamydospores scanty, 16-28 × 14-25 µm, submerged in the agar. Crystals absent. Temperature optimum: 21°C (14-21 mm diam.). No or very little growth at 27°C.

STRAINS EXAMINED:

IMI 113078 = CBS 101265, ex millipede droppings, UK, 1965, T.F. Hering.

CBS 383.70a, ex garden soil, Netherlands, 1970, H.A. van der Aa.

CBS 248.83, ex eggs of *Heterodera avenae*, Sweden, 1983, C. Dackman, **ex-type**.

CBS 817.83, ex eggs of *H. avenae*, Sweden, C. Dackman.

CBS 789.85, ex eggs of *Lymantria dispar* (gipsy moth), USA, G.C. Carroll.

CBS 495.90, ex soil, Canada, G. Thorn.

CBS 416.95, ex worm on dead leaf of *Roystonia regia*, Cuba, 1994, R.F. Castañeda.

No dictyochlamydospores were observed in strains IMI 113078, CBS 817.83 and CBS 789.85, but these strains otherwise conform well with the taxon, and have RFLP patterns identical with those of dictyochlamydosporic isolates.

5. **Pochonia rubescens** Zare, W. Gams & López-Llorca, sp. nov. Fig. 10

Coloniae humiles, albae, reverso rubescente (praecipue in agaro PDA), fere celeriter crescentes. Phialides singulae vel 2-4 verticillatae, 18-25 × 0.7-1.0 µm. Conidia in capitulis siccis cohaerentia, globosa vel subglobosa, levia, 2.5-3.5 × 2.0-3.0 µm. Dictyochlamydosporae parcae, e cellulis catenatis vel irregularibus constantes, saepe in agaro submersae. Cristalla absentia.

Holotypus CBS 464.88, isolatus ex ovis *Heteroderae avenae* in Scotia a L. López-Llorca 1988 (herb. CBS).

Colonies rather fast-growing, reaching 25-29 mm diam. in 10 days, thin, white, reverse red (at least on PDA), with a reddish pigment diffusing into the agar after 10 days. Conidiophores usually prostrate, rarely erect but not thick-walled. Phialides

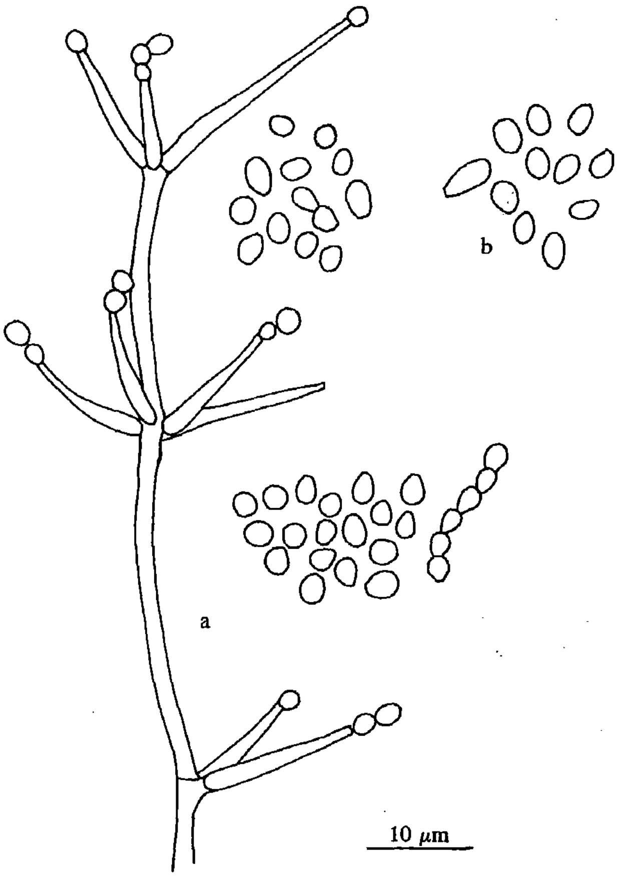

Fig. 9. *Pochonia suchlasporia* var. *catenata*. a. Conidiophore and conidia of CBS 876.85 on MEA, b. conidia of CBS 248.83.

solitary or up to 2-4 per node, 18-25 × 0.7-1.0 µm. Conidia formed in dry heads, globose to subglobose, smooth-walled, measuring 2.5-3.5 × 2.0-3.0 µm. Dictyochlamydospores scanty, scattered in chains or loosely held together forming irregular shapes, usually deeply submerged in the agar, sometimes totally absent or very difficult to detect. Crystals absent. Temperature optimum: 24°C (30-32°C diam.). No growth at 33°C.

STRAINS EXAMINED:

CBS 352.70, ex soil from *Thuja-Abies* bog, USA, 1967, W.F. Whittingham.

CBS 405.70, ex agricultural soil, Netherlands, 1968, J. W. Veenbaas-Rijks.

CBS 425.80a, ex cysts of *Heterodera schachtii*, 1980, G.J. Bollen.

IMI 293909 = CBS 101238, ex eggs of *Heterodera avenae*, UK, 1985, J.M. Duncan.

CBS 464.88 = ATCC 76547, ex eggs of *Heterodera avenae*, UK, Scotland, 1988, L. López-Llorca, **ex-type**.

Conidia of this species resemble those of *P. suchlasporia*. *Pochonia rubescens* is distinct mainly by its red pigment on the colony reverse and also the reddish yellow

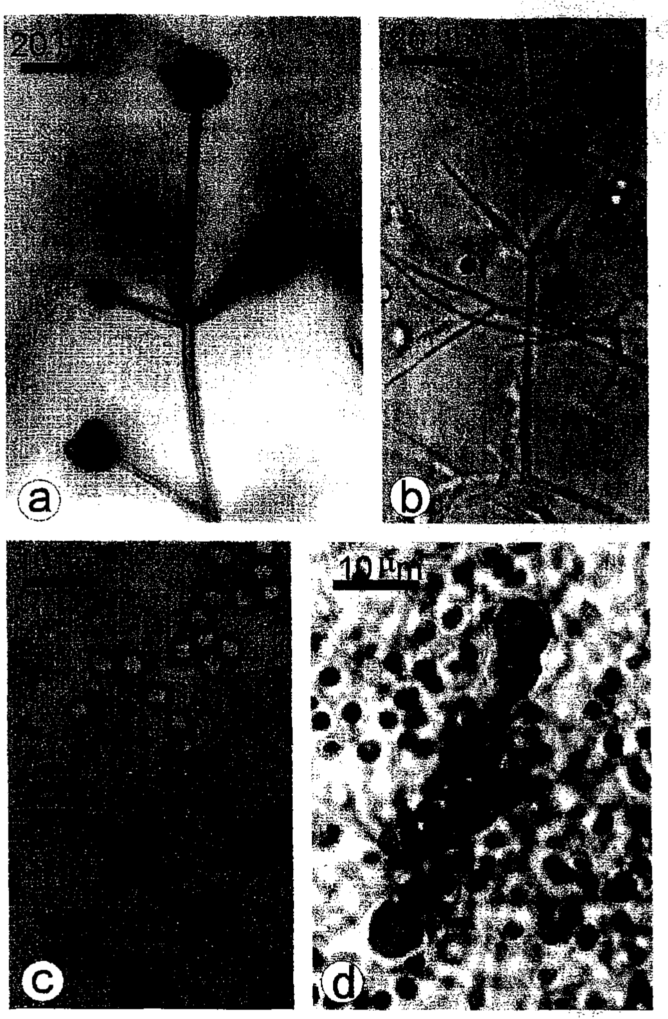

Fig. 10. *Pochonia rubescens*. a, b. Conidiophores, c. conidia, d. submerged dictyochlamydospores. a, b, c. CBS 352.70; d. CBS 425.80A. d. stained in cotton blue.

pigment diffusing into the agar. Dictyochlamydospores are very rare in *P. rubescens*; they appear as single cells or loosely compacted cell aggregates composed of irregular shapes or scattered chains; sometimes they are totally absent.

Five strains represent this taxon, three of which were isolated either from cysts of *Heterodera schachtii* or eggs of the cereal cyst nematode, *H. avenae*. The other two were obtained from soil. The ex-type strain was reported as an egg parasite on *H. avenae* (López-Llorca & Duncan 1988; López-Llorca 1990). Gams (1988) placed this strain under *V. suchlasporium*. The species has a distinct ITS RFLP pattern, that of the *β*-tubulin gene is the same as in *P. suchlasporia* and mtDNA is too variable to draw any conclusion.

The characteristic red pigment, most abundantly produced on acidic media, was also noted by López-Llorca et al. (1994) and López-Llorca & Olivares-Bernabeu (1998) in strain CBS 464.88. These authors extracted the pigment in chloroform/methanol and proved its inhibitory effect (mycotoxicity) on the growth of *Cladosporium cucumerinum*. They also showed that the extract had nematicidal effect on the potato root cyst nematode, *Globodera rostochiensis*.

6. **Pochonia gonioides** (Drechsler) Zare & W. Gams, comb. nov. Fig. 11

≡ *Acrostalagmus gonioides* Drechsler, J. Washington Acad. Sci. 32: 347, 1942 (basionym).

≡ *Verticillium gonioides* (Drechsler) W. Gams & Stalpers, Netherlands J. Pl. Pathol. 94: 143, 1988.

Colonies reaching 14-16 mm diam. in 10 days, white, with brownish cream reverse, moderately slow-growing. Phialides arising mostly in whorls of 2-5 on prostrate hyphae, measuring 13-30 × 1-2 µm, tapering distally to 0.5 µm. Conidia held together in heads, 1.8-2.5 µm diam., with irregularly polyhedral to tuberculate outline. Dictyochlamydospores irregular, mostly submerged, formed as lateral branches with swollen cells. Crystals absent. Temperature optimum: 18°C (CBS 611.89 with 4-5 mm diam.) or 21°C (CBS 891.72 with 21 mm diam.). No growth at 27°C (CBS 611.89) or 30°C (CBS 891.72).

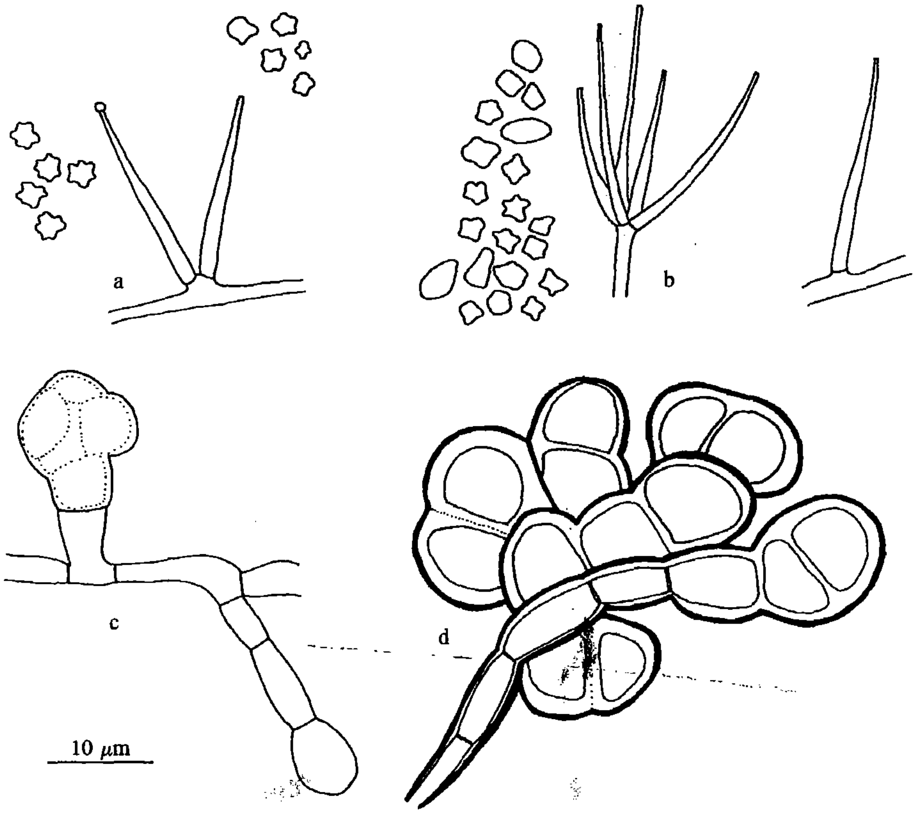

Fig. 11. *Pochonia gonioides*. a, b. Conidiophores and conidia of CBS 611.89 and 241.80 on PCA and MEA, c. young and d. old dictyochlamydospores of CBS 241.80 on SEA.

STRAINS EXAMINED:

CBS 891.72, ex *Pulcherricium caeruleum*, Germany, 1972, J.A. Stalpers, **ex-neotype** (Gams 1988).

CBS 611.89, ex litter of *Pinus sylvestris*, Germany, 1989, G. Kraepelin.

Drechsler (1942) found this fungus attacking cysts and eggs of *Heterodera* species and as an endoparasite of *Rhabditis terricola*. No living strains isolated from nematodes is available at the moment.

The species can be distinguished from all other taxa of the genus by its isodiametric-polyhedral and smaller conidia. The two isolates vary in the degree of lobulation of the conidia and differ strongly in growth rate, but have identical RFLP patterns of the ITS region and the β-tubulin gene.

7. **Pochonia bulbillosa** (W. Gams & Malla) Zare & W. Gams, comb. nov. Fig. 12

≡ *Verticillium bulbillosum* W. Gams & Malla, *Cephalosporium*-artige Schimmelpilze, p. 189, 1971 (basionym).

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

Colonies reaching 20-35 diam in 10 days, conidiophores and phialides similar to those of *P. chlamydosporia* var. *chlamydosporia*. Conidia produced in globose heads, of two types: falcate with blunt ends, 4-6.3 × 1.5-2.0 µm, and subglobose to ovoid, 2.2-3.0 × 1.3-2.0 µm. Dictyochlamydospores more or less scanty, produced on the agar surface, irregular or sometimes forming chains or reduced to irregularly swollen hyphae. Crystals absent. Temperature optimum: 21-24°C (21-30 mm diam.). No growth at 30°C.

STRAINS EXAMINED:

CBS 247.68, ex agricultural soil, Germany, 1964, W. Gams, ex-type of *V. cephalosporum*.

CBS 145.70, ex root of *Picea abies*, Denmark, 1970, D.S. Malla, **ex-type**.

CBS 578.78, ex plant material, New Zealand, 1978, G.F. Laundon.

CBS 426.81, ex paramo soil, Colombia, 1981, sample taken by T. van der Hammen & R. Jaramillo, isol. W. Gams.

This taxon can be readily distinguished from all other taxa of *Pochonia* by its falcate conidia. They are generally shorter and blunter than those of *Lecanicillium psalliotae* and related species, in which the conidia typically sit transversely on the phialide tip. The synonymy of *V. cephalosporum* (at least for the ex-type strain) was demonstrated by Gams (1988).

Pochonia bulbillosa is commonly isolated from forest soils. Synthetically produced mycorrhizae of *Picea abies* with *Laccaria laccata* were damaged by toxic metabolites and mycoparasitism, but mycorrhizae formed with *Hebeloma crustuliniforme* were not (Marchetti & Varese 1997).

8. **Pochonia microbactrospora** W. Gams & Zare, sp. nov. Figs 13, 14

Coloniae humiles, dilute flavidae, reversum flavum, ad 15 mm diam. post 10 dies. Phialides solitariae vel 2-3 verticillatae, deorsum inflatae et parte media angustatae. Conidia in capitulis parvis mucidis

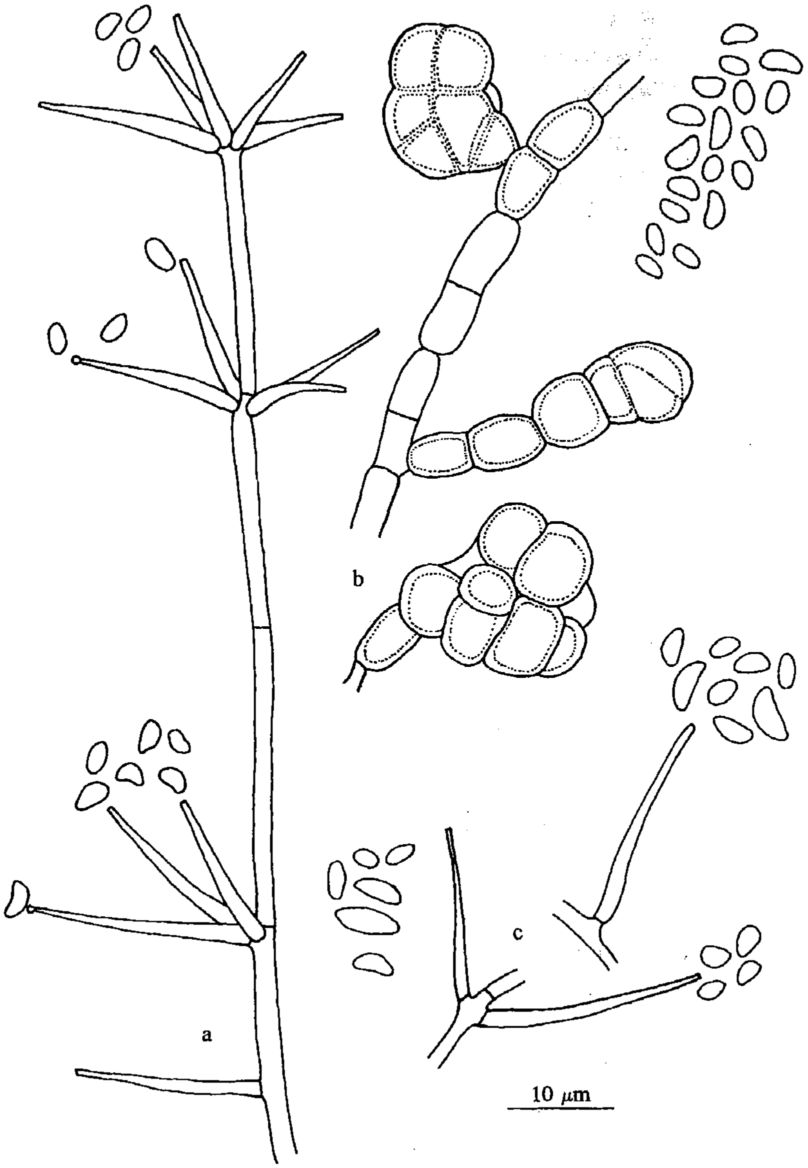

Fig. 12. *Pochonia bulbillosa*. a. Conidiophore and conidia of PD 82/32, b. irregular dictyochlamydospores and conidia of CBS 145.70 on OA, c. phialides and conidia of CBS 145.70.

cohaerentia, ellipsoidea vel bacilliformia, 2.0-2.5 × 0.7-1.0 µm. Cristalla praesentia. Dictyochlamydosporae irregulares, e cellulis catenatis vel laxe aggregatis constantes.

Holotypus CBS 101433, cultura sicca, isolata a S.L. Glockling e rotiferis in Japonia, 1996 (herb. CBS).

Colonies reaching up to 15 mm diam. in 10 days, thin, pale yellow to white, reverse yellow, rather slow-growing. Phialides solitary or verticillate up to 2-3 per node, swollen at the base and narrowed in the middle. Conidia produced in small slimy heads, ellipsoidal to rod-shaped, 2-2.5 × 0.7-1.0 µm. Dictyochlamydospores of

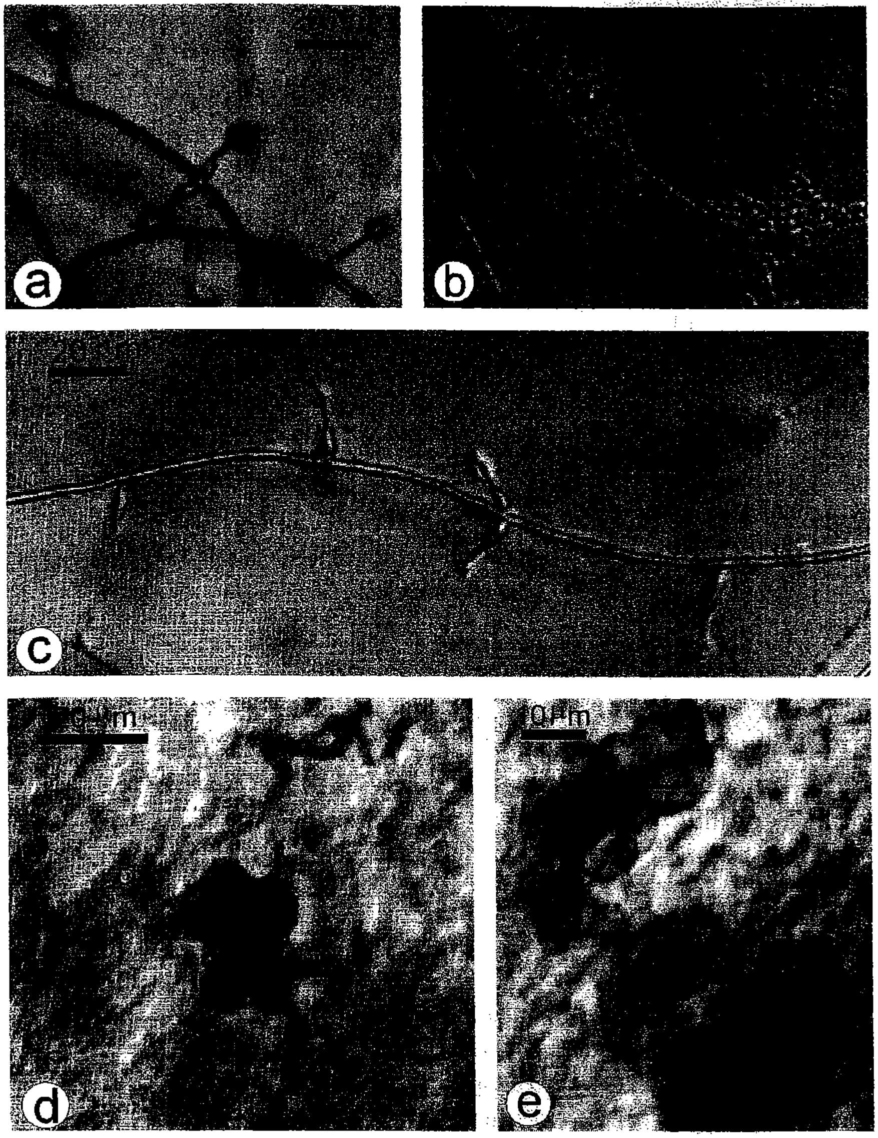

Fig. 13. *Pochonia microbactrospora*. a. Conidial heads, b. conidia, c. phialides, d, e. dictyochlamydospores. a-e. CBS 101433, DIC.

irregular shape, in chains or loosely aggregated cells. Octahedral crystals present. Temperature optimum: 21°C (7 mm diam.). No growth at 33°C.

STRAIN EXAMINED:

CBS 101433, isolated by S.L. Glockling, ex rotifers in pine litter, Japan, 1996, ex-type.

Glockling (1998 a) identified this strain as *Verticillium bactrosporum* (Drechsler) Subram., but, because of its smaller and non-adhesive conidia, and also based on molecular evidence (see Fig. 1), we consider this identification inappropriate and describe the very distinct fungus as a new species of *Pochonia*. This species resembles

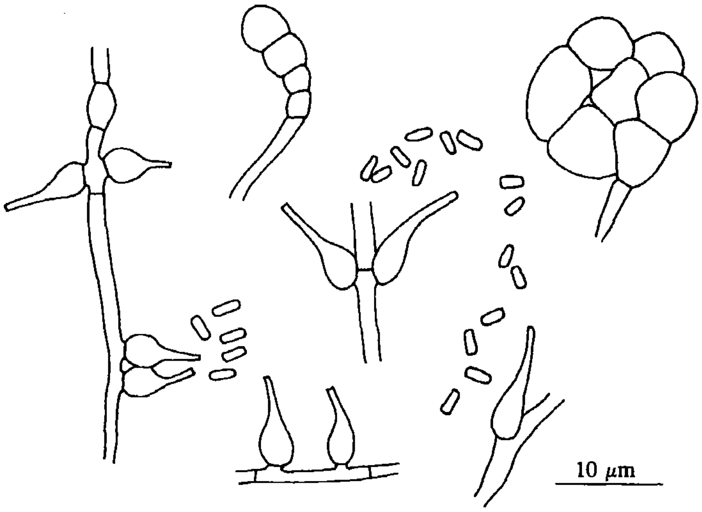

Fig. 14. *Pochonia microbactrospora.* Incipient dictyochlamydospores, phialides and conidia of CBS 101433 on PCA and SEA.

Verticillium campanulatum Glockling & Dick (1997), but it has conidia that are only of one type and are smaller than those of *V. campanulatum.* Drechsler (1941) described and illustrated *Acrostalagmus bactrosporus* with an intermediate size (2-3 × 1.3-1.6 µm) of adhesive conidia. That species is currently unavailable but obviously belongs to *Haptocillium.*

Rotiferophthora Barron, Canad. J. Bot. 69: 495, 1991.

Colonies very slow-growing. Conidiophores simple or sparingly branched; phialides either discrete, single, paired or in whorls, and flask-shaped, or intercalary, with short narrow fertile necks, and overtopped by a terminal phialide. Conidia globose, short-ellipsoidal to fusiform, clavate or lunate, containing one or more conspicuous oil droplets which are visible in water and lactic acid mounts. Dictyochlamydospores usually abundant, more or less applanate. Type species *Rotiferophthora globispora* Barron.

The genus *Rotiferophthora* was introduced by Barron (1991) to include parasites of bdelloid rotifers. A few species were previously classified in *Acrostalagmus* or *Diheterospora.* Over 25 species have been described, mostly based on minute differences in conidial shape (Drechsler 1942; Barron 1973, 1980, 1985, 1991; Glockling & Dick 1997; Glockling 1998 b). Very few of them have been grown in pure culture and at the moment only a small number of species are available in culture collections. Representatives of *Rotiferophthora* are exclusively known as specialized endoparasites of bdelloid rotifers, mainly *Adineta* species (Barron 1985). Conidia and chlamydospores are produced outside the host body (Glockling 1998 b). All species produce dictyochlamydospores. Conidia adhering in heads are produced from flask-shaped or elongate phialides and often also from short cylindrical conidiogenous necks of intercalary phialides (Barron 1991, Glockling 1998 a). The animals become infected by ingesting the conidia (Barron 1980, 1985).

Rotiferophthora and *Pochonia* are considered closely related. The differences between the two genera are summarized in Table II (extracted from Barron 1985; Glockling & Dick 1997; Glockling 1998 b).

Strains of two species received from Dr S.L. Glockling were included in this study.

Table II. Differences between *Pochonia* and *Rotiferophthora*.

Feature	*Pochonia*	*Rotiferophthora*
Hosts	nematode cysts and eggs	only rotifers
Dictyochlamydospores	more or less globose	usually flat
Verticillate phialides	long, gradually tapering from base to apex	more or less short, usually flask-shaped, with a swollen base and a narrow cylindrical neck
Intercalary phialides	absent	present
Conidia	without mucoid sheath or oil droplet	held in a mucoid sheath, with a large oil droplet

Rotiferophthora angustispora (Barron) Barron, Canad. J. Bot. 69: 495, 1991

≡ *Diheterospora angustispora* Barron, Canad. J. Bot. 63: 214, 1985.

Colonies reaching 15 mm diam. in 10 days, cream-coloured, with pale-brown reverse. Conidiophores more or less erect, up to 200 µm tall, 2.5-4 µm wide, bearing lateral branches in whorls, especially near the base. Phialides solitary or up to 5 on each node, 13-22 × 2.0-2.5 µm, swollen near the base and tapering gradually to a narrow apex which is often irregularly reflexed upwards. Intercalary phialides with a short neck, infrequent, appr. 6 × 0.8-1.3 µm. Conidia narrowly cylindrical or sausage-shaped, 6.5-8 × 1.0-1.3 µm. Because of the narrow conidia, the oil droplet at the distal end is difficult to see. Dictyochlamydospores flat, 15-25 × 10-12 µm. Temperature optimum 18-21°C (10-12 mm diam.). No growth at 27°C.

STRAIN EXAMINED:

CBS 101437, isolated by S.L. Glockling from a rotifer in decaying straw, England, 1997.

This species was originally recovered from bdelloid rotifers in farmyard soil in Guelph, Canada (Barron 1985).

Rotiferophthora minutispora S.L. Glockling, Mycol. Res. 102: 1145, 1998

Colonies very slow-growing, reaching 6 mm diam. in 10 days, pinkish red, with dark cream-coloured reverse. Conidiophores up to 300 µm tall, with up to 6 whorls of phialides, which are elongate and tapering, measuring 16 × 2 µm. Conidia produced in heads, spherical, 2.0-2.2 µm diam. Dictyochlamydospores 14-16 µm diam., bulbous. Temperature optimum: 21-24°C (about 6 mm diam.). No growth at 33°C.

STRAIN EXAMINED:

CBS 101436 = IMI 372229, isolated by S.L. Glockling from a rotifer in Japan, **ex-type**.

Residual group

Verticillium incurvum W. Helfer, Libri Bot. 1: 77, 1991 Fig. 15

Colonies very slow-growing, reaching 5 mm diam. in 10 days, white, with brownish-cream reverse. Phialides in whorls, measuring 16-26 × 1.0-1.7 µm, producing single conidia at the apex. Conidia falcate, gently curved and blunt-ended, 0(-1)-septate, 9-15 × 1.5-2.0 µm. Chlamydospores produced abundantly in the mycelium, of irregular shape, consisting of small globose cells, each cell 8-11 µm diam.

STRAIN EXAMINED:

CBS 460.88, isolated by I. Nuss from *Ganoderma lipsiense*, Bayerischer Wald, Germany, 1987, ex-type.

These observations are very close to Helfer's (1991) original description, who would have classified the species in sect. *Albo-erecta* of *Verticillium* had he not seen 'dictyochlamydospores'. Therefore we compared this species with *Pochonia* species. Its monomorphic conidia are much longer than those of *P. bulbillosa*. Its abundant catenate chlamydospores differ from the dictyochlamydospores of *Pochonia*. The ITS sequences of this species were so different from *Pochonia* species that they could not be aligned and analysed together. According to LSU + SSU sequences of rDNA, the species is classified in the Nectriaceae (Sung et al. 2001), thus *Verticillium* sect. *Albo-erecta*.

Verticillium epiphytum Hansford, Proc. Linn. Soc. Lond. 155: 41, 1943 Figs 16, 17

?= *Cephalosporium curtipes* var. *uredinicola* Sukap. & Thirum., Bull. Torrey Bot. Club 93: 307, 1966.

Colonies rather fast-growing, reaching 15-30 mm diam. in 10 days, thin, white, reverse yellow to yellowish cream, with brownish tinges. Most strains producing a yellow pigment diffusing into the agar. Hyphae hyaline, septate, 1.0-1.5 µm wide. Phialides relatively long, 30-60 × 1.0-2.5 µm, usually solitary, arising from prostrate hyphae, forming globose to ellipsoidal conidial heads. Conidia falcate with blunt ends, always 1-celled, measuring 3.5-10.5 × 1-2 µm. Microconidia absent. Chlamydospores mostly present (though scanty), terminal, generally 1-celled, globose to sub-globose to reniform or slightly constricted in the middle, sometimes slightly curved and appearing 1-septate with a small second cell, hyaline, thick-walled with a rough chromophilic surface, measuring 4-12 × 3.5-11.5 µm. Crystals present or absent. Temperature optimum: 24(-27)°C (16 mm diam., CBS 384.81, or 26 mm diam., CBS 154.61). No growth at 33°C.

STRAINS EXAMINED:

CBS 154.61 = IMI 090246 = ATCC 14494 = HACC 105, isolated by M.J. Thirumalachar from India from uredinia of a rust in 1961, ex-type of *Cephalosporium curtipes* var. *uredinicola*.

IMI 071315 = CBS 384.81 = ATCC 22593, isolated by E.F. Vestal from the coffee rust, *Hemileia vastatrix*, in Thailand in 1957, the only authentic strain of *V. epiphytum*.

IMI 286186 = CBS 101285, ex *Phakopsora pachyrhizi*, Thailand, 1984.

CBS 650.85 = ATCC 16541 = HACC 188, India, 1985, deposited as *Cephalosporium pimprina* Thirum. ined., producer of antiamoebin.

IMI 338015, ex *Hemileia vastatrix*, Uganda, 1990, C. Prior.

IMI 346243 = CBS 101296, ex rust pustules, India, 1991, D.H. Smith.

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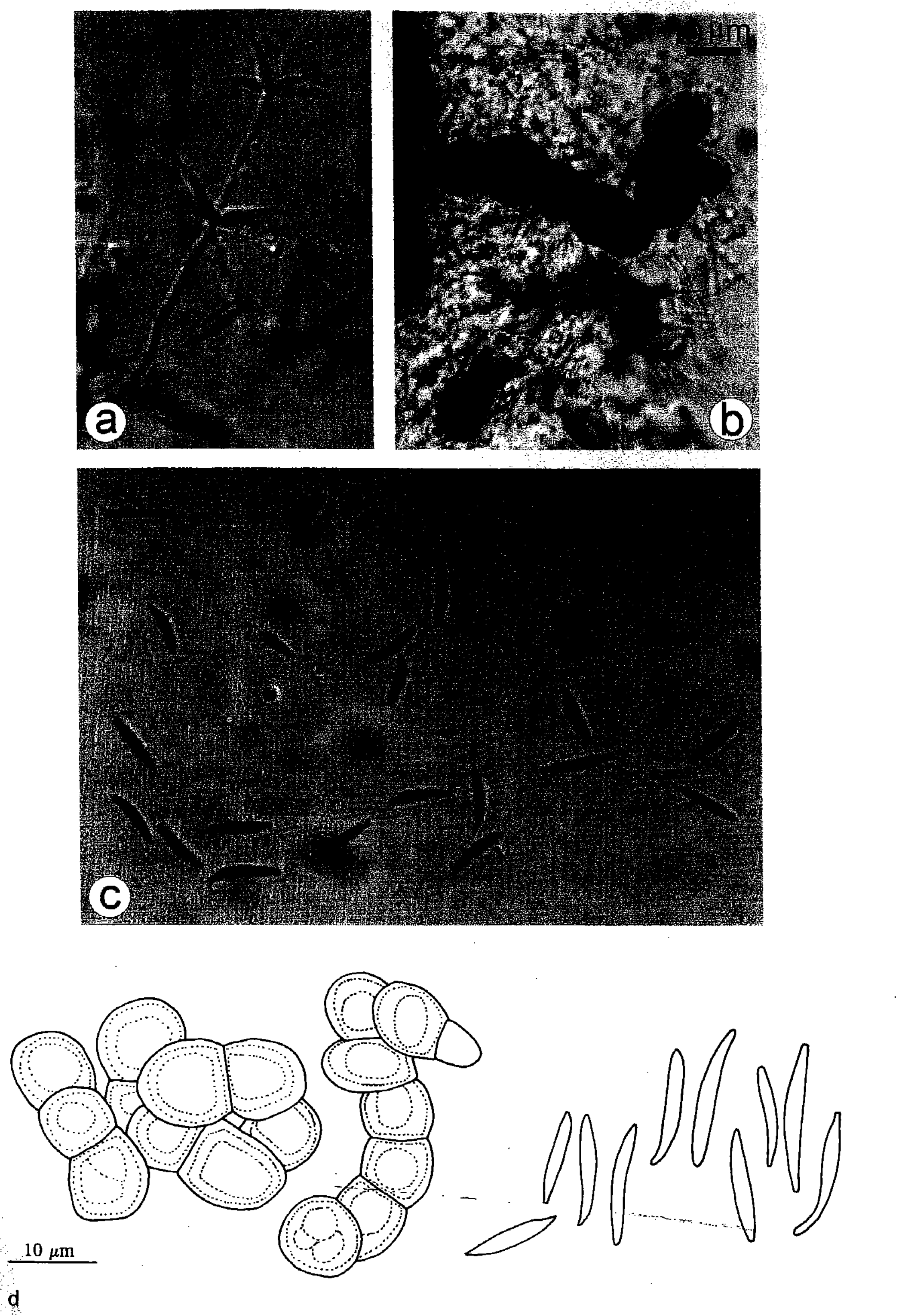

Fig. 15. *Verticillium incurvum*. a. Conidiophore, b. chlamydospores, c. conidia, DIC, b, c. stained in cotton blue. d. Chlamydospores and conidia. a-c. CBS 460.88.

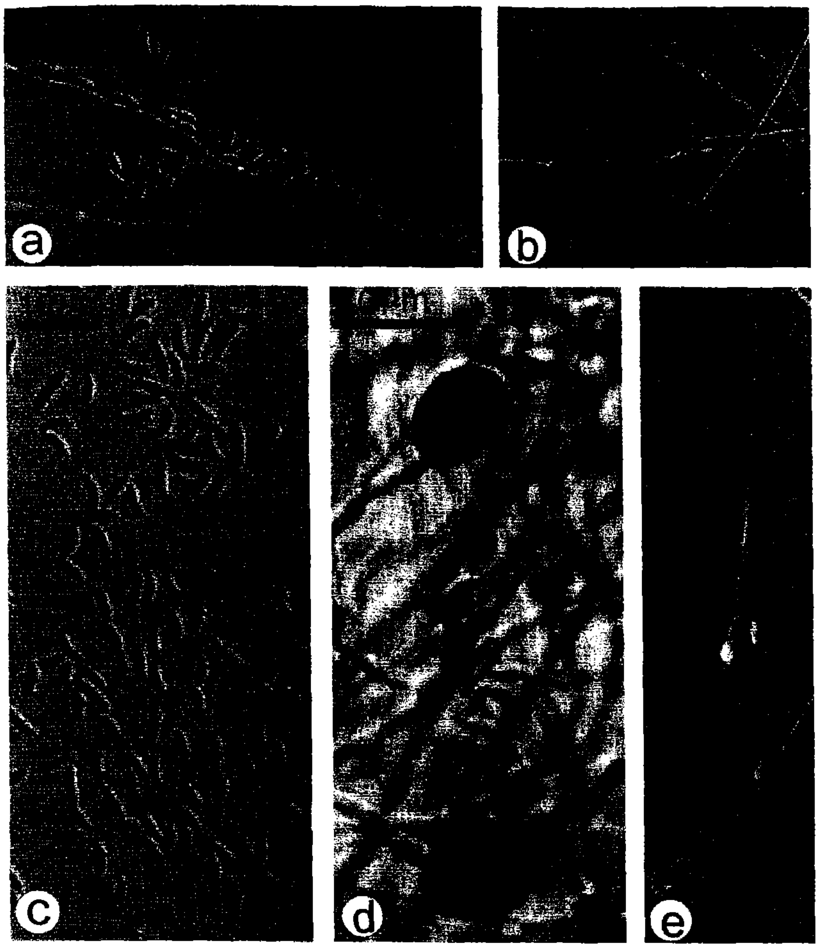

Fig. 16. *Verticillium epiphytum*. a, c, Conidia, b. phialides, d, e. chlamydospores. a, b, e. CBS 384.81; c, d. CBS 650.85, a-e. DIC.

HERBARIUM MATERIAL:

Type material of *V. epiphytum*, numbered 771, collected by Hansford in Kampala, Uganda, on *Helminthosporium triumfettae* on *Triumfetta* sp., 1926 (K).

A specimen numbered 1187, on *Cladosporium herbarum*, collected by Hansford on *Lantana trifolia* in 1930, Kampala, Uganda (K).

Conidia of the type specimen were slightly shrunken and smaller than in CBS 384.81. The specimen is not in good condition and we could not find any chlamydospores. On Hansford's specimen 1187 from Uganda it was almost impossible to find the fungus.

Cephalosporium curtipes var. *uredinicola* could not clearly be separated from *V. epiphytum* using morphological and molecular (sequences of ribosomal RNA genes and spacers) features. Although *Lecanicillium psalliotae* has also been isolated from rust fungi, it seems that most foliicolous verticillium-like mycoparasites from tropical countries belong to this taxon.

Sukapure & Thirumalachar (1966) did not mention the thick-walled chlamydospores in *Cephalosporium curtipes* var. *uredinicola*; however, the ex-type of this taxon does

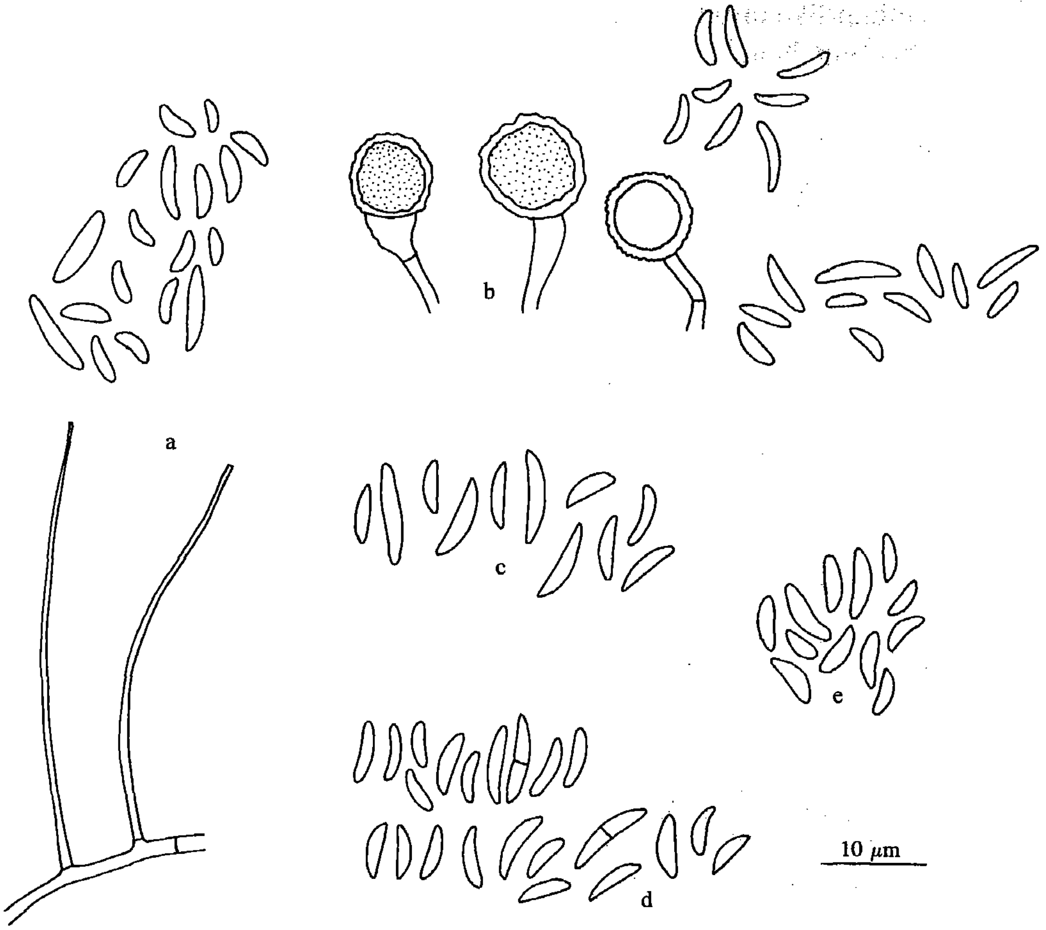

Fig. 17. *Verticillium epiphytum.* a. Phialides and conidia of CBS 154.61 on PCA, b. chlamydospores and conidia of CBS 650.85 on PCA, c-e. conidia of CBS 101296, CBS 384.81 and IMI 338015 on various media.

produce them. The strains showed some variation: IMI 346243 has larger conidia than the average. Strains IMI 346243 and IMI 338015 did not produce any chlamydospores, and no crystals were observed in CBS 650.85 and IMI 338015.

Gams (1971) placed this species under *Verticillium psalliotae*. *Verticillium epiphytum* is, however, distinct in its blunt-ended conidia held in globose heads, wider hyphae and phialides, longer phialides, presence of terminal chlamydospores and the lack of red pigment diffusing into the agar. The same features differentiate this fungus from all other previously described species.

Verticillium epiphytum appeared close to *Pochonia* in a phylogeny inferred from ITS sequences (Zare et al. 2001). According to sequences of LSU + SSU (Sung et al. 2001), it is sufficiently distinct from *Pochonia* and not monophyletic with it. Because we have not seen much material and the phylogenetic position is so far poorly resolved, we refrain from a formal classification. This may be one of the many verticillium-like taxa that are very difficult to distinguish generically and can be left, for the time being, in an informal aggregate of *Verticillium.*

Verticillium pseudohemipterigenum H.C. Evans & Y. Jun, Mycol. Res. 101: 1245, 1997 Figs 18, 19

Colonies reaching 25 mm diam. in 10 days, compact, white, with cream to brownish cream reverse, without discoloration of the agar. Phialides almost exclusively in

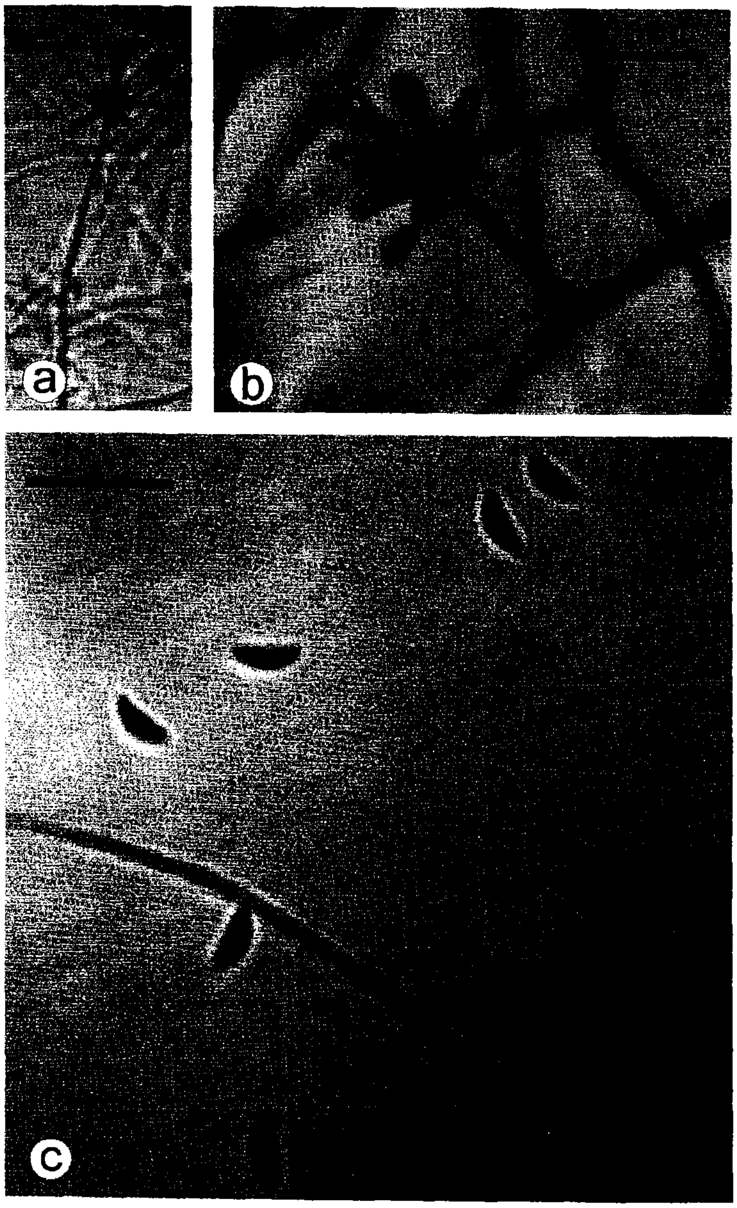

Fig. 18. *Verticillium pseudohemipterigenum.* a, b. Conidiophores, c. conidia in cotton blue. IMI 331563, DIC.

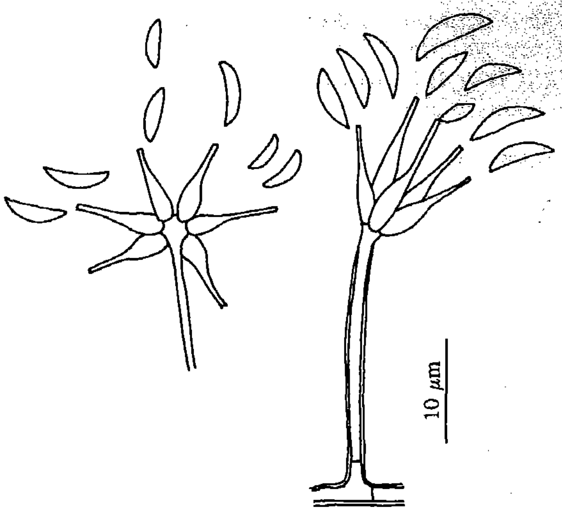

Fig. 19. *Verticillium pseudohemipterigenum.* Conidiophores and conidia, IMI 331563, 8 days on PCA.

whorls of 4-8(-10) on erect conidiophores, hyaline, smooth-walled, (8-)10-16(-20) × 2-5 µm, often inflated at the base, tapering to a needle-like, less than 0.3 µm wide, 4-10 µm long neck. Solitary phialides awl-shaped scanty, up to 25 µm in length, tapering gradually from 1-1.5 to 0.3-0.5 µm. Conidia produced singly, hyaline, aseptate, smooth, narrowly fusiform to ellipsoidal, often in the shape of an orange segment (3.5-)4.5-6.5 × 1.5-2 µm. Teleomorph unknown. Temperature optimum: 24-27°C (24-26 mm diam.). No growth at 33°C (but 2 days at this temperature are survived).

STRAINS EXAMINED:

IMI 331563 = I 96-1013 = CBS 102069, isolated by C. Prior from *Coccus viridis* (coffee green scale) in Trinidad, 1985, ex-type.

I 96-1014 = CBS 102070, ex insect, Surinam, 1996. H.C. Evans.

This taxon is not closely related to any other taxa in this group. Its position could not be resolved using morphology and sequences of ITS regions and 5.8S gene. Therefore, the species is retained in its original genus for the time being. It resembles *Verticillium hemipterigenum* Petch (Petch 1932), especially in the shape and arrangement of phialides and solitary production of conidia, but it is distinguished by its asymmetrically falcate conidia. The two species were studied in detail by Hywel-Jones et al. (1997). *Verticillium hemipterigenum* has not been studied with molecular methods.

Acknowledgement

We have received a number of strains from Sally Glockling (Newcastle). We are grateful to her and other authors who deposited cultures at CBS and CABI Bioscience. Drs K.A. Seifert and R.C. Summerbell kindly contributed to improving the text. Dr A. Culham is thanked for his contribution in data analysis. Mrs C. van den Tweel-Vermeulen inked the drawings and Mrs A. van Iperen carried out the temperature experiments. R. Zare thanks the Iranian Ministry of Agriculture for receiving a PhD award.

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