

# Phylogenetic and morphotaxonomic revision of *Ramichloridium* and allied genera

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**Abstract:** The phylogeny of the genera *Periconiella*, *Ramichloridium*, *Rhinoctadiella* and *Veronaea* was explored by means of partial sequences of the 28S (LSU) rDNA gene and the ITS region (ITS1, 5.8S rDNA and ITS2). Based on the LSU sequence data, ramichloridium-like species segregate into eight distinct clusters. These include the *Capnodiales* (*Mycosphaerellaceae* and *Teratosphaeriaceae*), the *Chaetothyriales* (*Herpotrichiellaceae*), the *Pleosporales*, and five ascomycete clades with uncertain affinities. The type species of *Ramichloridium*, *R. apiculatum*, together with *R. musae*, *R. biverticillatum*, *R. cerophilum*, *R. verrucosum*, *R. pini*, and three new species isolated from *Strelitzia*, *Musa* and forest soil, respectively, reside in the *Capnodiales* clade. The human-pathogenic species *R. mackenziei* and *R. basitonum*, together with *R. fasciculatum* and *R. anceps*, cluster with *Rhinoctadiella* (type species: *Rh. atrovirens*, *Herpotrichiellaceae*, *Chaetothyriales*), and are allocated to this genus. *Veronaea botryosa*, the type species of the genus *Veronaea*, also resides in the *Chaetothyriales* clade, whereas *Veronaea simplex* clusters as a sister taxon to the *Venturiaceae* (*Pleosporales*), and is placed in a new genus, *Veronaeopsis*. *Ramichloridium obovoideum* clusters with *Carpoligna pleurothecii* (anamorph: *Pleurothecium* sp., *Chaetosphaeriales*), and a new combination is proposed in *Pleurothecium*. Other ramichloridium-like clades include *R. subulatum* and *R. epichloë* (*incertae sedis*, *Sordariomycetes*), for which a new genus, *Radulidium* is erected. *Ramichloridium schulzeri* and its varieties are placed in a new genus, *Myrmecridium* (*incertae sedis*, *Sordariomycetes*). The genus *Pseudovirgaria* (*incertae sedis*) is introduced to accommodate ramichloridium-like isolates occurring on various species of rust fungi. A veronaea-like isolate from *Bertia moriformis* with phylogenetic affinity to the *Annulatascaceae* (*Sordariomycetidae*) is placed in a new genus, *Rhodoveronaea*. Besides *Ramichloridium*, *Periconiella* is also polyphyletic. *Thysanorea* is introduced to accommodate *Periconiella papuana* (*Herpotrichiellaceae*), which is unrelated to the type species, *P. velutina* (*Mycosphaerellaceae*).

**Taxonomic novelties:** *Myrmecridium* Arzanlou, W. Gams & Crous, gen. nov., *Myrmecridium flexuosum* (de Hoog) Arzanlou, W. Gams & Crous, comb. et stat. nov., *Myrmecridium schulzeri* (Sacc.) Arzanlou, W. Gams & Crous var. *schulzeri*, comb. nov., *Myrmecridium schulzeri* var. *tritici* (M.B. Ellis) Arzanlou, W. Gams & Crous, comb. nov., *Periconiella arcuata* Arzanlou, S. Lee & Crous, sp. nov., *Periconiella levispora* Arzanlou, W. Gams & Crous, sp. nov., *Pleurothecium obovoideum* (Matsush.) Arzanlou & Crous, comb. nov., *Pseudovirgaria* H.D. Shin, U. Braun, Arzanlou & Crous, gen. nov., *Pseudovirgaria hyperparasitica* H.D. Shin, U. Braun, Arzanlou & Crous, sp. nov., *Radulidium* Arzanlou, W. Gams & Crous, gen. nov., *Radulidium epichloë* (Ellis & Dearn.) Arzanlou, W. Gams & Crous, comb. nov., *Radulidium subulatum* (de Hoog) Arzanlou, W. Gams & Crous, comb. nov., *Ramichloridium australiense* Arzanlou & Crous, sp. nov., *Ramichloridium biverticillatum* Arzanlou & Crous, nom. nov., *Ramichloridium brasilianum* Arzanlou & Crous, sp. nov., *Ramichloridium strelitziae* Arzanlou, W. Gams & Crous, sp. nov., *Rhinoctadiella basitona* (de Hoog) Arzanlou & Crous, comb. nov., *Rhinoctadiella fasciculata* (V. Rao & de Hoog) Arzanlou & Crous, comb. nov., *Rhinoctadiella mackenziei* (C.K. Campb. & Al-Hedaithy) Arzanlou & Crous, comb. nov., *Rhodoveronaea* Arzanlou, W. Gams & Crous, gen. nov., *Rhodoveronaea varioseptata* Arzanlou, W. Gams & Crous, sp. nov., *Thysanorea* Arzanlou, W. Gams & Crous, gen. nov., *Thysanorea papuana* (Aptroot) Arzanlou, W. Gams & Crous, comb. nov., *Veronaea japonica* Arzanlou, W. Gams & Crous, sp. nov., *Veronaeopsis* Arzanlou & Crous, gen. nov., *Veronaeopsis simplex* (Papendorf) Arzanlou & Crous, comb. nov.

**Key words:** *Capnodiales*, *Chaetothyriales*, *Mycosphaerella*, *Periconiella*, phylogeny, *Rhinoctadiella*, *Veronaea*.

## INTRODUCTION

The anamorph genus *Ramichloridium* Stahel ex de Hoog 1977 presently accommodates a wide range of species with erect, dark, more or less differentiated, branched or unbranched conidiophores and predominantly aseptate conidia produced on a sympodially proliferating rachis (de Hoog 1977). This heterogeneous group of anamorphic fungi includes species with diverse life styles, viz. saprobes, human and plant pathogens, most of which were classified by Schol-Schwarz (1968) in *Rhinoctadiella* Nannf. according to a very broad generic concept. *Ramichloridium* was originally erected by Stahel (1937) with *R. musae* Stahel as type species. However, because his publication lacked a Latin diagnosis, the genus was invalid. Stahel also invalidly described *Chloridium musae* Stahel for a fungus causing leaf spots (tropical speckle disease) on banana. Ellis (1976) validated *Chloridium musae* as *Veronaea musae* M.B. Ellis, and *Ramichloridium musae* as *Periconiella musae* Stahel ex M.B. Ellis.

*Periconiella* Sacc. (1885) [type species *P. velutina* (G. Winter) Sacc.] differs from *Veronaea* Cif. & Montemart. chiefly based on its dark brown, apically branched conidiophores. However, de Hoog (1977) observed numerous specimens of *V. musae* to exhibit branched conidiophores in culture, as did Stahel (1937) for *Ramichloridium musae*. De Hoog (1977) subsequently re-introduced *Ramichloridium*, but typified it with *R. apiculatum* (J.H.

Mill., Giddens & A.A. Foster) de Hoog. He regarded *V. musae* and *P. musae* to be conspecific, and applied the name *R. musae* (Stahel ex M.B. Ellis) de Hoog to both species, regarding *Periconiella musae* as basionym. The circumscription by de Hoog was based on their similar morphology and ecology. Central in his genus concept was the observed presence of more or less differentiated and pigmented conidiophores, with predominantly aseptate conidia produced on a sympodially proliferating rachis. De Hoog (1977) also used some ecological features as additional characters to discriminate *Ramichloridium* from other genera, noting, for instance, that species in *Ramichloridium* were non-pathogenic to humans (de Hoog 1977, Campbell & Al-Hedaithy 1993). This delimitation, however, was not commonly accepted (McGinnis & Schell 1980). De Hoog *et al.* (1983) further discussed the problematic separation of *Ramichloridium* from genera such as *Rhinoctadiella*, *Veronaea* and *Cladosporium* Link. It was further noted that the main feature to distinguish *Ramichloridium* from *Rhinoctadiella*, was the presence of exophiala-type budding cells in species of *Rhinoctadiella* (de Hoog 1977, de Hoog *et al.* 1983, Veerkamp & Gams 1983). The separation of *Veronaea* from this complex is more problematic, as the circumscriptions provided by Ellis (1976) and Morgan-Jones (1979, 1982) overlap with that of *Ramichloridium sensu* de Hoog (1977). *Cladosporium* is more distinct, having very conspicuous, protuberant, darkened and thickened, coronate conidial scars, and catenate conidia (David 1997, Braun *et al.* 2003, Schubert *et al.* 2007 – this volume).

To date 26 species have been named in *Ramichloridium*; they not only differ in morphology, but also in life style. *Ramichloridium mackenziei* C.K. Campb. & Al-Hedaithy is a serious human pathogen, causing cerebral phaeohyphomycosis (Al-Hedaithy *et al.* 1988, Campbell & Al-Hedaithy 1993), whereas *R. musae* causes tropical speckle disease on members of the *Musaceae* (Stahel 1937, Jones 2000). Another plant-pathogenic species, *R. pini* de Hoog & Rahman, causes a needle disease on *Pinus contorta* (de Hoog *et al.* 1983). Other clinically relevant species of *Ramichloridium* are *R. basitonum* de Hoog and occasionally *R. schulzeri* (Sacc.) de Hoog, while the remaining species tend to be common soil saprobes.

No teleomorph has thus far been linked to species of *Ramichloridium*. The main question that remains is whether shared morphology among the species in this genus reflects common ancestry (Seifert 1993, Untereiner & Naveau 1999). To delineate anamorphic genera adequately, morphology and conidial ontogeny alone are no longer satisfactory (Crous *et al.* 2006a, b), and DNA data provide additional characters to help delineate species and genera (Taylor *et al.* 2000, Mostert *et al.* 2006, Zipfel *et al.* 2006). The aim of the present study was to integrate morphological and cultural features with DNA sequence data to resolve the species concepts and generic limits of the taxa currently placed in *Periconiella*, *Ramichloridium*, *Rhinocladia* and *Veronaea*, and to resolve the status of several new cultures that were isolated during the course of this study.

## MATERIALS AND METHODS

### Isolates

Species names, substrates, geographical origins and GenBank accession numbers of the isolates included in this study are listed in Table 1. Fungal isolates are maintained in the culture collection of the Centraalbureau voor Schimmelcultures (CBS) in Utrecht, the Netherlands.

### DNA extraction, amplification and sequence analysis

Genomic DNA was extracted from colonies grown on 2 % malt extract agar (MEA, Difco) (Gams *et al.* 2007) using the FastDNA kit (BIO101, Carlsbad, CA, U.S.A.). The primers ITS1 and ITS4 (White *et al.* 1990) were used to amplify the internal transcribed spacer region (ITS) of the nuclear ribosomal RNA operon, including: the 3' end of the 18S rRNA gene, the first internal transcribed spacer region (ITS1), the 5.8S rRNA gene, the second internal transcribed spacer region (ITS2) and the 5' end of 28S rRNA gene. Part of the large subunit 28S rRNA (LSU) gene was amplified with primers LR0R (Rehner & Samuels 1994) and LR5 (Vilgalys & Hester 1990). The ITS region was sequenced only for those isolates for which these data were not available. The ITS analyses confirmed the proposed classification based on LSU analysis for each major clade and are not presented here in detail; but the sequences are deposited in GenBank where applicable. The PCR reaction was performed in a mixture with 0.5 units *Taq* polymerase (Bioline, London, U.K.), 1× PCR buffer, 0.5 mM MgCl<sub>2</sub>, 0.2 mM of each dNTP, 5 pmol of each primer, approximately 10–15 ng of fungal genomic DNA, with the total volume adjusted to 25 µL with sterile water. Reactions were performed on a GeneAmp PCR System 9700 (Applied Biosystems, Foster City, CA) with cycling conditions consisting of 5 min at 96 °C for primary denaturation, followed by 36 cycles at 96 °C (30 s), 52 °C (30 s), and 72 °C (60 s), with a final 7 min extension step at 72 °C to complete the

reaction. The amplicons were sequenced using BigDye Terminator v. 3.1 (Applied Biosystems, Foster City, CA) or DYEnamicET Terminator (Amersham Biosciences, Freiburg, Germany) Cycle Sequencing Kits and analysed on an ABI Prism 3700 (Applied Biosystems, Foster City, CA) under conditions recommended by the manufacturer. Newly generated sequences were subjected to a Blast search of the NCBI databases, sequences with high similarity were downloaded from GenBank and comparisons were made based on the alignment of the obtained sequences. Sequences from GenBank were also selected for similar taxa. The LSU tree was rooted using sequences of *Athelia epiphylla* Pers. and *Paulliticortium ansatum* Libertas as outgroups. Phylogenetic analysis was performed with PAUP (Phylogenetic Analysis Using Parsimony) v. 4.0b10 (Swofford 2003), using the neighbour-joining algorithm with the uncorrected ("p"), the Kimura 2-parameter and the HKY85 substitution models. Alignment gaps longer than 10 bases were coded as single events for the phylogenetic analyses; the remaining gaps were treated as missing data. Any ties were broken randomly when encountered. Phylogenetic relationships were also inferred with the parsimony algorithm using the heuristic search option with simple taxon additions and tree bisection and reconstruction (TBR) as the branch-swapping algorithm; alignment gaps were treated as a fifth character state and all characters were unordered and of equal weight. Branches of zero length were collapsed and all multiple, equally parsimonious trees were saved. Only the first 5 000 equally most parsimonious trees were saved. Other measures calculated included tree length, consistency index, retention index and rescaled consistency index (TL, CI, RI and RC, respectively). The robustness of the obtained trees was evaluated by 1 000 bootstrap replications. Bayesian analysis was performed following the methods of Crous *et al.* (2006c). The best nucleotide substitution model was determined using MrModeltest v. 2.2 (Nylander 2004). MRBAYES v. 3.1.2 (Ronquist & Huelsenbeck 2003) was used to perform phylogenetic analyses, using a general time-reversible (GTR) substitution model with inverse gamma rates, dirichlet base frequencies and the temp value set to 0.5. New sequences were lodged with NCBI's GenBank (Table 1) and the alignment and trees with TreeBASE ([www.treebase.org](http://www.treebase.org)).

### Morphology

Cultural growth rates and morphology were recorded from colonies grown on MEA for 2 wk at 24 °C in the dark, and colony colours were determined by reference to the colour charts of Rayner (1970). Microscopic observations were made from colonies cultivated on MEA and OA (oatmeal agar, Gams *et al.* 2007), using a slide culture technique. Slide cultures were set up in Petri dishes containing 2 mL of sterile water, into which a U-shaped glass rod was placed, extending above the water surface. A block of freshly growing fungal colony, approx. 1 cm square was placed onto a sterile microscope slide, covered with a somewhat larger, sterile glass cover slip, and incubated in the moist chamber. Fungal sporulation was monitored over time, and when optimal, images were captured by means of a Nikon camera system (Digital Sight DS-5M, Nikon Corporation, Japan). Structures were mounted in lactic acid, and 30 measurements (× 1 000 magnification) determined wherever possible, with the extremes of spore measurements given in parentheses.

**Table 1.** Isolates of *Ramichloridium* and similar genera used for DNA analysis and morphological studies.

Species	Accession number <sup>1</sup>	Source	Origin	GenBank numbers (LSU, ITS)
<i>Myrmecridium flexuosum</i>	CBS 398.76*; IMI 203547	Soil	Suriname	EU041825, EU041768
<i>Myrmecridium schulzeri</i>	CBS 100.54; JCM 6974	Soil	Zaire	EU041826, EU041769
	CBS 134.68; ATCC 16310	Soil	Germany	EU041827, EU041770
	CBS 156.63	<i>Homo sapiens</i>	Netherlands	EU041828, EU041771
	CBS 188.96	Soil	Papua New Guinea	EU041829, EU041772
	CBS 304.73	Wheat straw	South Africa	EU041830, EU041773
	CBS 305.73; JCM 6967	Wheat straw	South Africa	EU041831, EU041774
	CBS 325.74; JCM 7234	<i>Triticum aestivum</i>	Netherlands	EU041832, EU041775
	CBS 381.87	—	Australia	EU041833, EU041776
	CBS 642.76	<i>Malus sylvestris</i>	Switzerland	EU041834, EU041777
	CBS 114996	<i>Cannomois virgata</i>	South Africa	EU041835, EU041778
<i>Periconiella arcuata</i>	CBS 113477*	<i>Ischyrolepsis subverticellata</i>	South Africa	EU041836, EU041779
<i>Periconiella levispora</i>	CBS 873.73*	<i>Turpinia pomifera</i>	Sri Lanka	EU041837, EU041780
<i>Periconiella velutina</i>	CBS 101948*; CPC 2262	<i>Brabejum stellatifolium</i>	South Africa	EU041838, EU041781
	CBS 101949; CPC 2263	<i>Brabejum stellatifolium</i>	South Africa	EU041839, EU041782
	CBS 101950; CPC 2264	<i>Brabejum stellatifolium</i>	South Africa	EU041840, EU041783
<i>Pleurothecium obovoideum</i>	CBS 209.95*; MFC 12477	<i>Pasania edulis</i>	Japan	EU041841, EU041784
<i>Pseudovirgaria hyperparasitica</i>	CBS 121735; CPC 10702	On <i>Phragmidium</i> sp. on <i>Rubus coreanus</i>	Korea	EU041822, EU041765
	CBS 121738; CPC 10704	On <i>Phragmidium</i> sp. on <i>Rubus coreanus</i>	Korea	EU041823, EU041766
	CBS 121739*; CPC 10753	On <i>Pucciniastrum agrimoniae</i> on <i>Agrimonia pilosa</i>	Korea	EU041824, EU041767
<i>Radulidium epichloës</i>	CBS 361.63*; MUCL 3124	<i>Epichloë typhina</i>	U.S.A.	EU041842, EU041785
<i>Radulidium</i> sp.	CBS 115704	<i>Poaceae</i>	Guyana	EU041843, EU041786
<i>Radulidium subulatum</i>	CBS 287.84	<i>Puccinia allii</i>	U.K.	EU041844, EU041787
	CBS 405.76*	<i>Phragmites australis</i>	Czech Republic	EU041845, EU041788
	CBS 912.96	Incubator for cell cultures	Germany	EU041846, EU041789
	CBS 101010	<i>Lasioptera arundinis</i>	Czech Republic	EU041847, EU041790
<i>Ramichloridium apiculatum</i>	CBS 156.59*; ATCC 13211; IMI 100716; JCM 6972; MUCL 7991; MUCL 15753; QM 7716	Forest soil	U.S.A.	EU041848, EU041791
	CBS 390.67	<i>Cucumis sativus</i>	South Africa	EU041849, EU041792
	CBS 391.67; JCM 6966	<i>Aloe</i> sp.	South Africa	EU041850, EU041793
	CBS 400.76; IMI 088021	Soil	Pakistan	EU041851, EU041794
<i>Ramichloridium australiense</i>	CBS 121710	<i>Musa banksii</i>	Australia	EU041852, EU041795
<i>Ramichloridium biverticillatum</i>	CBS 335.36	<i>Musa sapientum</i>	—	EU041853, EU041796
<i>Ramichloridium brasilianum</i>	CBS 283.92*	Forest soil	Brazil	EU041854, EU041797
<i>Ramichloridium cerophilum</i>	CBS 103.59*	<i>Sasa</i> sp.	Japan	EU041855, EU041798
<i>Ramichloridium indicum</i>	CBS 171.96	—	—	EU041856, EU041799
<i>Ramichloridium musae</i>	CBS 190.63; MUCL 9557	<i>Musa sapientum</i>	—	EU041857, EU041800
	CBS 365.36*; JCM 6973; MUCL 9556	<i>Musa sapientum</i>	Surinam	EU041858, EU041801
<i>Ramichloridium pini</i>	CBS 461.82*; MUCL 28942	<i>Pinus contorta</i>	U.K.	EU041859, EU041802
<i>Ramichloridium strelitziae</i>	CBS 121711	<i>Strelitzia</i> sp.	South Africa	EU041860, EU041803
<i>Rhinochlaidiella anceps</i>	CBS 157.54; ATCC 15680; MUCL 1081; MUCL 7992; MUCL 15756	<i>Fagus sylvatica</i>	France	EU041861, EU041804
	CBS 181.65*; ATCC 18655; DAOM 84422; IMI 134453; MUCL 8233; OAC 10215	Soil	Canada	EU041862, EU041805
<i>Rhinochlaidiella basitona</i>	CBS 101460*; IFM 47593	<i>Homo sapiens</i>	Japan	EU041863, EU041806
<i>Rhinochlaidiella fasciculata</i>	CBS 132.86*	Decayed wood	India	EU041864, EU041807
<i>Rhinochlaidiella mackenziei</i>	CBS 367.92; NCPF 2738; UTMB 3169	<i>Homo sapiens</i>	Israel	EU041865, EU041808

Table 1. (Continued).

Species	Accession number <sup>1</sup>	Source	Origin	GenBank numbers (LSU, ITS)
	CBS 368.92; UTMB 3170	<i>Homo sapiens</i>	Israel	EU041866, EU041809
	CBS 102590; NCPF 2853	<i>Homo sapiens</i>	United Arab Emirates	EU041867, EU041810
<i>Rhinochadiella phaeophora</i>	CBS 496.78*; IMI 287527	Soil	Colombia	EU041868, EU041811
<i>Rhinochadiella</i> sp.	CBS 264.49; MUCL 9904	Honey	France	EU041869, EU041812
<i>Rhodoveronaea varioseptata</i>	CBS 431.88*	<i>Bertia moriformis</i>	Germany	EU041870, EU041813
<i>Thysanorea papuana</i>	CBS 212.96*	—	Papua New Guinea	EU041871, EU041814
<i>Veronaea botryosa</i>	CBS 121.92	<i>Xanthorrhoea preissii</i>	Australia	EU041872, EU041815
	CBS 254.57*; IMI 070233; MUCL 9821	—	Italy	EU041873, EU041816
	CBS 350.65; IMI 115127; MUCL 7972	Goat dung	India	EU041874, EU041817
<i>Veronaea compacta</i>	CBS 268.75*	—	South Africa	EU041876, EU041819
<i>Veronaea japonica</i>	CBS 776.83*	On dead bamboo culm	Japan	EU041875, EU041818
<i>Veronaeopsis simplex</i>	CBS 588.66*; IMI 203547	<i>Acacia karroo</i>	South Africa	EU041877, EU041820
<i>Zasmidium cellare</i>	CBS 146.36	Wine cellar	—	EU041878, EU041821

<sup>1</sup>ATCC: American Type Culture Collection, Virginia, U.S.A.; CBS: Centraalbureau voor Schimmelcultures, Utrecht, The Netherlands; CPC: Culture collection of Pedro Crous, housed at CBS; DAOM: Plant Research Institute, Department of Agriculture (Mycology), Ottawa, Canada; IFM: Research Center for Pathogenic Fungi and Microbial Toxicoses, Chiba University, Chiba, Japan; IMI: International Mycological Institute, CABI-Bioscience, U.K.; JCM: Japan Collection of Microorganism, RIKEN BioResource Center, Japan; MFC: Matsushima Fungus Collection, Kobe, Japan; MUCL: Mycotheque de l' Université Catholique de Louvain, Louvain-la-Neuve, Belgium; NCPF: The National Collection of Pathogenic Fungi, Holborn, London, U.K.; OAC: Department of Botany and Genetics, University of Guelph, Ont., Canada; QM: Quartermaster Research and Development Center, U.S. Army, MA, U.S.A.; UTMB: University of Texas Medical Branch, Texas, U.S.A.

\*Ex-type cultures.

## RESULTS

### Phylogeny

The manually adjusted alignment of the 28S rDNA data contained 137 sequences (including the two outgroups) and 995 characters including alignment gaps. Of the 748 characters used in the phylogenetic analysis, 373 were parsimony-informative, 61 were variable and parsimony-uninformative, and 314 were constant. Neighbour-joining analysis using the three substitution models on the LSU alignment yielded trees with similar topology and bootstrap values. Parsimony analysis of the alignment yielded 5 000 equally most parsimonious trees, one of which is shown in Fig. 1 (TL = 2 157, CI = 0.377, RI = 0.875, RC = 0.330). The Markov Chain Monte Carlo (MCMC) analysis of four chains started from a random tree topology and lasted 2 000 000 generations. Trees were saved each 1 000 generations, resulting in 2 000 trees. Burn-in was set at 500 000 generations after which the likelihood values were stationary, leaving 1 500 trees from which the consensus tree (Fig. 2) and posterior probabilities (PP's) were calculated. The average standard deviation of split frequencies was 0.043910 at the end of the run. Among the neighbour-joining, Bayesian and parsimony analyses, the trees differed in the hierarchical order of the main families and the support values (data not shown; e.g. the support within of the *Capnodiales* in Figs 1–2).

The phylogenetic trees (Figs 1–2) show that the *Ramichloridium* species segregate into eight distinct clades, residing in the *Capnodiales* (*Mycosphaerellaceae* and *Teratosphaeriaceae*), the *Chaetothyriales* (*Herpotrichiellaceae*), the *Pleosporales*, and five other clades of which the relationships remain to be elucidated. The type species of *Ramichloridium*, *R. apiculatum*, together with *R. musae*, *R. cerophilum* (Tubaki) de Hoog, *R. indicum* (Subram.) de Hoog, *R. pini* and three new species respectively isolated from *Musa banksii*, *Strelitzia nicolai*, and forest soil, reside in different parts of the *Capnodiales* clade (all in the *Mycosphaerellaceae*, except for the

species from forest soil which clusters in the *Teratosphaeriaceae*). The second clade (in the *Chaetothyriomycetes* clade), including the human-pathogenic species *R. mackenziei* and *R. basitonum*, together with *R. fasciculatum* V. Rao & de Hoog and *R. anceps* (Sacc. & Ellis) de Hoog, groups together with *Rhinochadiella* in the *Herpotrichiellaceae*. The third clade (in the *Sordariomycetes* clade) includes *R. obovoideum* (Matsush.) de Hoog, which in a Blast search was found to have affinity with *Carpoligna pleurothecii* F.A. Fernández & Huhndorf (*Chaetosphaeriales*). The fourth clade (in the *Sordariomycetes* clade) includes a veronaea-like isolate from *Bertia moriformis*, with phylogenetic affinity to the *Annulatascaceae* (*Sordariomycetidae*). The fifth clade (in the *Sordariomycetes* clade) includes *R. schulzeri* var. *schulzeri* and *R. schulzeri* var. *flexuosum* de Hoog, the closest relatives being *Thyridium vestitum* (Fr.) Fuckel in the *Thyridiaceae* and *Magnaporthe grisea* (T.T. Hebert) M.E. Barr in the *Magnaportheaceae*. The sixth clade (in the *Incertae sedis* clade) includes *R. subulatum* de Hoog, *R. epichloës* (Ellis & Dearn.) de Hoog and a species isolated from the *Poaceae*. Three ramichloridium-like isolates from *Rubus coreanus* and *Agrimonia pilosa* form another unique clade (in the *Incertae sedis* clade) with uncertain affinity. *Veronaea simplex* Papendorf clusters as sister taxon to the *Venturiaceae* representing the eighth clade (*Dothideomycetes*). The type species of *Periconiella*, *P. velutina*, clusters within the *Mycosphaerellaceae* (*Capnodiales* clade), whereas *P. papuana* Aptroot resides in the *Herpotrichiellaceae* (*Chaetothyriales* clade). *Veronaea botryosa* Cif. & Montemart., the type species of *Veronaea*, also resides in the *Herpotrichiellaceae*.

### Taxonomy

The species previously described in *Ramichloridium* share some morphological features, including erect, pigmented, more or less differentiated conidiophores, sympodially proliferating conidiogenous cells and predominantly aseptate conidia. Other than conidial morphology, features of the conidiogenous apparatus that

appear to be more phylogenetically informative include pigmentation of vegetative hyphae, conidiophores and conidia, denticle density on the rachis, and structure of the scars. By integrating these data

with the molecular data set, more natural genera are delineated, which are discussed below.

### Key to ramichloridium-like genera

1. Conidiogenous cells integrated, terminal and lateral on creeping or ascending hyphae (differentiation between branched vegetative hyphae and conidiophores barely possible); conidiogenous loci bulging, more or less umbonate, apex rounded; occurring on rust pustules ..... ***Pseudovirgaria***
1. Conidiogenous cells integrated in distinct conidiophores; conidiogenous loci non-umbonate (flat, not prominent; subcylindrical or conical denticles; or terminally flat-tipped; or thickened and darkened); rarely occurring on rust pustules, but if so, with a raduliform rachis and distinct denticles ..... 2
2. Conidia 0–2(–3)-septate, conidial base truncate, retaining a marginal frill after liberation [anamorphs of *Sordariomycetes*] ..... ***Rhodoveronaea***
2. Conidial base without marginal frill ..... 3
3. Conidiophores composed of a well-developed erect stalk and a terminal branched head ..... 4
3. Conidiophores unbranched or, if branched, branches loose, irregular or dichotomous, but not distinctly separated into stalk and branched head ..... 5
4. Conidiophores dimorphic, either macronematous, dark brown with a dense apical cluster of branches or micronematous, undifferentiated, resembling vegetative hyphae; both kinds with a denticulate rachis; conidia predominantly 1-septate [anamorph of *Chaetothyriales*] ..... ***Thysanorea***
4. Conidiophores monomorphic; branched head with fewer branches and looser; conidiogenous loci usually flat, non-prominent, less denticle-like; conidia aseptate to pluriseptate [anamorphs of *Capnodiales*] ..... ***Periconiella***
5. Rachis with denticles 1–1.5 µm long, denticles almost cylindrical; conidia at least partly in short chains ..... ***Pleurothecium***
5. Rachis with denticles less than 1 µm long, denticles not cylindrical or denticles lacking, rachis with flat, barely prominent scars ..... 6
6. Conidia predominantly septate ..... 7
6. Conidia predominantly aseptate ..... 8
7. Conidiophores up to 200 µm long; rachis straight, not to slightly geniculate; conidiogenous loci more or less flat, barely prominent, unthickened, slightly darkened [anamorphs of *Chaetothyriales*, *Herpotrichiellaceae*] ..... ***Veronaea***
7. Conidiophores up to 60 µm long; rachis distinctly geniculate; conidiogenous loci denticle-like, prominent, up to 0.5 µm high, slightly thickened and darkened [anamorph of *Pleosporales*, *Venturiaceae*] ..... ***Veronaeopsis***
8. Vegetative mycelium entirely hyaline; rachis long, hyaline, with widely scattered pimple-shaped, terminally pointed, unpigmented denticles ..... ***Myrmecridium***
8. Vegetative mycelium at least partly pigmented; conidiogenous loci distinct, non-denticulate, somewhat darkened-refractive, or denticles, if present, neither pimple-shaped nor pointed ..... 9
9. Rachis distinctly raduliform, with distinct, prominent blunt denticles, 0.5–1 µm long; scars and hila unthickened, but pigmented ..... ***Radulidium***
9. Rachis not distinctly raduliform, at most subdenticulate; scars flat or only slightly prominent (subdenticulate), shorter ..... 10
10. Conidiophores usually poorly differentiated from the vegetative hyphae; conidial apparatus often loosely branched; exophiala-like budding cells usually present in culture [anamorphs of *Chaetothyriales*, *Herpotrichiellaceae*] ..... ***Rhinocladia***
10. Conidiophores usually well differentiated from the vegetative mycelium (macronematous), usually unbranched; without exophiala-like states [anamorphs of *Capnodiales*] ..... ***Ramichloridium***

### ***Capnodiales* (*Mycosphaerellaceae*, *Teratosphaeriaceae*)**

The type species of *Ramichloridium*, *R. apiculatum*, together with *R. indicum* cluster as a sister group to the *Dissoconium* de Hoog, Oorschot & Hijwegen clade in the *Mycosphaerellaceae*. Some other *Ramichloridium* species, including *R. musae*, *R. biverticillatum* Arzanlou & Crous, *R. pini* and *R. cerophilum*, are also allied with members of the *Mycosphaerellaceae*. Three additional new species are introduced for *Ramichloridium* isolates

from *Musa banksii*, *Strelitzia nicolai*, and forest soil. *Periconiella velutina*, the type species of *Periconiella*, which also resides in the *Mycosphaerellaceae*, is morphologically sufficiently distinct to retain its generic status. Two new species of *Periconiella* are introduced for isolates obtained from *Turpinia pomifera* and *Ischyrolepis subverticellata* in South Africa. *Zasmidium cellare* (Pers.) Fr., the type species of *Zasmidium* (Pers.) Fr., is also shown to cluster within the *Mycosphaerellaceae*.



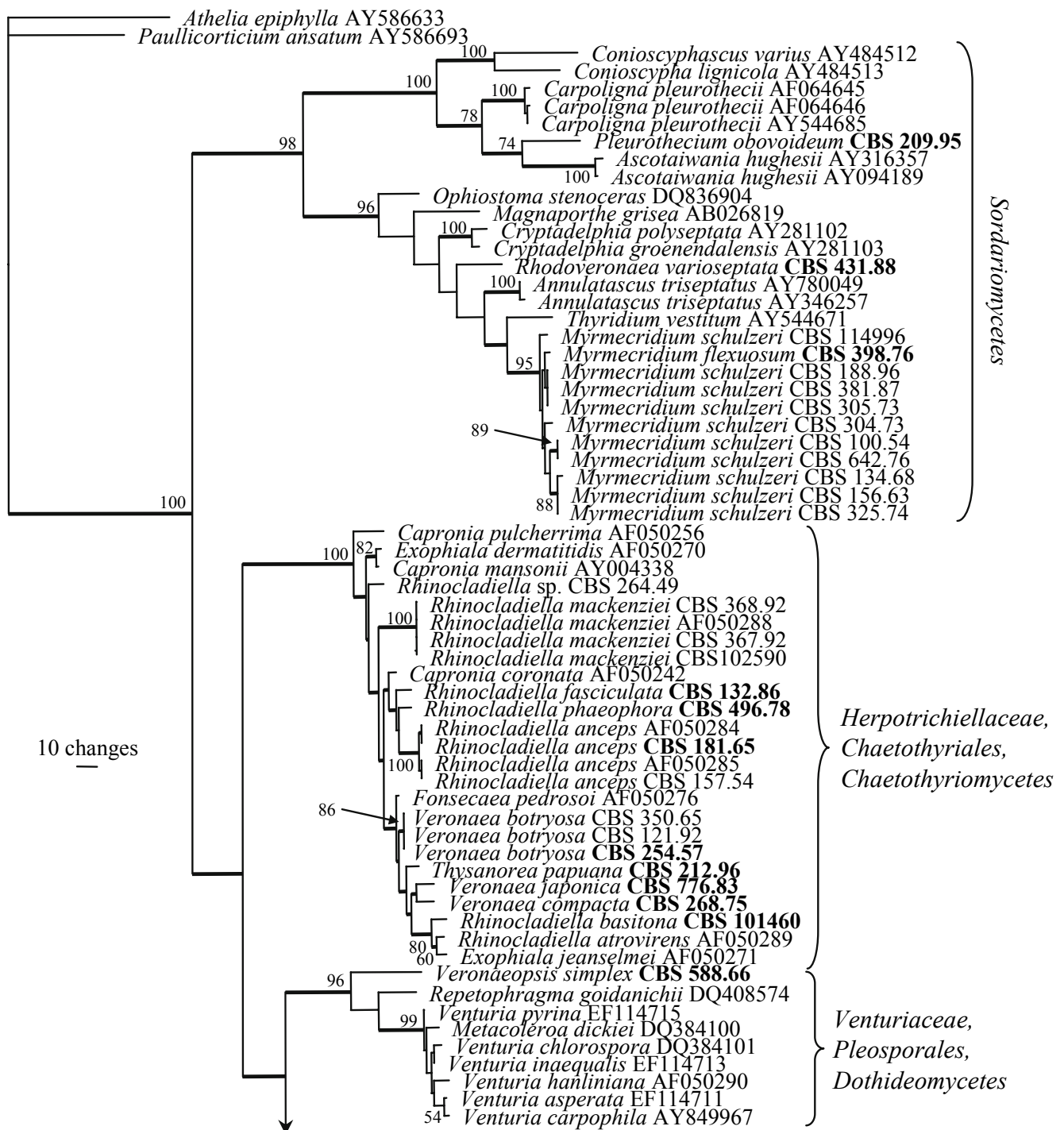


Fig. 1. (Page 62–63). One of 5 000 equally most parsimonious trees obtained from a heuristic search with simple taxon additions of the LSU sequence alignment using PAUP v. 4.0b10. The scale bar shows 10 changes; bootstrap support values from 1 000 replicates are shown at the nodes. Thickened lines indicate the strict consensus branches and ex-type sequences are printed in bold face. The tree was rooted to two sequences obtained from GenBank (*Athelia epiphylla* AY586633 and *Paullicorticium ansatum* AY586693).

*Periconiella* Sacc., in Sacc. & Berlese, Atti Ist. Veneto Sci., Ser. 6, 3: 727. 1885.

*In vitro*: Colonies with entire margin; aerial mycelium rather compact, raised, velvety, olivaceous-grey; reverse olivaceous-black. *Submerged hyphae* verrucose, hyaline, thin-walled, 1–3 µm wide; *aerial hyphae* subhyaline, later becoming dark brown, thick-walled, smooth. *Conidiophores* arising vertically from creeping hyphae, straight or flexuose, up to 260 µm long, dark brown at the base, paler towards the apex, thick-walled; in the upper part bearing short branches. *Conidiogenous cells* terminally integrated, polyblastic, smooth or verrucose, subcylindrical, mostly not or barely

geniculate-sinuous, variable in length, subhyaline, later becoming pale brown, fertile part as wide as the basal part, proliferating sympodially, sometimes becoming septate and forming a short, straight rachis with pigmented, slightly thickened and hardly prominent, more or less flat scars. *Conidia* solitary, occasionally in short chains, 0–multi-septate, subhyaline to rather pale olivaceous or olivaceous-brown, smooth to verrucose, globose, ellipsoidal to obovoid or obclavate, with a slightly darkened and thickened hilum; conidial secession schizolytic.

*Type species*: *P. velutina* (G. Winter) Sacc., *Miscell. mycol.* 2: 17. 1884.

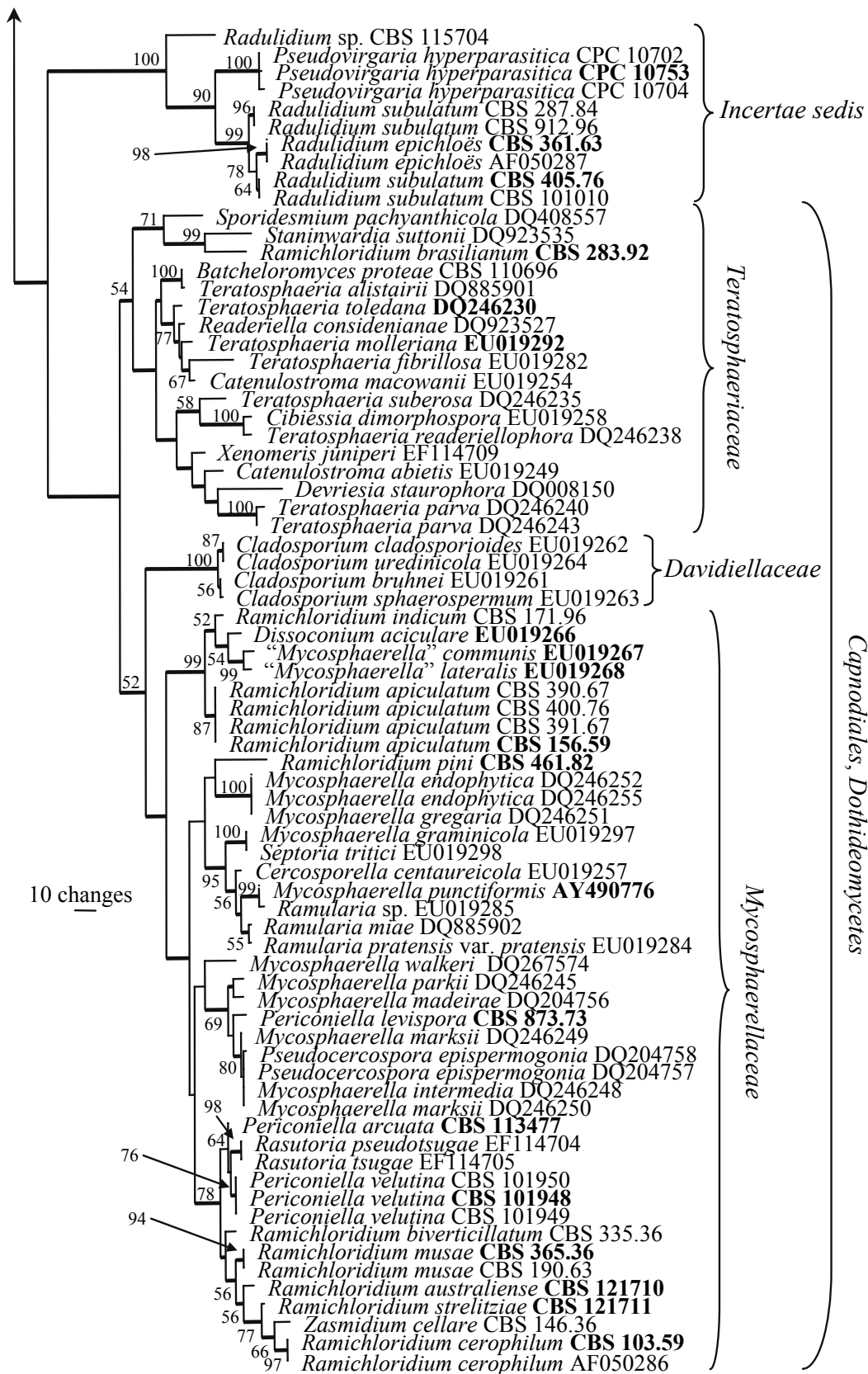


Fig. 1. (Continued).

Notes: *Periconiella* is distinct from other ramichloridium-like genera by its conidiophores that are prominently branched in the upper part, and by its darkened, thickened conidial scars, that are more or less flat and non-prominent. Although conidiophores are also branched in the upper part in *Thysanorea* Arzanlou, W. Gams & Crous, the branching pattern in the latter genus is different from

that of *Periconiella*. *Thysanorea* has a complex head consisting of up to six levels of branches, while in *Periconiella* the branching is limited, with mainly primary and secondary branches. Furthermore, *Thysanorea* is characterised by having dimorphic conidiophores and more or less prominent denticle-like conidiogenous loci.

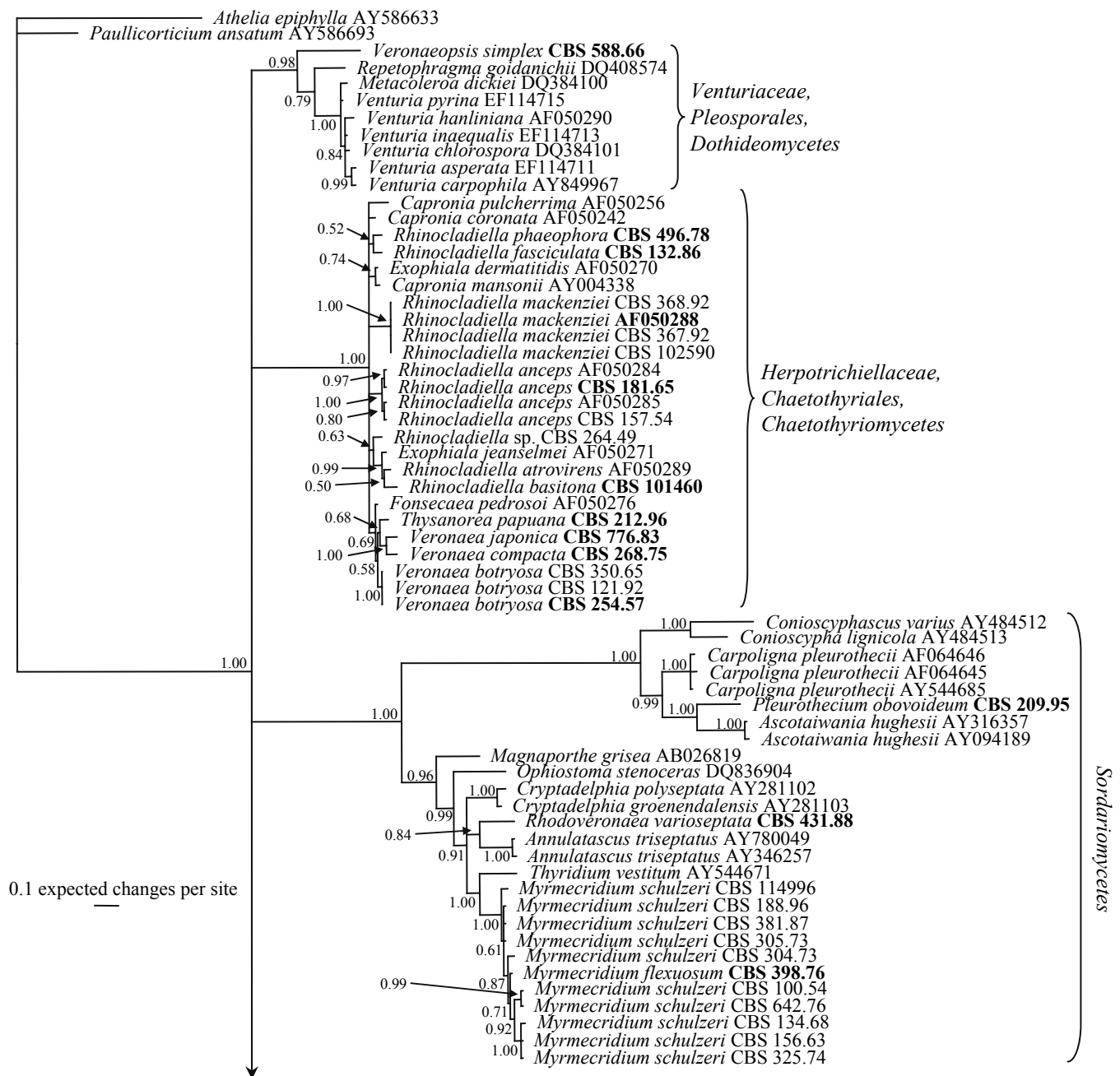


Fig. 2. (Page 64–65). Consensus phylogram (50 % majority rule) of 1 500 trees resulting from a Bayesian analysis of the LSU sequence alignment using MrBAYES v. 3.1.2. Bayesian posterior probabilities are indicated at the nodes. Ex-type sequences are printed in bold face. The tree was rooted to two sequences obtained from GenBank (*Athelia epiphylla* AY586633 and *Paullicorticium ansatum* AY586693).

*Periconiella velutina* (G. Winter) Sacc., *Miscell. mycol.* 2: 17. 1884. Fig. 3.

*Basionym*: *Periconia velutina* G. Winter, *Hedwigia* 23: 174. 1884.

*In vitro*: Submerged hyphae verrucose, hyaline, thin-walled, 1–3 µm wide; aerial hyphae subhyaline, later becoming dark brown, thick-walled, smooth. Conidiophores arising vertically from creeping hyphae, straight or flexuose, up to 260 µm long, dark brown at the base, paler towards the apex, thick-walled; in the upper part bearing short branches, 10–35 µm long. Conidiogenous cells mostly terminally integrated, sometimes discrete, smooth or verrucose, cylindrical, variable in length, subhyaline, later becoming pale brown, fertile part as wide as the basal part, proliferating sympodially, sometimes becoming septate and forming a short, straight rachis with pigmented, slightly thickened and hardly prominent, more

or less flat scars, less than 1 µm diam. Conidia 0(–)1-septate, subhyaline, thin-walled, verrucose or smooth, globose, ellipsoidal to obovoid, (7)–8–9(–11) × (2.5)–3(–4) µm, with a slightly darkened and thickened hilum, 1.5–2 µm diam.

*Cultural characteristics*: Colonies on MEA slow-growing, reaching 4 mm diam after 14 d at 24 °C, with entire margin; aerial mycelium rather compact, raised, velvety, olivaceous-grey; reverse olivaceous-black.

*Specimens examined*: South Africa, Cape Town, on *Brabejum stellatifolium*, P. MacOwan, herb. G. Winter (B), **lectotype selected here**; Cape Town, on leaves of *Brabejum stellatifolium* (= *B. stellatum*), P. MacOwan, PAD, F42165, F462166, **isolectotypes**; Stellenbosch, Jonkershoek Nature Reserve, on *Brabejum stellatifolium*, 21 Jan. 1999, J.E. Taylor, **epitype designated here** CBS H-15612, cultures ex-epitype CBS 101948–101950.



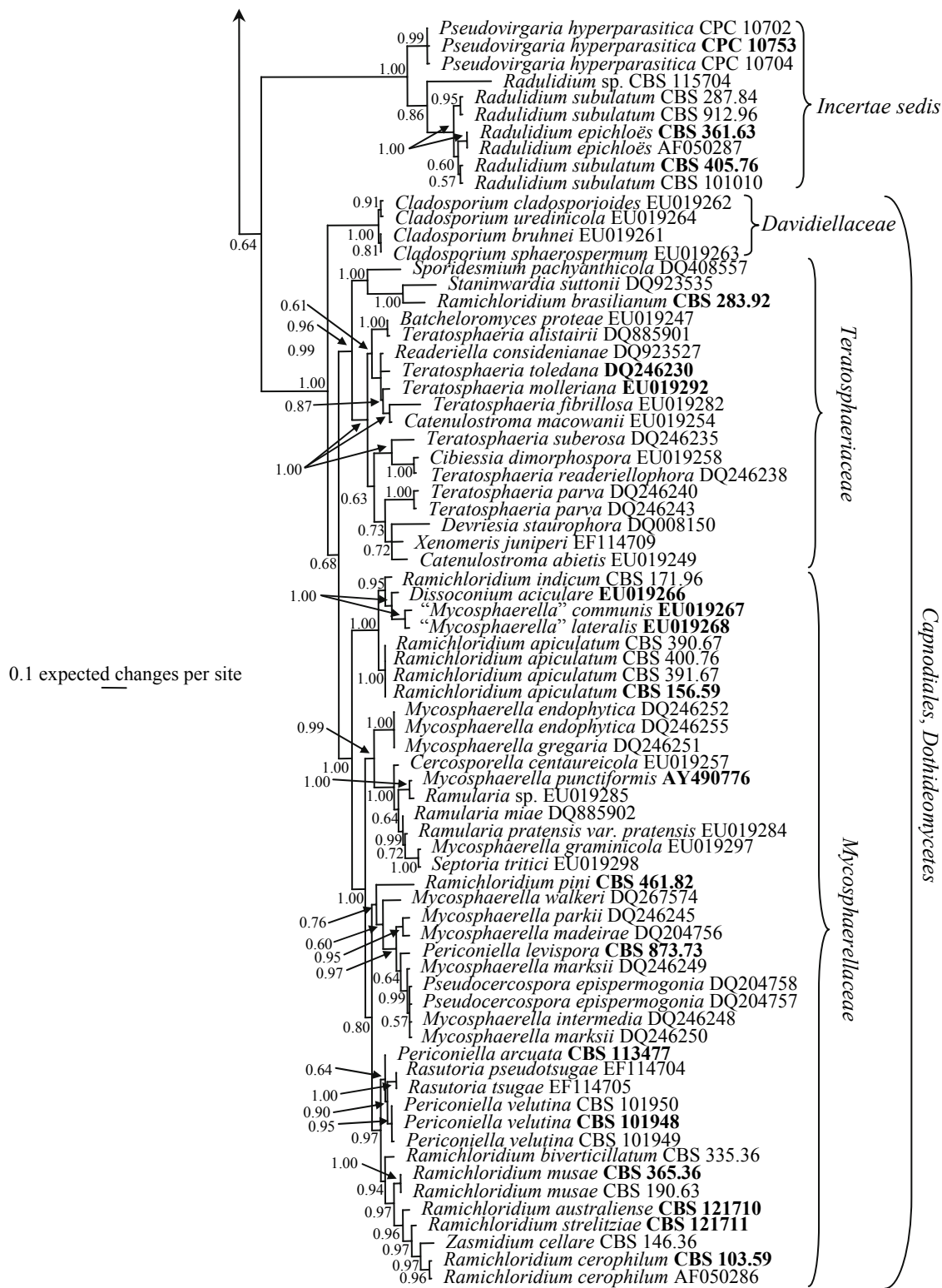


Fig. 2. (Continued).

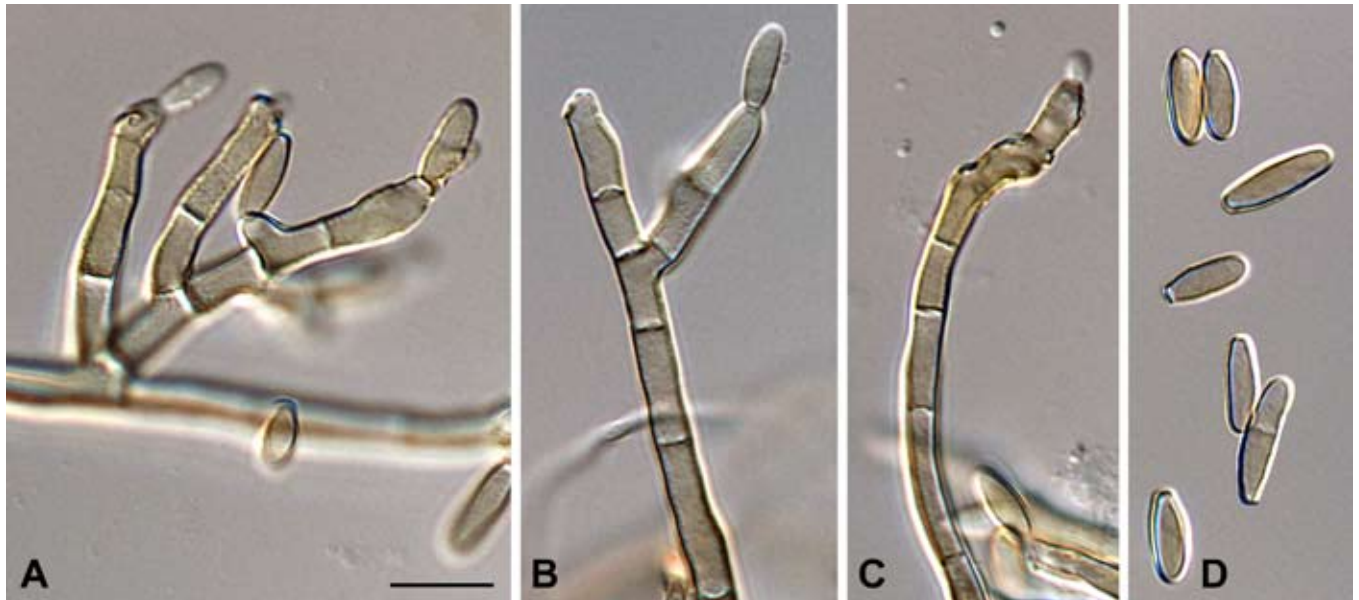
*Periconiella arcuata* Arzanlou, S. Lee & Crous, **sp. nov.** MycoBank MB504547. Figs 4, 7A.

*Etymology*: Named after its curved conidia.

Ab aliis speciebus *Periconiellae* conidiis obclavatis, rectis vel curvatis, (30–)53–61(–79) × (3–)5(–7) µm, distinguenda.

*Submerged hyphae* smooth, hyaline, thin-walled, 2 µm wide; *aerial hyphae* pale brown, smooth or verrucose, slightly narrower. *Conidiophores* arising vertically from creeping hyphae, straight or flexuose, up to 300 µm long, dark brown at the base, paler

towards the apex, thick-walled; loosely branched in the upper part, bearing short branches. *Conidiogenous cells* integrated, cylindrical, variable in length, 20–50 µm long, subhyaline, later becoming pale brown, fertile part as wide as the basal part, proliferating sympodially, forming a geniculate conidium-bearing rachis with pigmented and thickened, prominent, cone-shaped scars, 1 µm diam. *Conidia* formed singly, obclavate, straight or mostly curved, 0(–4)-septate, coarsely verrucose, pale olive, thin-walled, tapering towards the apex, (30–)53–61(–79) × (3–)5(–7) µm, with a narrowly truncate base and a darkened, hardly thickened hilum, 2 µm diam; microcyclic conidiation observed in culture.

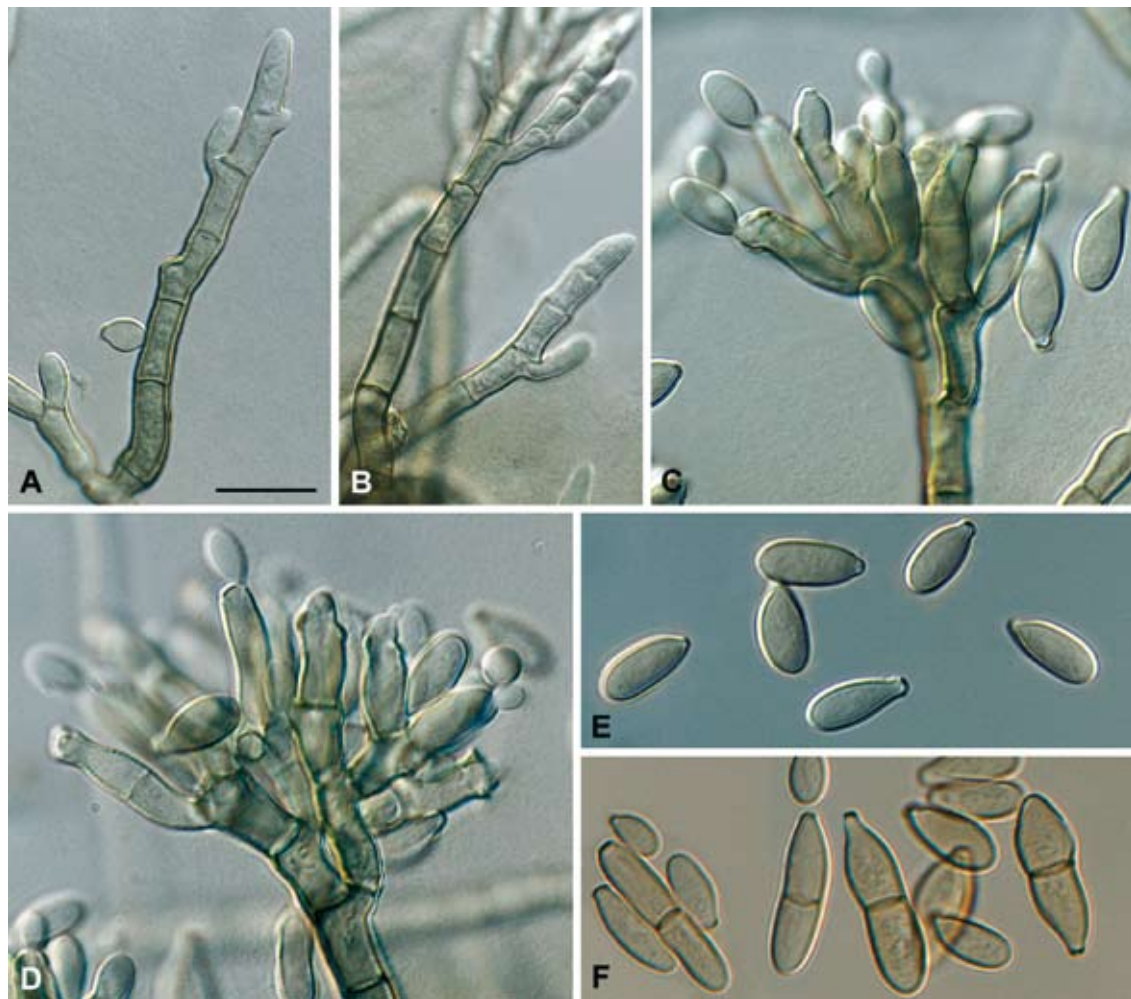


**Fig. 3.** *Periconiella velutina* (CBS 101948). A–B. Macronematous conidiophores with short branches in the upper part. C. Sympodially proliferating conidiogenous cell with darkened and slightly thickened scars. D. Conidia. Scale bar = 10  $\mu$ m.

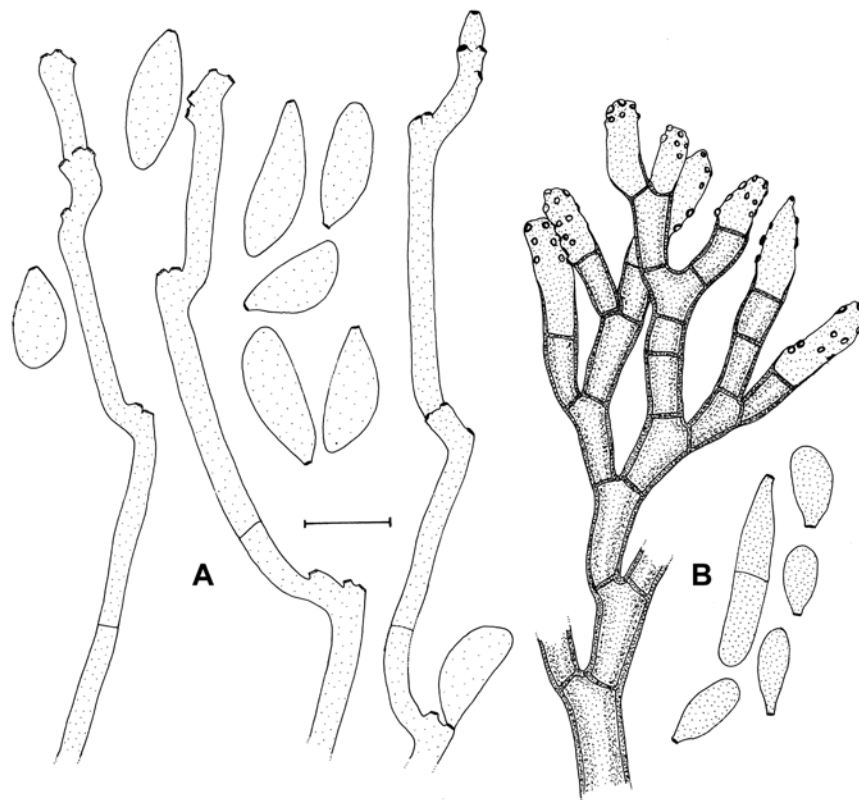


**Fig. 4.** *Periconiella arcuata* (CBS 113477). A–B. Sympodially proliferating conidiogenous cells with darkened, thickened and cone-shaped scars. C–E. Macronematous conidiophores with loose branches in the upper part. F–I. Conidia. Scale bar = 10  $\mu$ m.





**Fig. 5.** *Periconiella levispora* (CBS 873.73). A–C. Conidial apparatus at different stages of development, which gives rise to macronematous conidiophores with dense branches in the upper part. D. Sympodially proliferating conidiogenous cells with darkened and somewhat protruding scars. E–F. Conidia with truncate base and darkened hilum. Scale bar = 10  $\mu$ m.



**Fig. 6.** A. *Pseudovirgaria hyperparasitica* (CBS 121739 = CPC 10753). B. *Periconiella levispora* (CBS 873.73). Scale bar = 10  $\mu$ m.

**Cultural characteristics:** Colonies on MEA reaching 12 mm diam after 14 d at 24 °C, with entire, smooth, sharp margin; mycelium compacted, becoming hairy, colonies up to 1 mm high; surface olivaceous to olivaceous-grey, reverse dark grey-olivaceous to olivaceous-black.

**Specimen examined:** **South Africa**, Western Cape Province, Kogelberg, on dead culms of *Ischyrolepis subverticillata*, May 2001, S. Lee, **holotype** CBS H-19927, culture ex-type CBS 113477.

***Periconiella levispora*** Arzanlou, W. Gams & Crous, **sp. nov.** MycoBank MB504546. Figs 5–6B.

**Etymology:** (Latin) *levis* = smooth.

A simili *Periconiella velutina* conidiis levibus et maioribus, ad 23 µm longis distinguenda.

**In vitro:** *Submerged hyphae* smooth, hyaline, thin-walled, 2–2.5 µm wide; *aerial hyphae* subhyaline, later becoming dark brown, thick-walled, smooth. *Conidiophores* arising vertically from creeping aerial hyphae, dark brown at the base, paler towards the apex, thick-walled; in the upper part bearing several short branches, up to 120 µm long. *Conidiogenous cells* integrated, occasionally discrete, cylindrical, variable in length, 10–20 µm long, subhyaline, later becoming pale brown, fertile part as wide as the basal part, proliferating sympodially, forming a short rachis with pigmented and slightly thickened, somewhat protruding scars, less than 1 µm diam. *Conidia* solitary, 0(–2)-septate, smooth, pale olivaceous, cylindrical, ellipsoidal, pyriform to clavate, (7–)11–14(–23) × (3–)4–5(–6) µm, with a truncate base and a darkened, slightly thickened hilum, 2 µm diam.

**Cultural characteristics:** Colonies on MEA slow-growing, reaching 5 mm diam after 14 d at 24 °C, with entire margin; aerial mycelium compact, raised, velvety, olivaceous-grey; reverse olivaceous-black.

**Specimen examined:** **Sri Lanka**, Hakgala Botanic Gardens, on dead leaves of *Turpinia pomifera*, Jan. 1973, W. Gams, **holotype** CBS H-15611, culture ex-type CBS 873.73.

***Ramichloridium*** Stahel ex de Hoog, Stud. Mycol. 15: 59. 1977.

**In vitro:** Colonies flat to raised, with entire margin; surface olivaceous-green to olivaceous-black. *Mycelium* consisting of submerged and aerial hyphae; submerged hyphae hyaline to subhyaline, thin-walled, aerial hyphae smooth or verrucose. *Conidiophores* straight, unbranched, rarely branched, thick-walled, dark brown (darker than the subtending hyphae), continuous or with several additional thin septa. *Conidiogenous cells* integrated, terminal, polyblastic, smooth, thick-walled, golden-brown, apical part subhyaline, with sympodial proliferation, straight or flexuose, geniculate or nodose, with conspicuous conidiogenous loci; scars crowded or scattered, unthickened, unpigmented to faintly pigmented, or slightly prominent denticles. *Conidia* solitary, 0–1-septate, subhyaline to pale brown, smooth to coarsely verrucose, rather thin-walled, obovate, obconical or globose to ellipsoidal, fusiform, with a somewhat prominent, slightly pigmented hilum; conidial secession schizolytic.

**Type species:** *R. apiculatum* (J.H. Mill., Giddens & A.A. Foster) de Hoog, Stud. Mycol. 15: 69. 1977.

***Ramichloridium apiculatum*** (J.H. Mill., Giddens & A.A. Foster) de Hoog, Stud. Mycol. 15: 69. 1977. Fig. 8.

**Basionym:** *Chloridium apiculatum* J.H. Mill., Giddens & A.A. Foster, Mycologia 49: 789. 1957.

= *Veronaea apiculata* (J.H. Mill., Giddens & A.A. Foster) M.B. Ellis, in Ellis, More Dematiaceous Hyphomycetes: 209. 1976.

[non *Rhinochadiella apiculata* Matsush., in Matsushima, *Icon. Microfung. Mats. lect.*: 122. 1975].

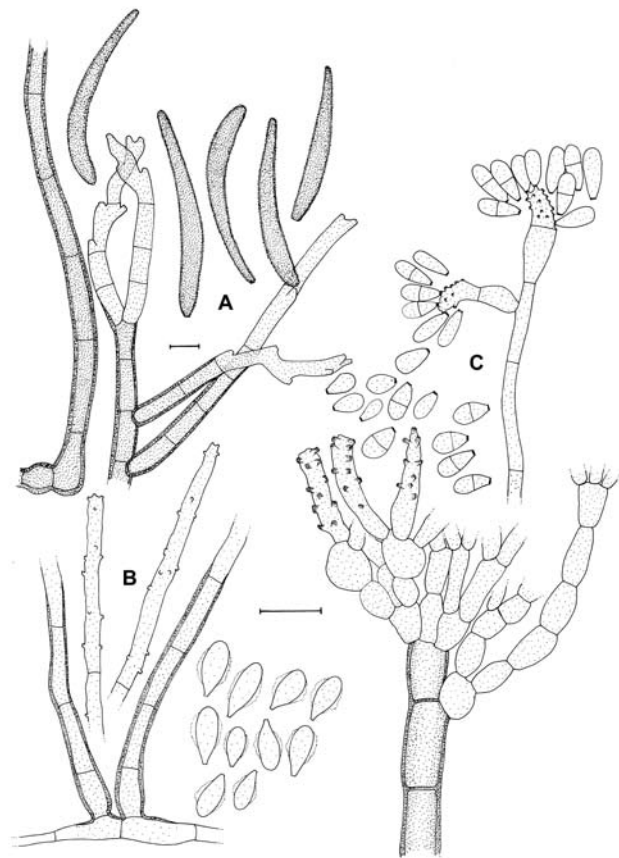
= *Rhinochadiella indica* Agarwal, Lloydia 32: 388. 1969.

[non *Chloridium indicum* Subram., Proc. Indian Acad. Sci., Sect. B, 42: 286. 1955].

**In vitro:** *Submerged hyphae* hyaline to subhyaline, thin-walled, 1–2.5 µm wide; *aerial hyphae* slightly darker, smooth-walled. *Conidiophores* generally arising at right angles from creeping aerial hyphae, straight, unbranched, thick-walled, dark brown, continuous or with 1–2(–3) additional thin septa, up to 100 µm long; intercalary cells 10–28 µm long. *Conidiogenous cells* integrated, terminal, smooth, thick-walled, golden-brown, straight, cylindrical, 25–37(–47) × 2–3.5 µm; proliferating sympodially, resulting in a straight rachis with conspicuous conidiogenous loci; scars prominent, crowded, slightly pigmented, less than 1 µm diam. *Conidia* solitary, obovate to obconical, pale brown, finely verrucose, (3–)5–5.5(–7.5) × (2–)2.5–3(–4) µm, hilum conspicuous, slightly pigmented, about 1 µm diam.

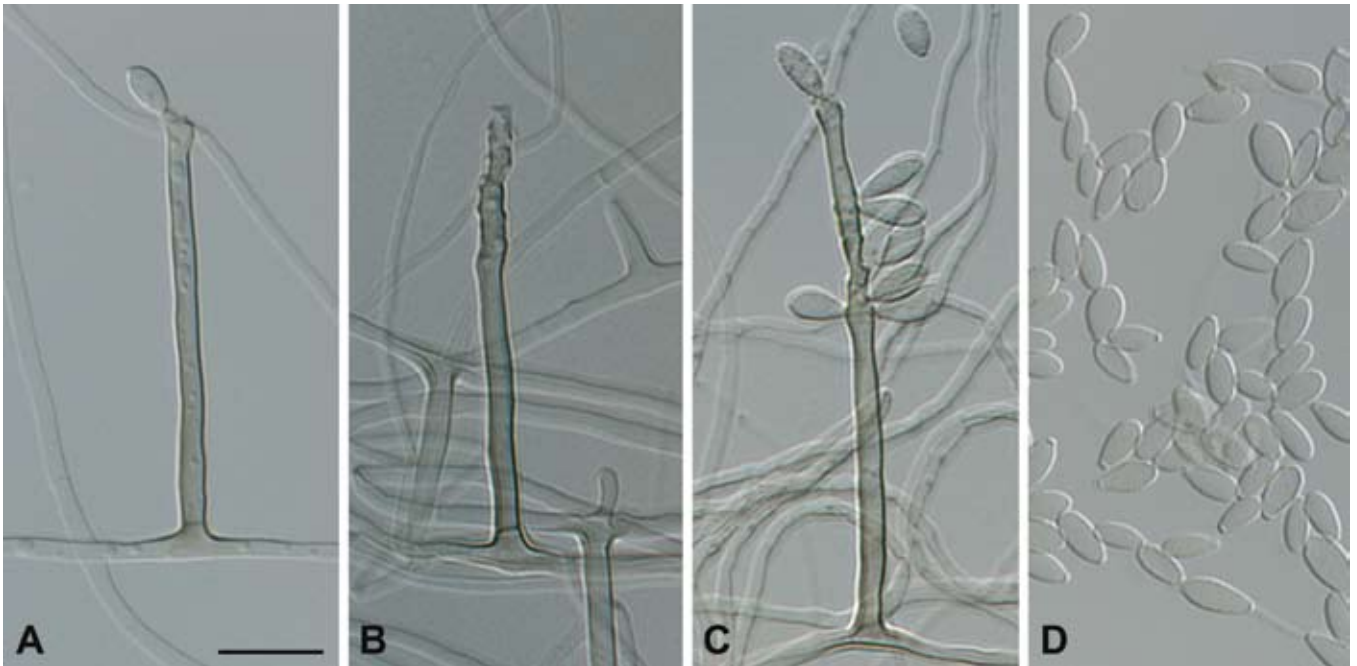
**Cultural characteristics:** Colonies on MEA reaching 35 mm diam after 14 d at 24 °C; minimum temperature for growth above 6 °C, optimum 24 °C, maximum 30 °C. Colonies raised, velvety, dense, with entire margin; surface olivaceous-green, reverse olivaceous-black, often with a diffusing citron-yellow pigment.

**Specimens examined:** **Pakistan**, Lahore, from soil, A. Kamal, CBS 400.76 = IMI 088021. **South Africa**, from preserved *Cucumis sativus* in 8-oxyquinoline sulphate, M.C. Papendorf, CBS 390.67; Potchefstroom, from *Aloe* sp., M.C. Papendorf, CBS 391.67. **U.S.A.**, Georgia, isolated from forest soil, CBS 156.59 = ATCC 13211 = IMI 100716 = QM 7716, **ex-type** culture.

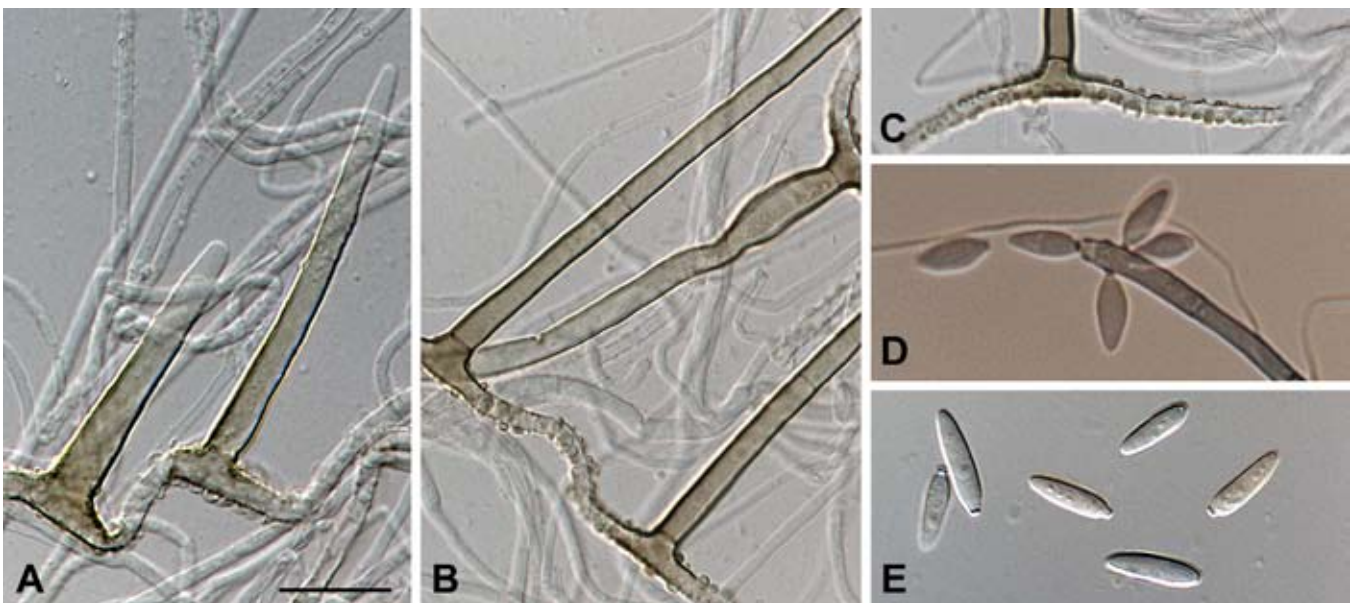


**Fig. 7.** A. *Periconiella arcuata* (CBS 113477). B. *Myrmecridium schulzeri* (CBS 325.74). C. *Thysanorea papuana* (CBS 212.96). Scale bars = 10 µm.





**Fig. 8.** *Ramichloridium apiculatum* (CBS 156.59). A–C. Macronematous conidiophores with sympodially proliferating conidiogenous cells, which give rise to a conidium-bearing rachis with crowded and prominent scars. D. Conidia. Scale bar = 10  $\mu$ m.



**Fig. 9.** *Ramichloridium australiense* (CBS 121710). A–C. Macronematous conidiophores with thick-walled and warted subtending hyphae. D. Sympodially proliferating conidiogenous cell, which results in a short rachis with darkened and slightly thickened scars. E. Conidia. Scale bar = 10  $\mu$ m.

***Ramichloridium australiense*** Arzanlou & Crous, **sp. nov.**  
MycoBank MB504548. Figs 9–10A.

**Etymology:** Named after its country of origin, Australia.

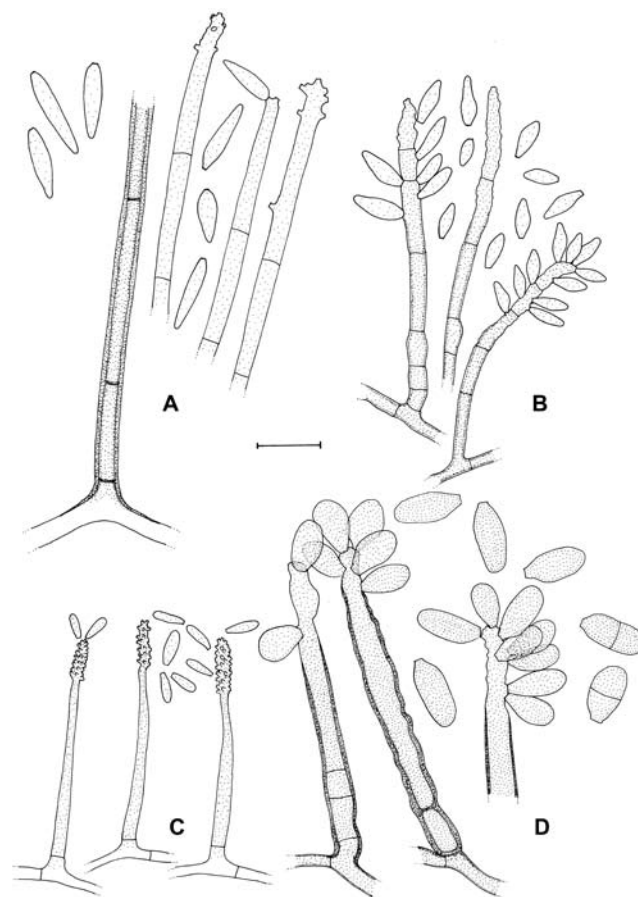
Ab aliis speciebus *Ramichloridii* conidiophoris ex hyphis verrucosis, crassitunicatis ortis distinguendum.

**In vitro:** *Submerged hyphae* hyaline, smooth, thin-walled, 1–2  $\mu$ m wide; *aerial hyphae* pale brown, warted. *Conidiophores* arising vertically and clearly differentiated from creeping aerial hyphae, up to 400  $\mu$ m tall, with several additional thin septa; intercalary cells, 8–40  $\times$  2–5  $\mu$ m, from the broadest part at the base tapering towards the apex, subhyaline, later becoming pale brown and warted in the lower part. Subtending hyphae thick-walled, warted. *Conidiogenous cells* integrated, terminal, 10–18  $\mu$ m long, proliferating sympodially,

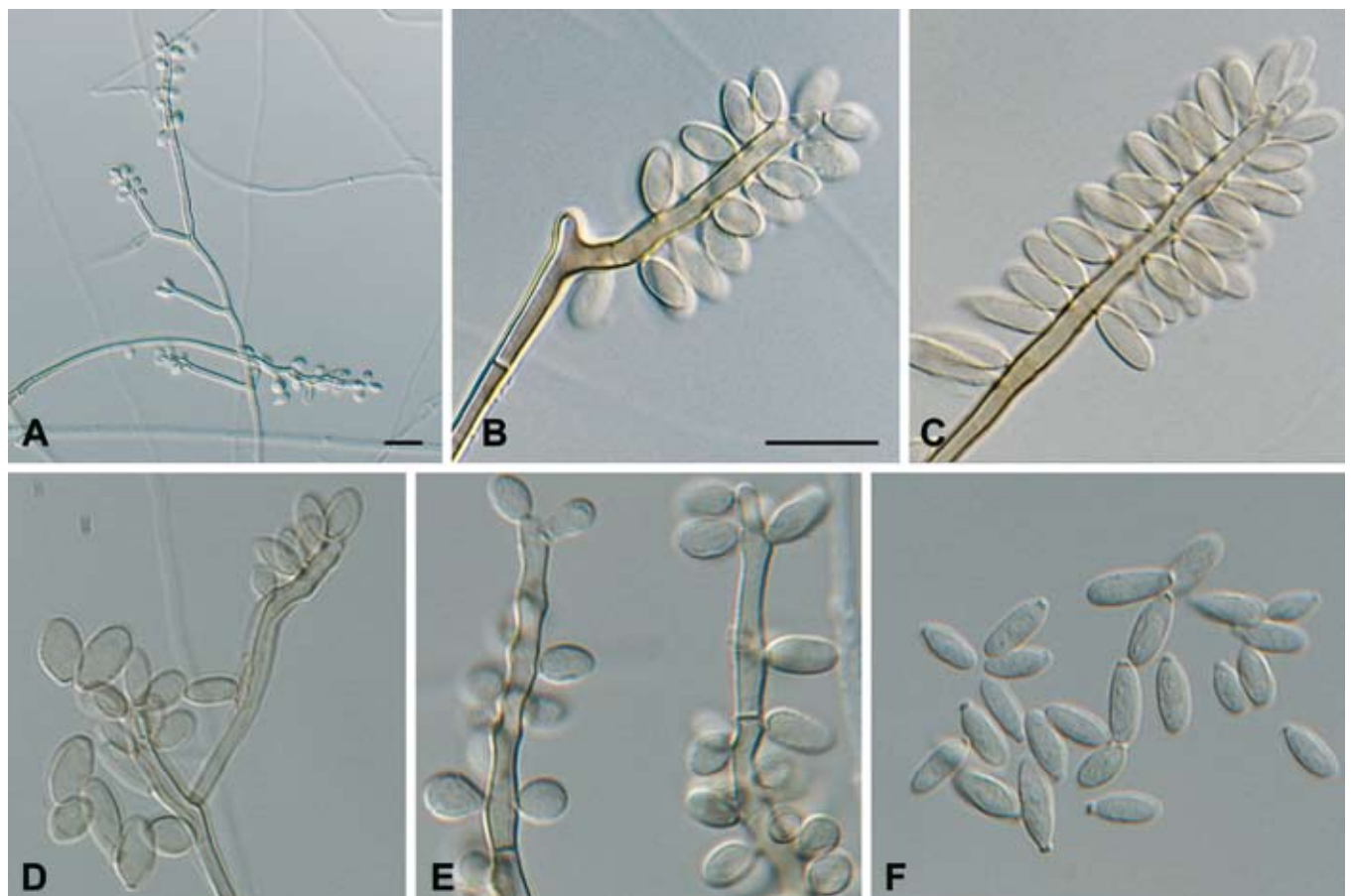
giving rise to a short rachis with conspicuous conidiogenous loci; scars slightly thickened and darkened, about 1  $\mu$ m diam. *Conidia* solitary, aseptate, thin-walled, smooth, subhyaline, subcylindrical to obclavate, (10–)12–15(–23)  $\times$  2.5–3  $\mu$ m, with a truncate base and a slightly darkened and thickened hilum, 1.5–2  $\mu$ m diam, rarely fusing at the basal part.

**Cultural characteristics:** Colonies on MEA rather slow growing, reaching 8 mm diam after 14 d at 24  $^{\circ}$ C, with entire, smooth margin; mycelium flat, olivaceous-grey, becoming granular, with gelatinous droplets at the margin developing with aging; reverse pale olivaceous-grey.

**Specimen examined:** **Australia**, Queensland, Mount Lewis, Mount Lewis Road, 16 $^{\circ}$ 34'47.2" S, 145 $^{\circ}$ 19'7" E, 538 m alt., on *Musa banksii* leaf, Aug. 2006, P.W. Crous and B. Summerell, **holotype** CBS H-19928, culture ex-type CBS 121710.

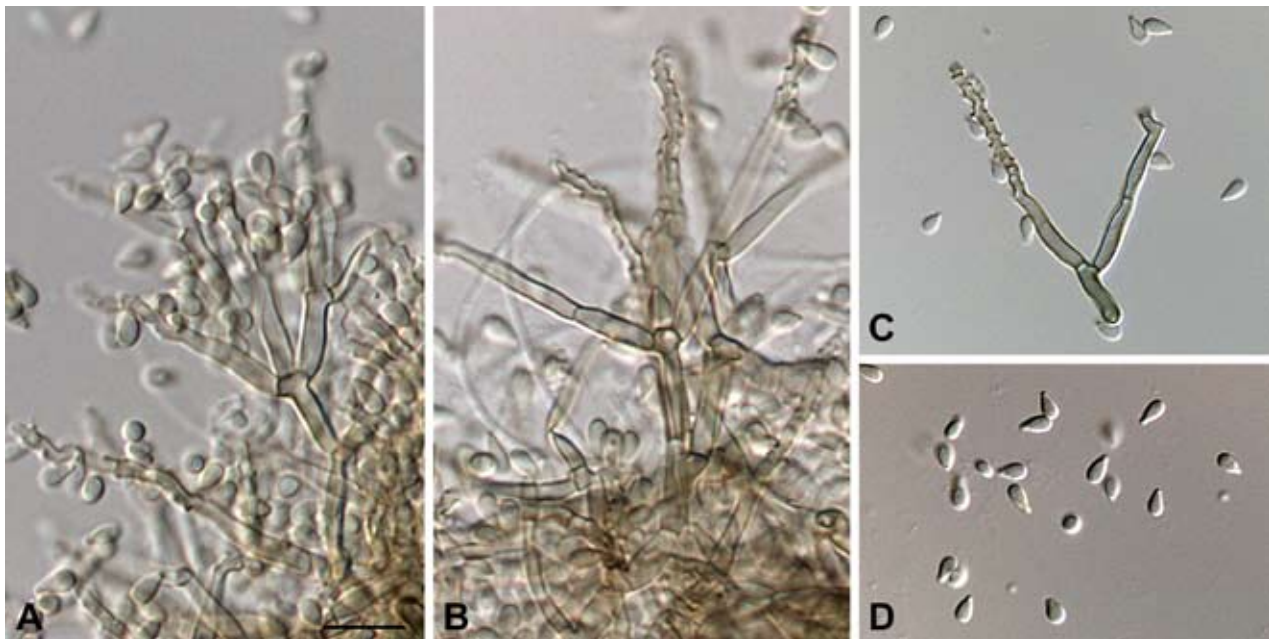


**Fig. 10.** A. *Ramichloridium australiense* (CBS 121710). B. *Ramichloridium brasilianum* (CBS 283.92). C. *Radulidium subulatum* (CBS 405.76). D. *Rhodoveronea varioseptata* (CBS 431.88). Scale bar = 10  $\mu$ m.

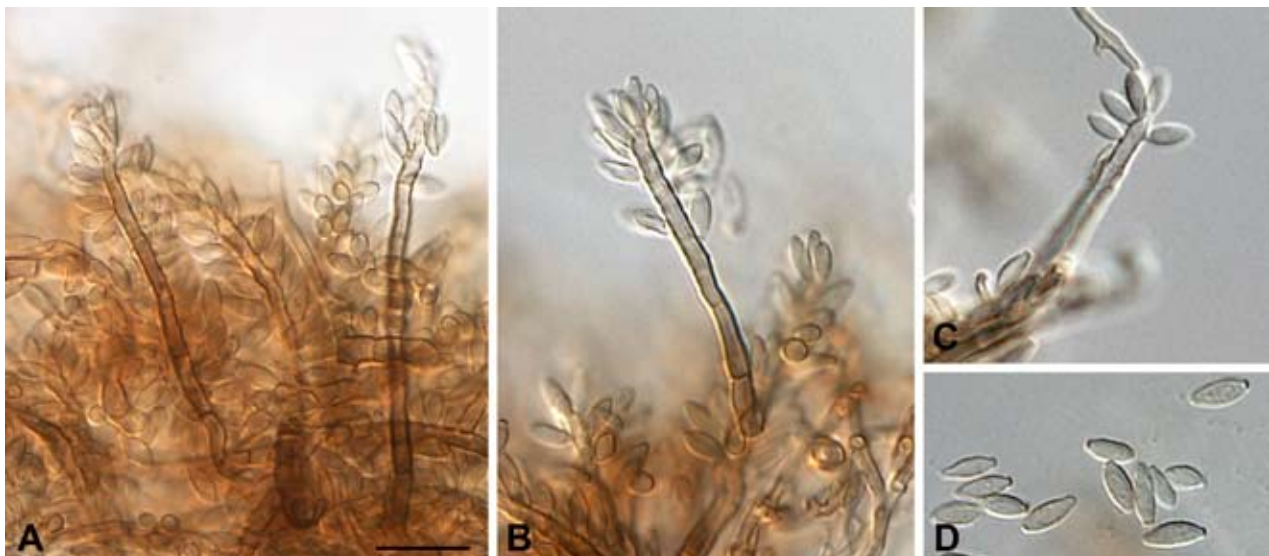


**Fig. 11.** *Ramichloridium musae* (CBS 365.36). A. Conidiophores with loose branches. B–D. Sympodially proliferating conidiogenous cells, resulting in a long conidium-bearing rachis. E. Rachis with hardly prominent, slightly darkened scars. F. Conidia. Scale bars = 10  $\mu$ m.

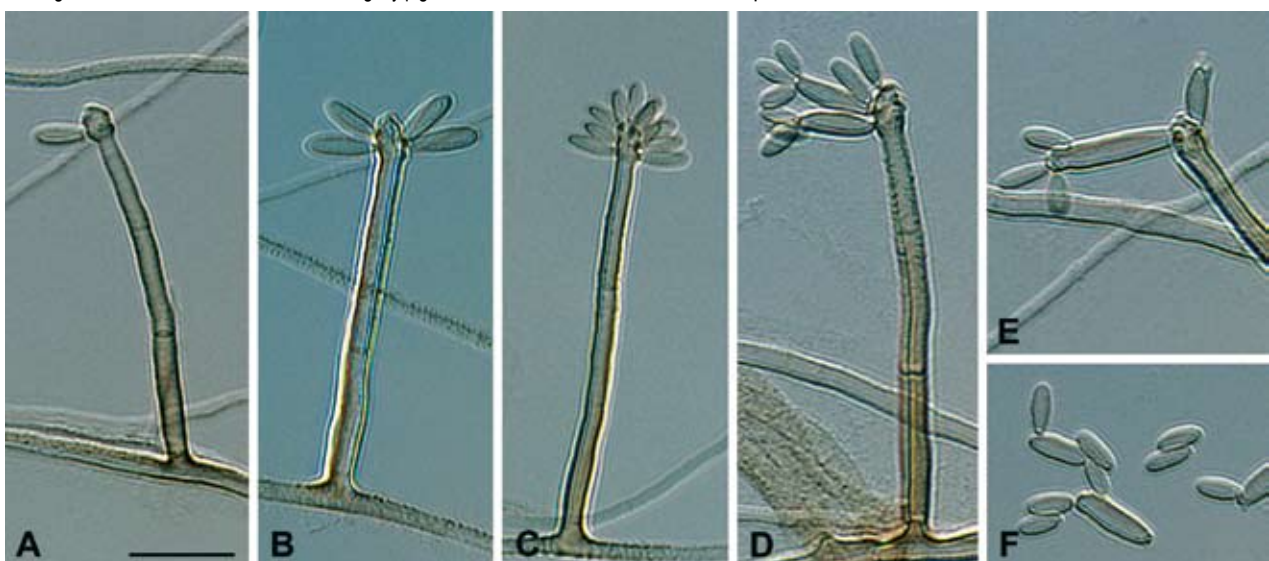




**Fig. 12.** *Ramichloridium biverticillatum* (CBS 335.36). A–B. Profusely branched and biverticillate conidiophores. C. Sympodially proliferating conidiogenous cells, which give rise to a conidium-bearing rachis with crowded, slightly pigmented and thickened scars. D. Conidia. Scale bar = 10  $\mu$ m.



**Fig. 13.** *Ramichloridium brasilianum* (CBS 283.92). A–B. Macronematous conidiophores with sympodially proliferating conidiogenous cells, resulting in a conidium-bearing rachis. C. Rachis with crowded and slightly pigmented scars. D. Conidia. Scale bar = 10  $\mu$ m.



**Fig. 14.** *Ramichloridium cerophilum* (CBS 103.59). A–C. Conidial apparatus at different stages of development, resulting in macronematous conidiophores and sympodially proliferating conidiogenous cells. D–E. Formation of secondary conidia. F. Conidia. Scale bar = 10  $\mu$ m.

**Ramichloridium musae** (Stahel ex M.B. Ellis) de Hoog, Stud. Mycol. 15: 62. 1977. Fig. 11.

*Basionym:* *Veronaea musae* Stahel ex M.B. Ellis, in Ellis, *More Dematiaceous Hyphomycetes*: 209. 1976.

≡ *Chloridium musae* Stahel, Trop. Agric., Trinidad 14: 43. 1937 (nom. inval. Art. 36).

*Misapplied name:* *Chloridium indicum* Subram., *sensu* Batista & Vital, Anais Soc. Biol. Pernambuco 15: 379. 1957.

*In vitro:* *Submerged hyphae* smooth, hyaline, thin-walled, 1–2 µm wide; *aerial hyphae* subhyaline, smooth. *Conidiophores* arising vertically and mostly sharply differentiated from creeping aerial hyphae, golden-brown; unbranched, rarely branched in the upper part, up to 250 µm tall, with up to 6 additional thin septa, cells 23–40 × 2–2.5 µm, basal cell occasionally inflated. *Conidiogenous cells* terminally integrated, cylindrical, variable in length, 10–40 µm long, golden-brown near the base, subhyaline to pale brown near the end, fertile part as wide as the basal part, later also becoming septate; rachis elongating sympodially, 2–2.5 µm wide, with hardly prominent, scattered, slightly pigmented scars, about 0.5 µm diam. *Conidia* solitary, aseptate, hyaline to subhyaline, ellipsoidal, (4–)7–8(–12) × 2–3 µm, smooth or verruculose, thin-walled, with slightly darkened hilum, about 1 µm diam.

*Cultural characteristics:* Colonies on MEA slow-growing, reaching 27 mm diam after 14 d at 24 °C, with entire, smooth, sharp margin; mycelium mostly submerged, some floccose to lanose aerial mycelium in the olivaceous-grey centre, becoming pale pinkish olivaceous towards the margin; reverse pale orange.

*Specimens examined:* **Cameroon**, from *Musa sapientum*, J.E. Heron, CBS 169.61 = ATCC 15681 = IMI 079492 = DAOM 84655 = MUCL 2689; from *Musa sapientum*, J. Brun, CBS 190.63 = MUCL 9557. **Surinam**, Paramaribo, from *Musa sapientum* leaf, G. Stahel, CBS 365.36 = JCM 6973 = MUCL 9556, **ex-type** strain of *Chloridium musae*; from *Musa sapientum*, G. Stahel, CBS 365.36; dried culture preserved as CBS H-19933.

**Ramichloridium biverticillatum** Arzanlou & Crous, **nom. nov.** MycoBank MB504549. Fig. 12.

*Basionym:* *Periconiella musae* Stahel ex M.B. Ellis, Mycol. Pap. 111: 5. 1967.

[non *Ramichloridium musae* (Stahel ex M.B. Ellis) de Hoog, 1977].  
≡ *Ramichloridium musae* Stahel, Trop. Agric., Trinidad 14: 43. 1937 (nom. inval. Art. 36).

= *Ramichloridium musae* (Stahel ex M.B. Ellis) de Hoog, Stud. Mycol. 15: 62. 1977, *sensu* de Hoog, p.p.

*Etymology:* Named after its biverticillate conidiophores.

*In vitro:* *Submerged hyphae* smooth, hyaline, thin-walled, 1–2 µm wide; *aerial hyphae* subhyaline, smooth, slightly darker. *Conidiophores* arising vertically from creeping aerial hyphae, pale brown, profusely branched, biverticillate, with up to three levels of main branches; branches tapering distally, 2–3 µm wide at the base, approx. 2 µm wide in the upper part, up to 250 µm long. *Conidiogenous cells* terminally integrated, cylindrical, variable in length, 15–50 µm long, rachis straight or geniculate, pale brown, as wide as the basal part; elongating sympodially, forming a rachis with crowded, slightly darkened and thickened minute scars, less than 0.5 µm wide. *Conidia* solitary, aseptate, hyaline to subhyaline, dacryoid to pyriform, (2–)3–4(–6) × (1.5–)2(–2.5) µm, smooth, thin-walled, with an inconspicuous hilum.

*Cultural characteristics:* Colonies on MEA slow-growing, reaching 16 mm diam after 14 d at 24 °C, with entire, smooth, sharp margin, rather compact, velvety; surface vinaceous-buff to olivaceous-buff; reverse buff.

*Specimen examined:* **Surinam**, from *Musa sapientum*, Aug. 1936, G. Stahel, CBS 335.36.

*Notes:* *Ramichloridium biverticillatum* is a new name based on *Periconiella musae*. The species is distinct from *R. musae* because of its profusely branched conidiophores, and conidia that are smaller (2–5 × 1.5–2.5 µm) than those of *R. musae* (5–11 × 2–3 µm).

**Ramichloridium brasilianum** Arzanlou & Crous, **sp. nov.** MycoBank MB504550. Figs 10B, 13.

*Etymology:* Named after its country of origin, Brazil.

A simili *Ramichloridio cerophilo* conidiis minoribus, ad 8 µm longis, et conidiis secundariis absentibus distinguendum.

*In vitro:* *Submerged hyphae* pale olivaceous, smooth or slightly rough, 1.5–2 µm wide; *aerial hyphae* olivaceous, smooth or rough, narrower and darker than the submerged hyphae. *Conidiophores* unbranched, arising vertically from creeping aerial hyphae, straight or flexuose, dark brown, with up to 10 additional septa, thick-walled, cylindrical, 2–2.5 µm wide and up to 70 µm long. *Conidiogenous cells* integrated, terminal, 10–30 µm long, proliferating sympodially, giving rise to a long, straight rachis with crowded, slightly darkened minute scars, about 0.5 µm diam. *Conidia* solitary, obovoid to fusiform with the widest part below the middle, thin-walled, verruculose, aseptate, pale brown, slightly rounded at the apex, truncate at the base, (4–)5–6(–8.5) × 2–2.5(–3) µm, with a slightly thickened and darkened hilum, 1–1.5 µm diam.

*Cultural characteristics:* Colonies on MEA slow-growing, reaching 6 mm diam after 14 d at 24 °C, velvety to hairy, colonies with entire margin, surface dark olivaceous-grey; black gelatinous exudate droplets produced on OA.

*Specimen examined:* **Brazil**, São Paulo, Peruibe, Jureia Ecological Reserve, forest soil, Jan. 1991, D. Attili, **holotype** CBS H-19929, culture ex-type CBS 283.92.

**Ramichloridium cerophilum** (Tubaki) de Hoog, Stud. Mycol. 15: 74. 1977. Fig. 14.

*Basionym:* *Acrotheca cerophila* Tubaki, J. Hattori Bot. Lab. 20: 143. 1958.

≡ *Cladosporium cerophilum* (Tubaki) Matsush., in Matsushima, *Icn. Microfung. Matsush. lect.* (Kobe): 34. 1975.

*In vitro:* *Submerged hyphae* pale olivaceous-brown, smooth or slightly rough, 1.5–3 µm wide; *aerial hyphae* olivaceous-brown, smooth or slightly rough, somewhat narrower and darker than the submerged hyphae. *Conidiophores* unbranched, arising vertically from creeping aerial hyphae, dark brown, thick-walled, smooth or verruculose, hardly tapering towards the apex, 2–3 µm wide, up to 50 µm long, with up to 3 additional septa. *Conidiogenous cells* integrated, terminal, proliferating sympodially, rachis short and straight, with crowded, prominent, pigmented unthickened scars, minute, approx. 0.5 µm diam. *Conidia* solitary, fusiform to clavate, thin-walled, smooth, 0(–1)-septate, subhyaline, (4–)6–7(–11) × (2–)2.5(–3) µm, with a conspicuous hilum, about 0.5 µm diam, slightly raised with an inconspicuous marginal frill, somehow resembling those of *Cladosporium*. Conidia sometimes producing 1–3(–4) short secondary conidia.

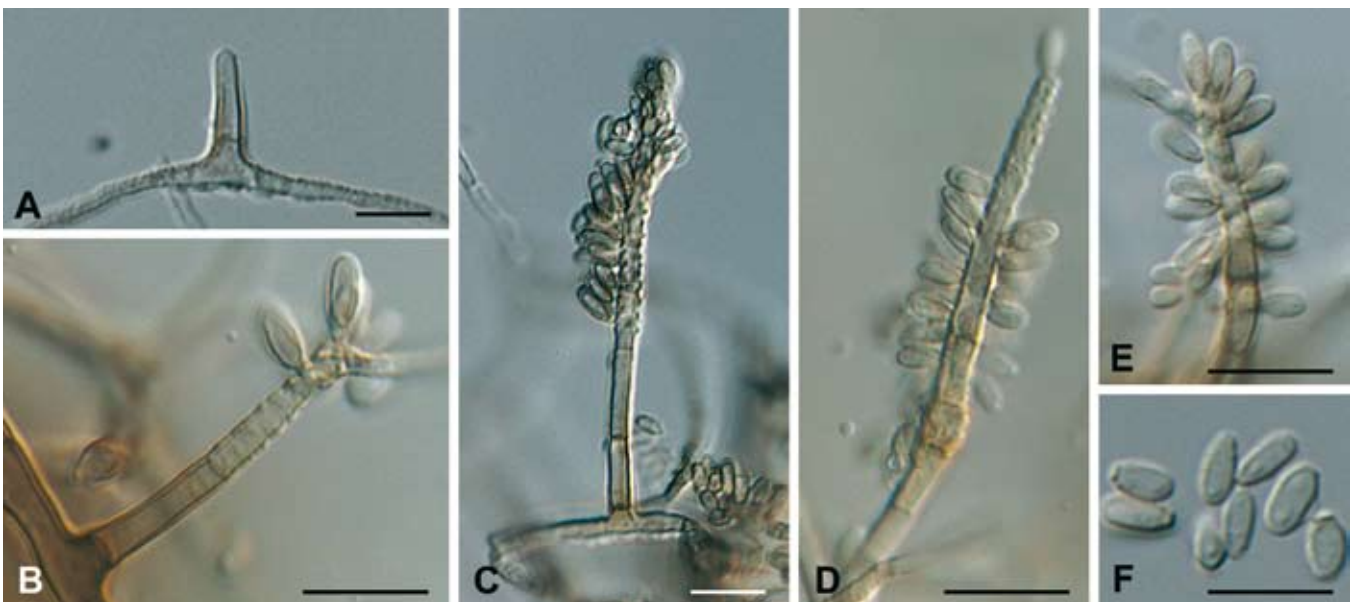
*Cultural characteristics:* Colonies on MEA rather slow-growing, reaching 12 mm diam after 14 d at 24 °C, velvety to hairy, with entire margin; surface dark olivaceous-grey, with black gelatinous exudate droplets on OA.

*Specimen examined:* **Japan**, isolated from *Sasa* sp., K. Tubaki, CBS 103.59, **ex-type**.





**Fig. 15.** *Ramichloridium indicum* (CBS 171.96). A–B. Macronematous conidiophores. C–E. Symphytally proliferating conidiogenous cells, resulting in a conidium-bearing rachis with pigmented and thickened scars. F. Conidia. Scale bar = 10  $\mu$ m.



**Fig. 16.** *Ramichloridium strelitziae* (CBS 121711). A–C. Conidial apparatus at different stages of development, resulting in macronematous conidiophores and symphytally proliferating conidiogenous cells. D–E. Rachis with crowded, slightly pigmented, thickened, circular scars. F. Conidia. Scale bars = 10  $\mu$ m.

**Notes:** Phylogenetically, this species together with *Ramichloridium apiculatum* and *R. musae* cluster within the *Mycosphaerellaceae* clade. *Ramichloridium cerophilum* can be distinguished from its relatives by the production of secondary conidia and its distinct conidial hila.

***Ramichloridium indicum*** (Subram.) de Hoog, *Stud. Mycol.* 15: 70. 1977. Fig. 15.

**Basionym:** *Chloridium indicum* Subram., *Proc. Indian Acad. Sci., Sect. B*, 42: 286. 1955 [non *Rhinochlaedia indica* Agarwal, *Lloydia* 32: 388. 1969].

≡ *Veronaea indica* (Subram.) M.B. Ellis, in Ellis, *More Dematiaceous Hyphomycetes*: 209. 1976.

= *Veronaea verrucosa* Geeson, *Trans. Brit. Mycol. Soc.* 64: 349. 1975.

**In vitro:** *Submerged hyphae* smooth, thin-walled, hyaline, 1–2.5  $\mu$ m wide, with thin septa; *aerial hyphae* coarsely verrucose, olivaceous-green, rather thick-walled, 2–2.5  $\mu$ m wide, with thin septa. *Conidiophores* arising vertically from creeping hyphae at right angles, straight, unbranched, thick-walled, smooth, dark brown, with up to 10 thin septa, up to 250  $\mu$ m long, 2–4  $\mu$ m wide, often with inflated basal cells. *Conidiogenous cells* terminally integrated, up to 165  $\mu$ m long, smooth, dark brown, symphytally proliferating, rachis straight or flexuose, geniculate or nodose, subhyaline; scars thickened and darkened, clustered at nodes, approx. 0.5  $\mu$ m diam. Microcyclic conidiation observed in culture. *Conidia* solitary, (0–)1-septate, not constricted at the septum, subhyaline to pale brown, smooth or coarsely verrucose, rather thin-walled, broadly ellipsoidal to globose, (5–)7–8(–10)  $\times$  (4–)6–6.5(–9)  $\mu$ m, with truncate base; hilum conspicuous, slightly darkened, not thickened, about 1  $\mu$ m diam.

**Cultural characteristics:** Colonies on MEA reaching 35 mm diam after 14 d at 24 °C. Colonies velvety, rather compact, slightly elevated, with entire, smooth, whitish margin, dark olivaceous-green in the central part.

**Specimen examined:** Living culture, Feb. 1996, L. Marvanová, CBS 171.96.

***Ramichloridium pini*** de Hoog & Rahman, Trans. Brit. Mycol. Soc. 81: 485. 1983.

**Specimen examined:** U.K., Scotland, Old Aberdeen, branch of *Pinus contorta* (Pinaceae), 1982, M.A. Rahman, **ex-type** strain, CBS 461.82 = MUCL 28942.

**Note:** The culture examined (CBS 461.82) was sterile. For a full description see de Hoog *et al.* (1983).

***Ramichloridium strelitziae*** Arzanlou, W. Gams & Crous, **sp. nov.** MycoBank MB504551. Figs 16–17A.

**Etymology:** Named after its host, *Strelitzia*.

**Ab aliis speciebus *Ramichloridii* conidiophoris brevibus, ad 40 µm longis, et cicatricibus rotundis, paulo protrudentibus distinguendum.**

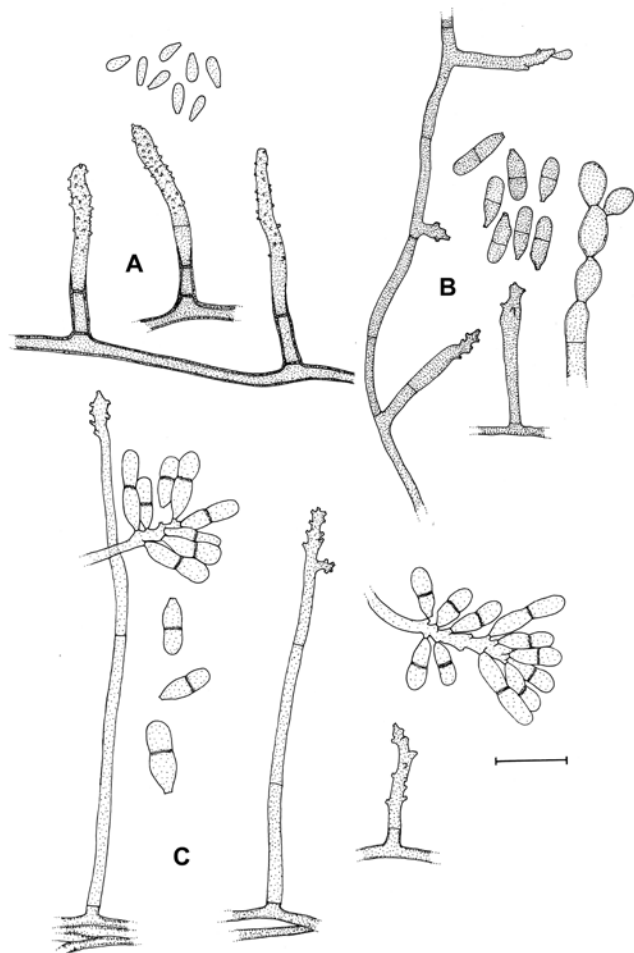
**In vitro:** *Submerged hyphae* smooth, hyaline, thin-walled, 2–2.5 µm wide; *aerial hyphae* pale brown, verrucose. *Conidiophores* arising vertically from creeping aerial hyphae, clearly differentiated from the vegetative hyphae, subhyaline, later becoming pale brown, thick-walled, smooth or verruculose, with 1–3 additional septa; up to 40 µm long and 2 µm wide. *Conidiogenous cells* integrated, terminal, cylindrical, variable in length, 10–35 µm long, subhyaline, later turning pale brown, fertile part as wide as the basal part, proliferating sympodially, forming a straight rachis with slightly thickened and darkened, circular, somewhat protruding scars, approx. 0.5 µm diam. *Conidia* solitary, aseptate, smooth or verruculose, subhyaline, oblong, ellipsoidal to clavate, (3–)4–5(–5.5) × (1–)2(–2.5) µm, with truncate base and unthickened, non-pigmented hilum.

**Cultural characteristics:** Colonies on MEA slow-growing, reaching 5 mm diam after 14 d at 24 °C, with entire margin; aerial mycelium rather compact, raised, dense, olivaceous-grey; reverse olivaceous-black.

**Specimen examined:** South Africa, KwaZulu-Natal, Durban, near Réunion, on leaves of *Strelitzia nicolai*, 5 Feb. 2005, W. Gams & H. Glen, CBS-H 19776, **holotype**, culture **ex-type** CBS 121711.

***Zasmidium* Fr., *Summa Veg. Scand.* 2: 407. 1849.**

**In vitro:** *Submerged hyphae* smooth, thin-walled, hyaline, with thin septa; *aerial hyphae* coarsely verrucose, olivaceous-green, thick-walled, with thin septa. *Conidiophores* not differentiated from vegetative hyphae, often reduced to conidiogenous

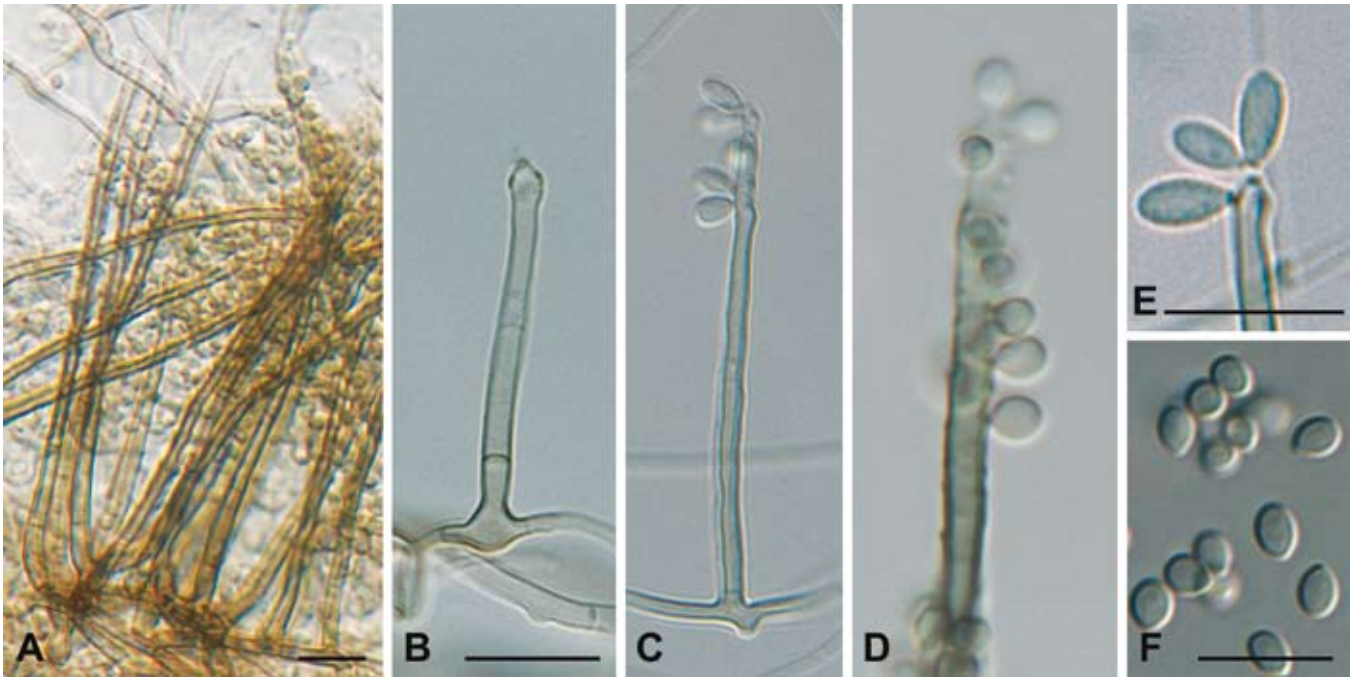


**Fig. 17.** A. *Ramichloridium strelitziae* (CBS 121711). B. *Veronaea japonica* (CBS 776.83). C. *Veronaeopsis simplex* (CBS 588.66). Scale bar = 10 µm.



**Fig. 18.** *Zasmidium cellare* (CBS 146.36). A–D. Micronematous conidiophores with terminal, integrated conidiogenous cells. E. Conidiogenous cell with pigmented, thickened and refractive scars. F–G. Primary and secondary conidia. Scale bar = 10 µm.





**Fig. 19.** *Rhinocladiella anceps* (CBS 181.65). A. Macronematous conidiophores. B–D. Conidial apparatus at different stages of development, resulting in semi-micronematous conidiophores and sympodially proliferating conidiogenous cells. E. Conidiogenous loci. F. Conidia. Scale bars = 10 µm.

cells. *Conidiogenous cells* integrated, predominantly terminal, sometimes lateral, arising from aerial hyphae, cylindrical, pale brown; polyblastic, proliferating sympodially producing crowded, conspicuously pigmented, almost flat, darkened, somewhat refractive scars. *Conidia* in short chains, cylindrical to fusiform, verrucose, obovate to obconical, pale brown, base truncate, with a conspicuous, slightly pigmented, thickened and refractive hilum. *Primary conidia* sometimes larger, subhyaline, verrucose or smooth-walled, 0–4-septate, variable in length, fusiform to cylindrical; conidial secession schizolytic.

*Type species:* *Zasmidium cellare* (Pers. : Fr.) Fr., *Summa Veg. Scand.* 2: 407. 1849.

***Zasmidium cellare*** (Pers. : Fr.) Fr., *Summa Veg. Scand.* 2: 407. 1849. Fig. 18.

*Basionym:* *Racodium cellare* Pers., *Neues Mag. Bot.* 1: 123. 1794.

≡ *Antennaria cellaris* (Pers. : Fr.) Fr., *Syst. Mycol.* 3: 229. 1829.

≡ *Cladosporium cellare* (Pers. : Fr.) Schanderl, *Zentralbl. Bakteriol.*, 2. Abt., 94: 117. 1936.

≡ *Rhinocladiella cellaris* (Pers. : Fr.) M.B. Ellis, in Ellis, *Dematiaceous Hyphomycetes*: 248. 1971.

*In vitro:* *Submerged hyphae* smooth, thin-walled, hyaline, 2–3 µm wide, with thin septa; *aerial hyphae* coarsely verrucose, olivaceous-green, rather thick-walled, 2–2.5 µm wide, with thin septa. *Conidiophores* not differentiated from vegetative hyphae, often reduced to conidiogenous cells. *Conidiogenous cells* integrated, predominantly terminal, sometimes lateral, arising from aerial hyphae, cylindrical, 20–60 µm long and 2–2.5 µm wide, pale brown, proliferating sympodially producing crowded, conspicuously pigmented scars that are thickened and refractive, about 1 µm diam. *Conidia* cylindrical to fusiform, verrucose, obovate to obconical, pale brown, with truncate base, (6–)9–14(–27) × 2–2.5 µm, with a conspicuous, slightly pigmented, refractive hilum, approx. 1 µm diam. *Primary conidia* sometimes subhyaline, verrucose or smooth-walled, thin-walled, 0–1(–4)-septate, variable in length, fusiform to cylindrical.

*Cultural characteristics:* Colonies reaching 7 mm diam after 14 d at 24 °C. Colonies velvety, rather compact, slightly elevated with entire margin; surface dark olivaceous-green in the central part, margin smooth, whitish.

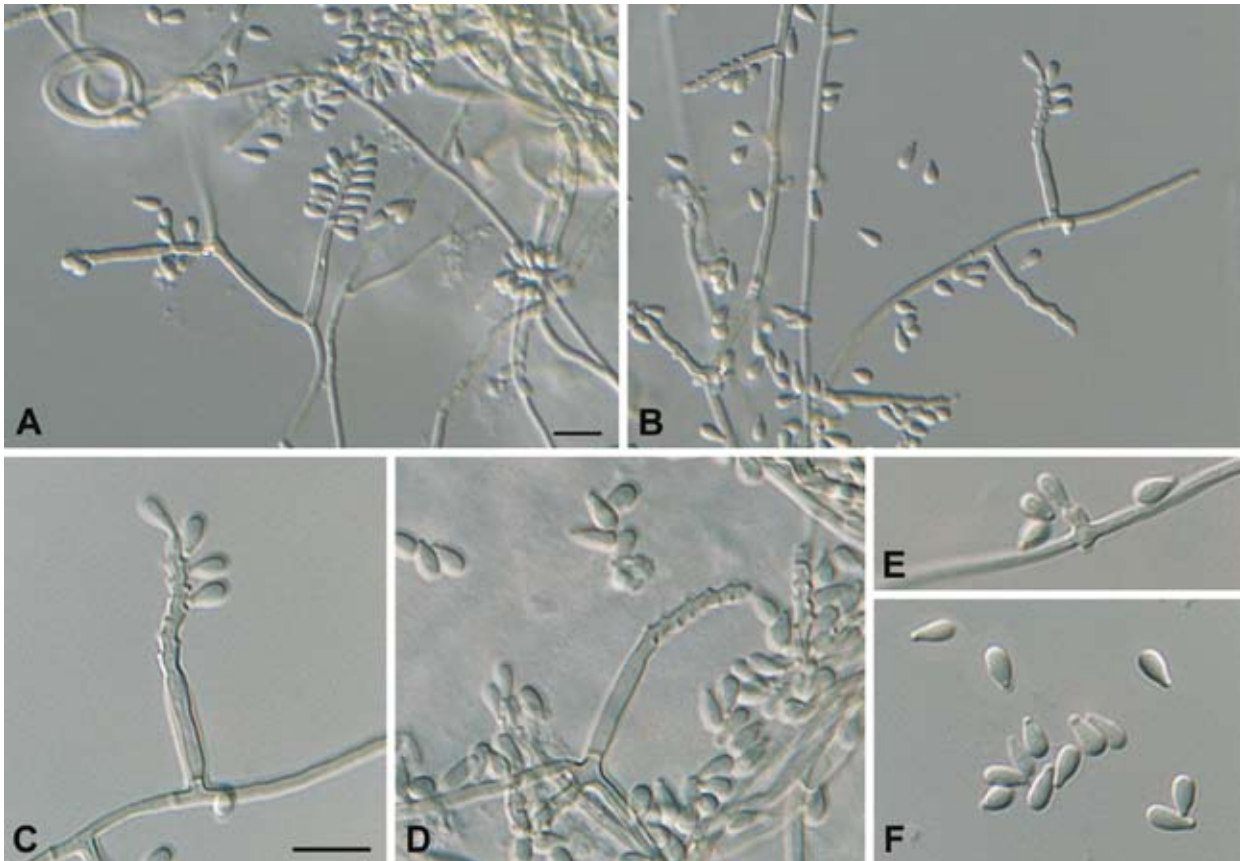
*Specimen examined:* Wall in wine cellar, Jun. 1936, H. Schanderl, ATCC 36951 = IFO 4862 = IMI 044943 = LCP 52.402 = LSHB BB274 = MUCL 10089 = CBS 146.36.

*Notes:* The name *Racodium* Fr., typified by *Ra. rupestre* Pers. : Fr., has been conserved over the older one by Persoon, with *Ra. cellare* as type species. De Hoog (1979) defended the use of *Zasmidium* in its place for the well-known wine-cellar fungus.

Morphologically *Zasmidium* resembles *Stenella* Syd., and both reside in the *Capnodiales*, though the type of *Stenella*, *S. araguata* Syd., clusters in the *Teratosphaeriaceae*, and the type of *Zasmidium*, *Z. cellare*, in the *Mycosphaerellaceae*. When accepting anamorph genera as polyphyletic within an order, preference would be given to the well-known name *Stenella* over the less known *Zasmidium*, even though the latter name is older. Further studies are required, however, to clarify if all *stenella*-like taxa should be accommodated in a single genus, *Stenella*. If this is indeed the case, a new combination for *Zasmidium cellare* will be proposed in *Stenella*, and the latter genus will have to be conserved over *Zasmidium*.

### ***Chaetothyriales (Herpotrichiellaceae)***

The four “*Ramichloridium*” species residing in the *Chaetothyriales* clade do not differ sufficiently in morphology to separate them from *Rhinocladiella* (type *Rh. atrovirens*). Because of the pale brown conidiophores, conidiogenous cells with crowded, slightly prominent scars and the occasional presence of an *Exophiala* J.W. Carmich. synanamorph, *Rhinocladiella* is a suitable genus to accommodate them. These four species chiefly differ from *Ramichloridium* in the morphology of their conidial apparatus, which is clearly differentiated from the vegetative hyphae. The appropriate combinations are therefore introduced for *Ramichloridium anceps*, *R. mackenziei*, *R. fasciculatum* and *R. basitonum*.



**Fig. 20.** *Rhinocladiella basitona* (CBS 101460). A–B. Semi-micronematous conidiophores with verticillate branching pattern. C–D. Sympodially proliferating conidiogenous cells, giving rise to a long rachis with slightly prominent, truncate conidium-bearing denticles. E. Intercalary conidiogenous cell. F. Conidia. Scale bars = 10 µm.

The genus *Veronaea* (type species: *V. botryosa*) also resides in the *Chaetothyriales* clade. *Veronaea* can be distinguished from *Rhinocladiella* by the absence of exophiala-type budding cells and its predominantly 1-septate conidia. Furthermore, the conidiogenous loci in *Veronaea* are rather flat, barely prominent.

***Rhinocladiella*** Nannf., Svensk Skogsvårdsfören. Tidskr., Häfte 32: 461. 1934.

*In vitro*: Colonies dark olivaceous-brown, slow-growing, almost moist. *Submerged hyphae* hyaline to pale olivaceous, smooth; *aerial hyphae*, if present, more darkly pigmented. Exophiala-type budding cells usually present in culture. *Conidial apparatus* usually branched, olivaceous-brown, consisting of either slightly differentiated tips of ascending hyphae or septate, markedly differentiated conidiophores. *Conidiogenous cells* intercalary or terminal, polyblastic, cylindrical to acicular, with a sympodially proliferating, subdenticulate rachis; scars unthickened, non-pigmented to somewhat darkened-refractive. *Conidia* solitary, hyaline to subhyaline, aseptate, thin-walled, smooth, subglobose, with a slightly pigmented hilum; conidial secession schizolytic.

*Type species*: *Rh. atrovirens* Nannf., Svenska Skogsvårdsfören. Tidskr. 32: 461. 1934.

***Rhinocladiella anceps*** (Sacc. & Ellis) S. Hughes, Canad. J. Bot. 36: 801. 1958. Fig. 19.

*Basionym*: *Sporotrichum anceps* Sacc. & Ellis, Michelia 2: 576. 1882.

= *Veronaea parvispora* M.B. Ellis, in Ellis, *More Dematiaceous Hyphomycetes*: 210. 1976.

*Misapplied name*: *Chloridium minus* Corda *sensu* Mangenot, Rev. Mycol. (Paris) 18: 137. 1953.

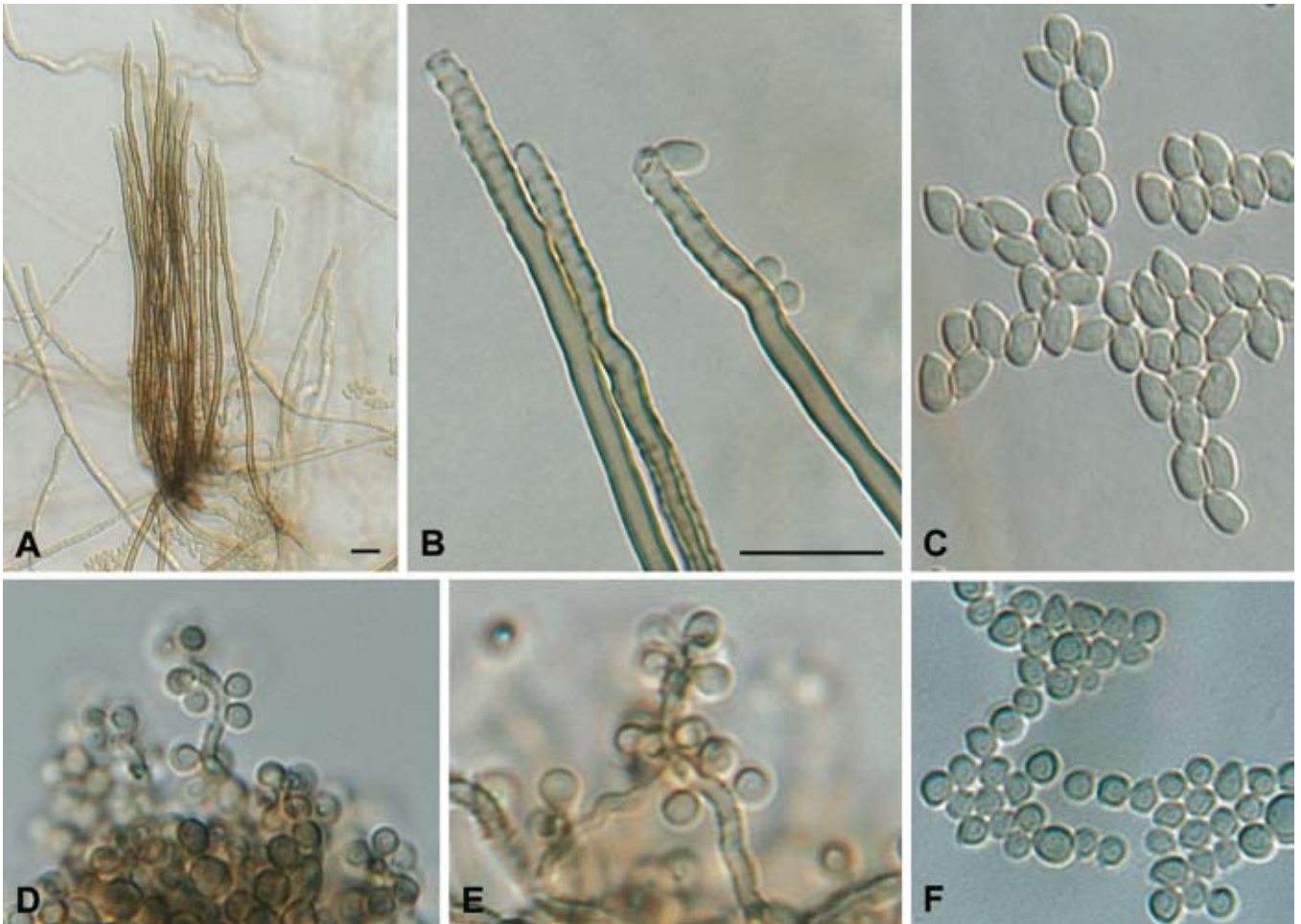
*In vitro*: *Submerged hyphae* subhyaline, smooth, thick-walled, 2–2.5 µm wide; *aerial hyphae* pale brown. Swollen germinating cells often present on MEA, giving rise to an *Exophiala* synanamorph. *Conidiophores* slightly differentiated from vegetative hyphae, arising from prostrate aerial hyphae, consisting of either unbranched or loosely branched stalks, thick-walled, golden to dark-brown, up to 350 µm tall, which may have up to 15 thin, additional septa, intercalary cells 9–14 µm long. *Conidiogenous cells* terminal, rarely lateral, cylindrical, occasionally intercalary, variable in length, smooth, golden to dark brown at the base, paler toward the apex, later becoming inconspicuously septate, fertile part as wide as the basal part, 15–40 × 1.5–2 µm; with crowded, slightly prominent, unpigmented, conidium-bearing denticles, about 0.5 µm diam. *Conidia* solitary, subhyaline, thin-walled, smooth, subglobose to ellipsoidal, 2.5–4 × 2–2.5 µm, with a less conspicuous, slightly darkened hilum, less than 0.5 µm diam.

*Cultural characteristics*: Colonies on MEA reaching 6–12 mm diam after 14 d at 24 °C, with entire, smooth, sharp margin; mycelium powdery, becoming hairy at centre; olivaceous-green to brown, reverse dark-olivaceous.

*Specimens examined*: **Canada**, Ontario, Campbellville, from soil under *Thuja plicata*, Apr. 1965, G. L. Barron, CBS H-7715 (isoneotype); CBS H-7716 (isoneotype); CBS H-7717 (isoneotype); CBS H-7718 (isoneotype); CBS H-7719 (isoneotype), **ex-type** strain, CBS 181.65 = ATCC 18655 = DAOM 84422 = IMI 134453 = MUCL 8233 = OAC 10215. **France**, from stem of *Fagus sylvatica*, 1953, F. Mangenot, CBS 157.54 = ATCC 15680 = MUCL 1081 = MUCL 7992 = MUCL 15756.

*Notes*: *Rhinocladiella anceps* (conidia 2.5–4 µm long) resembles *Rh. phaeophora* Veerkamp & W. Gams (1983) (conidia 5.5–6 µm long), but has shorter conidia.





**Fig. 21.** *Rhinocladiella fasciculata* (CBS 132.86). A. Conidiophores. B. Symphytally proliferating conidiogenous cells, which give rise to a long rachis with slightly prominent, unthickened scars. C. Conidia. D–E. Synanamorph consisting of conidiogenous cells with percurrent proliferation. F. Conidia. Scale bars = 10  $\mu\text{m}$ .

***Rhinocladiella basitona*** (de Hoog) Arzanlou & Crous, **comb. nov.** MycoBank MB504552. Fig. 20.

*Basionym:* *Ramichloridium basitonum* de Hoog, J. Clin. Microbiol. 41: 4774. 2003.

*In vitro:* *Submerged hyphae* hyaline, smooth, thin-walled, 2  $\mu\text{m}$  wide; *aerial hyphae* rather thick-walled, pale brown. *Conidiophores* slightly differentiated from vegetative hyphae, profusely and mostly verticillately branched, straight or flexuose, pale-brown, 2–2.5  $\mu\text{m}$  wide. *Conidiogenous cells* terminal, variable in length, 10–100  $\mu\text{m}$  long, pale brown, straight or geniculate, proliferating sympodially, giving rise to a long, 2–2.5  $\mu\text{m}$  wide rachis, with slightly prominent, truncate conidium-bearing denticles, slightly darkened. *Conidia* solitary, hyaline, thin-walled, smooth, pyriform to clavate, with a round apex, and slightly truncate base, (1–)3–4(–5)  $\times$  1–2  $\mu\text{m}$ , hilum conspicuous, slightly darkened and thickened, less than 0.5  $\mu\text{m}$  diam.

*Cultural characteristics:* Colonies on MEA reaching 19 mm diam after 14 d at 24  $^{\circ}\text{C}$ , with entire, smooth, sharp margin; mycelium rather flat and slightly elevated in the centre, pale olivaceous-grey to olivaceous-grey; reverse olivaceous-black.

*Specimen examined:* **Japan**, Hamamatsu, from subcutaneous lesion with fistula on knee of 70-year-old male, Y. Suzuki, **ex-type** culture CBS 101460 = IFM 47593.

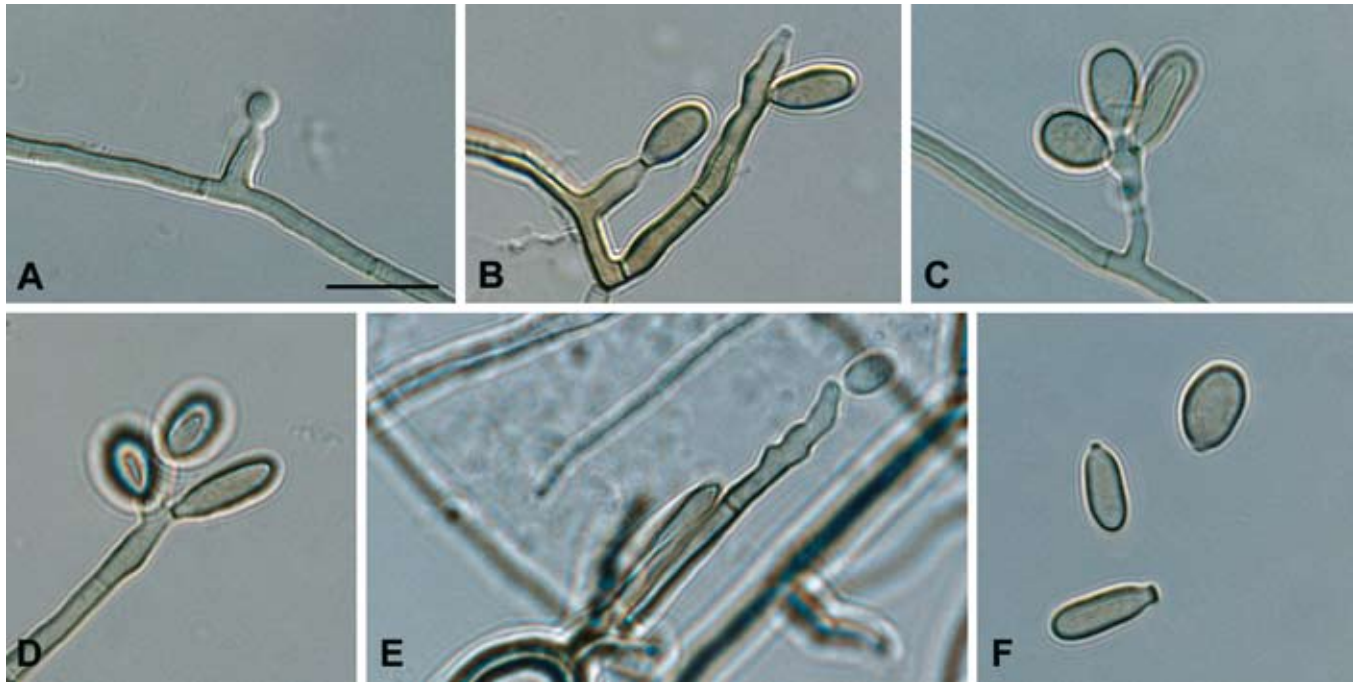
***Rhinocladiella fasciculata*** (V. Rao & de Hoog) Arzanlou & Crous, **comb. nov.** MycoBank MB504553. Fig. 21.

*Basionym:* *Ramichloridium fasciculatum* V. Rao & de Hoog, Stud. Mycol. 28: 39. 1986.

*In vitro:* *Submerged hyphae* subhyaline, smooth, thick-walled, 2–2.5  $\mu\text{m}$  wide; *aerial hyphae* pale brown. *Conidiophores* arising vertically from ascending hyphae in loose fascicles, unbranched or loosely branched at acute angles, cylindrical, smooth, brown and thick-walled at the base, up to 220  $\mu\text{m}$  long and 2–3  $\mu\text{m}$  wide, with 0–5 thin additional septa. *Conidiogenous cells* terminal, cylindrical, 30–100  $\mu\text{m}$  long, thin-walled, smooth, pale brown, fertile part as wide as the basal part, up to 2  $\mu\text{m}$  wide, proliferating sympodially, giving rise to a rachis with hardly prominent, slightly pigmented, not thickened scars, less than 0.5  $\mu\text{m}$  diam. *Conidia* solitary, smooth, thin-walled, subhyaline, ellipsoidal, (2.5–)4–5(–6)  $\times$  2–3  $\mu\text{m}$ , with truncate, slightly pigmented hilum, about 0.5  $\mu\text{m}$  diam. *Synanamorph* forming on torulose hyphae originating from giant cells; compact heads of densely branched hyphae forming thin-walled, lateral, subglobose cells, on which conidiogenous cells are formed; conidiogenous cells proliferating percurrently, giving rise to tubular annellated zones with inconspicuous annellations, up to 12  $\mu\text{m}$  long, 1–1.5  $\mu\text{m}$  wide. *Conidia* smooth, thin-walled, aseptate, subhyaline, globose, 2–2.5  $\mu\text{m}$  diam.

*Cultural characteristics:* Colonies on MEA reaching 8 mm diam after 14 d at 24  $^{\circ}\text{C}$ , with entire, smooth, sharp margin; mycelium velvety, becoming farinose in the centre due to abundant sporulation, olivaceous-green to brown, reverse dark olivaceous. Blackish droplets often produced at the centre, which contain masses of *Exophiala* conidia.

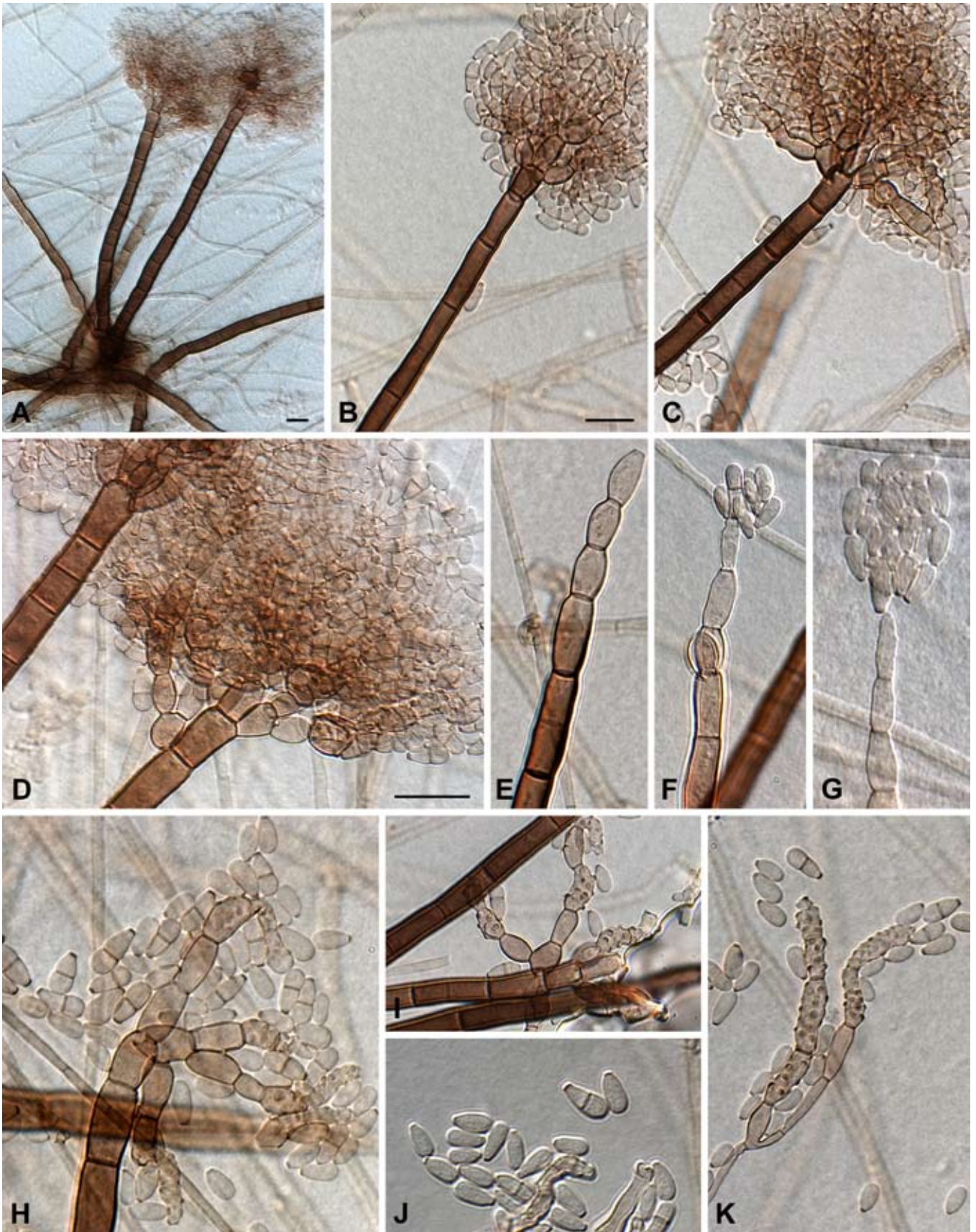
*Specimen examined:* **India**, Karnataka, Thirathahalli, isolated by V. Rao from decayed wood, **holotype** CBS-H 3866, culture **ex-type** CBS 132.86.



**Fig. 22.** *Rhinocladiella mackenziei* (CBS 368.92). A. Intercalary conidiogenous cell. B–E. Semi-micronematous conidiophores and sympodially proliferating conidiogenous cells, resulting in a rachis with slightly prominent, unthickened scars. F. Conidia. Scale bar = 10  $\mu$ m.







**Fig. 24.** *Thysanorea papuana* (CBS 212.96), periconiella-like synanamorph. A. Macronematous conidiophores. B–C. Conidiophores with dense apical branches. D. Branches with different levels of branchlets. E–I. Conidiogenous cells at different stages of development; sympodially proliferating conidiogenous cells give rise to a denticulate rachis. J–K. Conidia. Scale bars = 10  $\mu$ m.

**Fig. 23.** (Page 78). *Thysanorea papuana* (CBS 212.96). A. Intercalary conidiogenous cell. B–I. Semi-micronematous conidiophores and sympodially proliferating conidiogenous cells, resulting in a rachis with prominent conidium bearing denticles. J–K. Microcyclic conidiation observed in slide cultures. L. Conidia. Scale bar = 10  $\mu$ m.



**Rhinocladiella mackenziei** (C.K. Campb. & Al-Hedaihy) Arzanlou & Crous, **comb. nov.** MycoBank MB504554. Fig. 22.

*Basionym:* *Ramichloridium mackenziei* C.K. Campb. & Al-Hedaihy, J. Med. Veterin. Mycol. 31: 330. 1993.

*In vitro:* *Submerged hyphae* subhyaline, smooth, thin-walled, 2–3 µm wide; *aerial hyphae* pale brown, slightly narrower. *Conidiophores* slightly or not differentiated from vegetative hyphae, arising laterally from aerial hyphae, with one or two additional septa, often reduced to a discrete or intercalary conidiogenous cell, pale-brown, 10–25 × 2.5–3.5 µm. *Conidiogenous cells* terminal or intercalary, variable in length, 5–15 µm long and 3–5 µm wide, occasionally slightly wider than the basal part, pale brown, rachis with slightly prominent, unpigmented, non-thickened scars, about 0.5 µm diam. *Conidia* golden-brown, thin-walled, smooth, ellipsoidal to obovate, subcylindrical, (5–)8–9(–12) × (2–)3–3.5(–5) µm, with darkened, inconspicuously thickened, protuberant or truncate hilum, less than 1 µm diam.

*Cultural characteristics:* Colonies on MEA reaching 5 mm diam after 14 d at 24 °C, with entire, smooth, sharp margin; mycelium densely lanose and elevated in the centre, olivaceous-green to brown; reverse dark olivaceous.

*Specimens examined:* **Israel**, Haifa, isolated from brain abscess, CBS 368.92 = UTMB 3170; human brain abscess, E. Lefler, CBS 367.92 = NCPF 2738 = UTMB 3169. **Saudi Arabia**, from phaeoerythromycosis of the brain, S.S.A. Al-Hedaihy, **ex-type** strain, CBS 650.93 = MUCL 40057 = NCPF 2808; from brain abscess, Pakistani male who travelled to Saudi Arabia, CBS 102592 = NCPF 7460. **United Arab Emirates**, from fatal brain abscess, CBS 102590 = NCPF 2853.

*Notes:* Morphologically *Rhinocladiella mackenziei* is somewhat similar to *Pleurothecium obovoideum* (Matsush.) Arzanlou & Crous, which was originally isolated from dead wood. However, *P. obovoideum* has distinct conidiophores, and the ascending hyphae are thick-walled, and the denticles cylindrical, up to 1.5 µm long. In contrast, *Rh. mackenziei* has only slightly prominent denticles. *Rhinocladiella mackenziei* is a member of the *Chaetothyriales*, while *P. obovoideum* clusters in the *Chaetosphaeriales*.

**Thysanorea** Arzanlou, W. Gams & Crous, **gen. nov.** MycoBank MB504555.

*Etymology:* (Greek) *thysano* = brush, referring to the brush-like branching pattern, suffix derived from *Veronaea*.

*Veronaeae* similis sed conidiophoris partim *Periconiae* similibus dense ramosis distinguenda.

*In vitro:* *Submerged hyphae* subhyaline, smooth, thin-walled; *aerial hyphae* pale brown, smooth or verrucose. *Conidiophores* dimorphic; *micronematous conidiophores* slightly differentiated from vegetative hyphae, branched or simple, multiseptate. *Conidiogenous cells* terminal, polyblastic, variable in length, smooth, golden- to dark brown at the base, paler towards the apex, later sometimes inconspicuously septate; fertile part often wider than the basal part, clavate to doliiform, with crowded, more or less prominent conidium-bearing denticles, unpigmented, but slightly thickened. *Macronematous conidiophores* consisting of well-differentiated, thick-walled, dark brown stalks; apically repeatedly densely branched, forming a complex head, each branchlet giving rise to a conidium-bearing denticulate rachis with slightly pigmented, thickened scars. *Conidia* of both kinds of conidiophore formed singly, smooth, pale brown, obovoidal to pyriform, (0–)1-septate, with a truncate base and darkened hilum; conidial secession schizolytic.

*Type species:* *Thysanorea papuana* (Aptroot) Arzanlou, W. Gams & Crous, **comb. nov.**

**Thysanorea papuana** (Aptroot) Arzanlou, W. Gams & Crous, **comb. nov.** MycoBank MB504556. Figs 7C, 23–24.

*Basionym:* *Periconiella papuana* Aptroot, Nova Hedwigia 67: 491. 1998.

*In vitro:* *Submerged hyphae* subhyaline, smooth, thin-walled, 1.5–3 µm wide; *aerial hyphae* pale brown, smooth to verrucose, 1.5–2 µm wide. *Conidiophores* dimorphic; *micronematous conidiophores* slightly differentiated from vegetative hyphae, branched or simple, up to 6-septate. *Conidiogenous cells* terminal or intercalary, variable in length, 5–20 µm long, thin-walled, smooth, golden- to dark brown at the base, paler toward the apex, later sometimes becoming inconspicuously septate, fertile part wider than basal part, often clavate, with crowded, more or less prominent conidium-bearing denticles, about 1 µm diam, unpigmented but slightly thickened. *Conidia* solitary, subhyaline, thin-walled, smooth, cylindrical to pyriform, rounded at the apex and truncate at the base, pale brown, (0–)1-septate, (5–)7–8(–11) × (2–)3(–4) µm, with a truncate base and darkened hilum, 1 µm diam. *Macronematous conidiophores* present in old cultures after 1 mo of incubation, consisting of well-differentiated, thick-walled, dark brown stalks, up to 220 µm long, (4–)5–6(–7) µm wide, with up to 15 additional septa, often with inflated basal cells; apically densely branched, forming a complex head, with up to five levels of branchlets, 20–50 µm long, each branchlet giving rise to a denticulate conidium-bearing rachis; scars slightly pigmented, thickened, about 1 µm diam. *Conidia* solitary, thin-walled, smooth, pale brown, obovoidal to pyriform, (0–)1-septate, (4–)5–6(–8) × (2–)3(–4) µm, with a truncate base and darkened hilum, 1–2 µm diam.

*Cultural characteristics:* Colonies on MEA reaching 10 mm diam after 14 d at 24 °C, with entire, sharp margin; mycelium velvety, elevated, with colonies up to 2 mm high, surface olivaceous-grey to iron-grey; reverse greenish black.

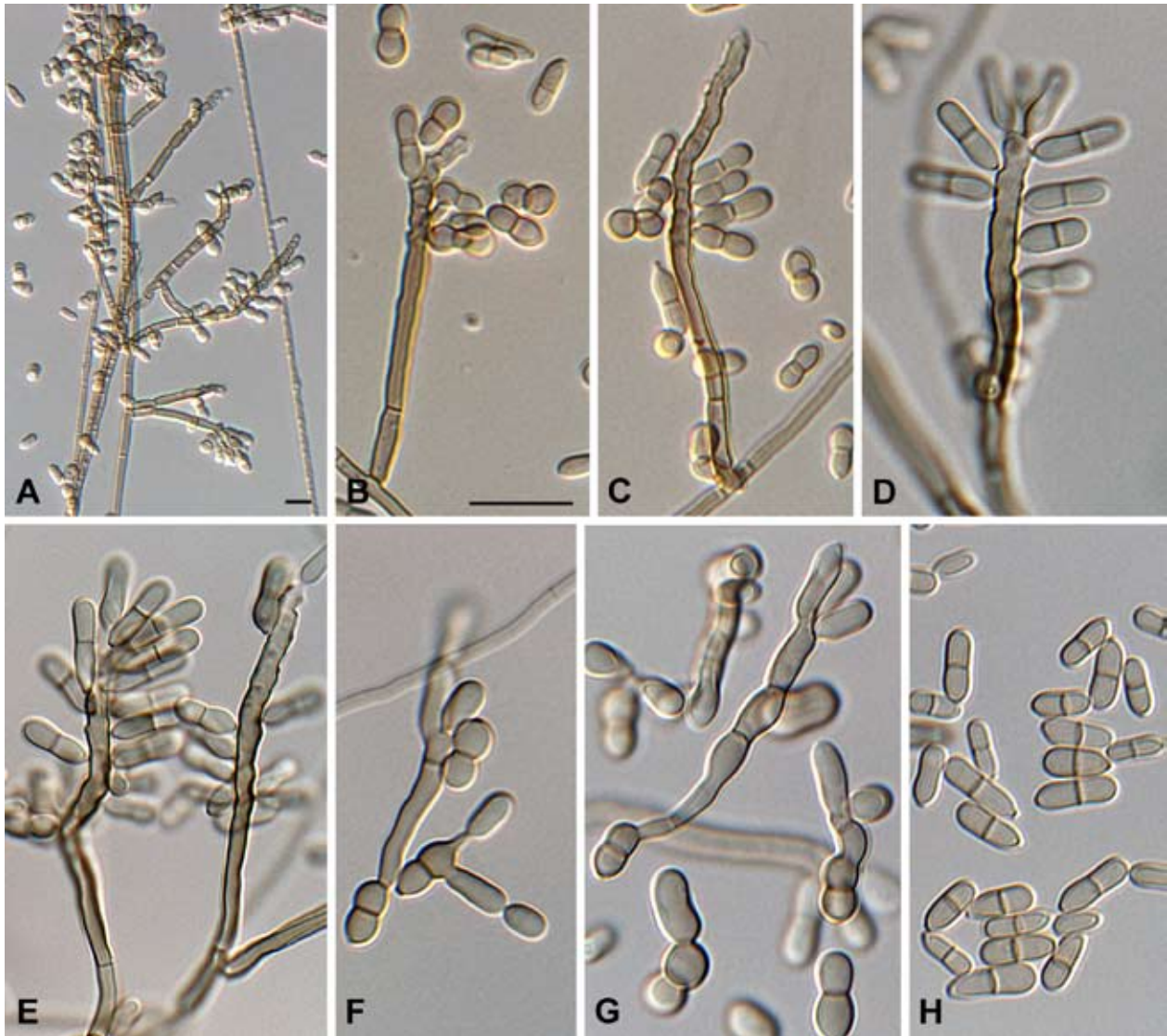
*Specimen examined:* **Papua New Guinea**, Madang Province, foothill of Finisterre range, 40.8 km along road Madang-Lae, alt. 200 m, isolated from unknown stipe, 2 Nov. 1995, A. Aptroot, **holotype** CBS-H 6351, culture *ex-type* CBS 212.96.

**Veronaea** Cif. & Montemart., Atti Ist. Bot. Lab. Crittog. Univ. Pavia, sér. 5, 15: 68. 1957.

*In vitro:* Colonies velvety, pale olivaceous-brown, moderately fast-growing. *Submerged hyphae* hyaline to pale olivaceous, smooth; *aerial hyphae*, more darkly pigmented. Exophiala-type budding cells absent in culture. *Conidiophores* erect, straight or flexuose, unbranched or occasionally loosely branched, sometimes geniculate, smooth-walled, pale to medium- or olivaceous-brown. *Conidiogenous cells* terminally integrated, polyblastic, occasionally intercalary, cylindrical, pale brown, later often becoming septate, fertile part subhyaline, often as wide as the basal part, rachis with crowded, flat to slightly prominent, faintly pigmented, unthickened scars. *Conidia* solitary, smooth, cylindrical to pyriform, rounded at the apex and truncate at the base, pale brown, 1(–2)-septate; conidial secession schizolytic.

*Type species:* *Veronaea botryosa* Cif. & Montemart., Atti Ist. Bot. Lab. Crittog. Univ. Pavia, sér. 5, 15: 68. 1957.

**Veronaea botryosa** Cif. & Montemart., Atti Ist. Bot. Lab. Crittog. Univ. Pavia, sér. 5, 15: 68. 1957. Fig. 25.



**Fig. 25.** *Veronaea botryosa* (CBS 254.57). A–C. Semi-micronematous conidiophores and sympodially proliferating conidiogenous cells. D–E. Rachis with crowded and flat scars. F–G. Microcyclic conidiation. H. Conidia. Scale bars = 10  $\mu$ m.

*In vitro*: Submerged hyphae hyaline to pale olivaceous, smooth; aerial hyphae more darkly pigmented. Conidiophores erect, straight or flexuose, unbranched or occasionally loosely branched, sometimes geniculate, smooth-walled, pale brown to olivaceous-brown, 2–3  $\mu$ m wide and up to 200  $\mu$ m long. Conidiogenous cells terminal, occasionally intercalary, cylindrical, 10–100  $\mu$ m long, pale brown, later often becoming septate, fertile part subhyaline, often as wide as the basal part, rachis with crowded, flat to slightly prominent, faintly pigmented, unthickened scars. Conidia solitary, smooth, cylindrical to pyriform, (3–)6.5–8.5(–12)  $\times$  (1.5–)2–2.5(–3)  $\mu$ m, rounded at the apex and truncate at the base, pale brown, 1(–2)-septate, with a faintly darkened, unthickened hilum, about 0.5  $\mu$ m diam.

**Cultural characteristics:** Colonies on MEA reaching 30 mm diam after 14 d at 24  $^{\circ}$ C, with entire, sharp margin; mycelium velvety, slightly elevated in the centre, surface olivaceous-grey to greyish-brown; reverse greenish black.

**Specimens examined:** **India**, Ramgarh, about 38 km from Jaipur, isolated from goat dung, 1 Sep. 1963, B.C. Lodha, CBS 350.65 = IMI 115127 = MUCL 7972. **Italy**, Tuscany, Pisa, isolated from Sansa olive slag, 1954, O. Verona, **ex-type** strain, CBS 254.57 = IMI 070233 = MUCL 9821.

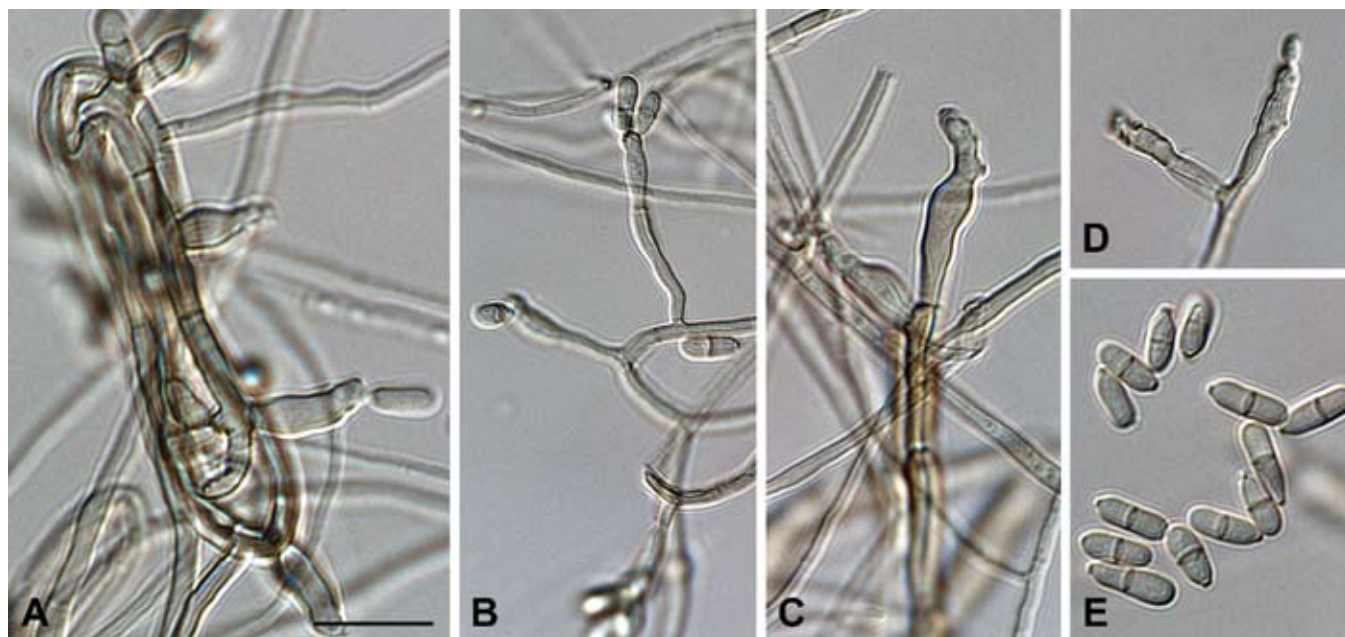
***Veronaea compacta*** Papendorf, Bothalia 12: 119. 1976. Fig. 26.

*In vitro*: Submerged hyphae subhyaline, smooth, thin-walled, 1.5–3  $\mu$ m wide; aerial hyphae rather thick-walled, pale brown. Conidiophores slightly differentiated from vegetative hyphae, lateral or occasionally terminal, often wider than the supporting hypha, up to 4  $\mu$ m wide, unbranched or branched at acute angles, with 1–3 additional septa, cells often inflated and flask-shaped, pale-brown, up to 60  $\mu$ m long. Conidiogenous cells terminal, occasionally intercalary, variable in length, up to 10  $\mu$ m long, pale brown, cylindrical to doliiform or flask-shaped, with hardly prominent denticles; scars flat, slightly pigmented, not thickened, about 0.5  $\mu$ m diam. Conidia solitary, pale brown, smooth, thin-walled, ellipsoidal to ovoid, 0–1(–2)-septate, often constricted at the septa, (4–)6–7(–9)  $\times$  2–3  $\mu$ m, with a round apex and truncate base; hilum prominent, slightly darkened, unthickened, about 0.5  $\mu$ m diam.

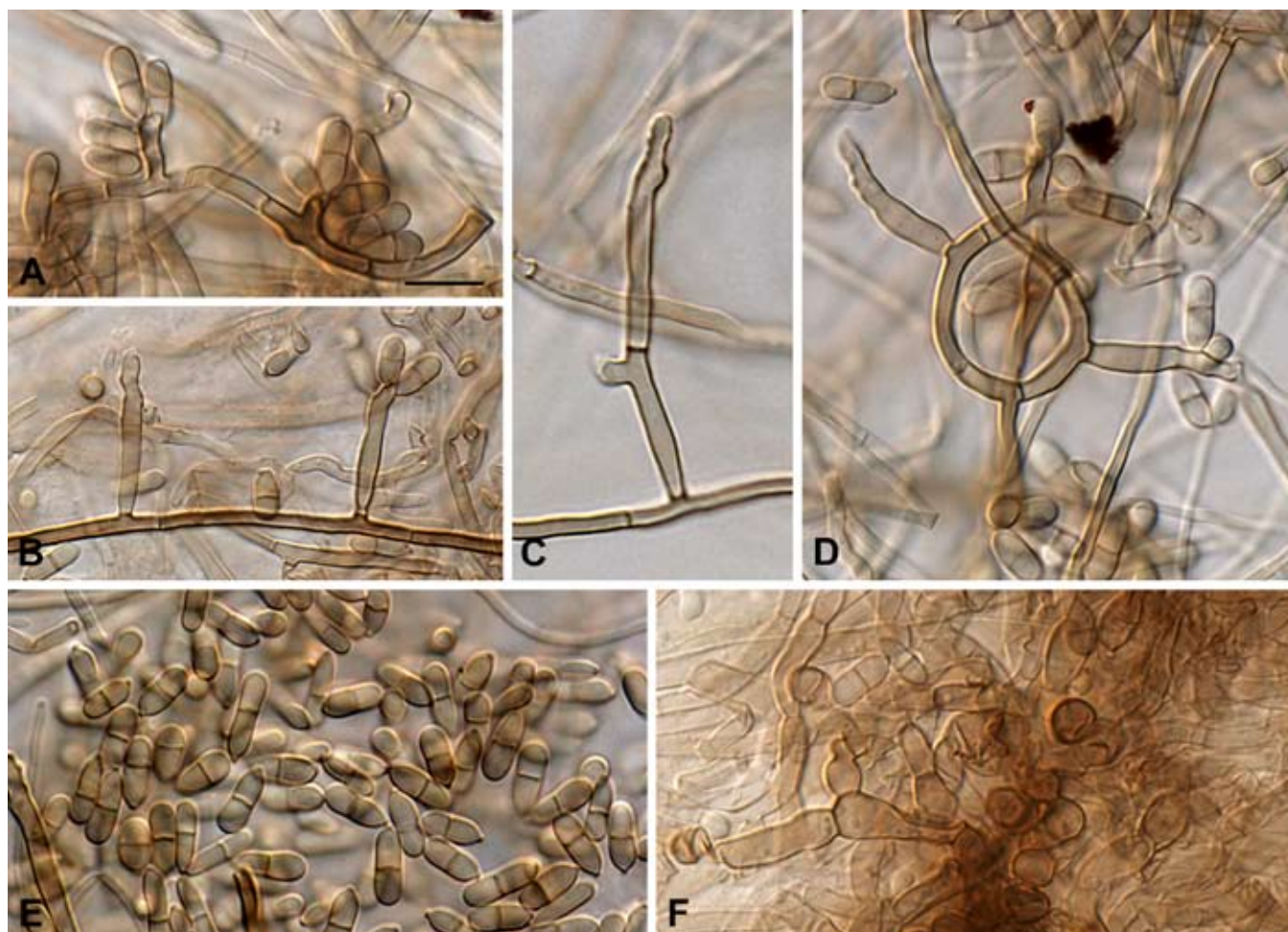
**Cultural characteristics:** Colonies rather slow growing, reaching 15 mm diam on MEA after 14 d at 24  $^{\circ}$ C; surface velvety to lanose, slightly raised in the centre, pale grey to pale brownish grey; reverse dark grey.

**Specimen examined:** **South Africa**, soil, M.C. Papendorf, **ex-type** culture CBS 268.75.





**Fig. 26.** *Veronaea compacta* (CBS 268.75). A–B. Semi-micronematous conidiophores and sympodially proliferating conidiogenous cells. C–D. Rachis with hardly prominent denticles. E. Conidia. Scale bar = 10  $\mu$ m.



**Fig. 27.** *Veronaea japonica* (CBS 776.83). A. Intercalary conidiogenous cells. B–D. Semi-micronematous conidiophores and sympodially proliferating conidiogenous cells. E. Conidia. F. Thick-walled, dark brown hyphal cells. Scale bar = 10  $\mu$ m.

***Veronaea japonica*** Arzanlou, W. Gams & Crous, **sp. nov.**  
Mycobank MB504557. Figs 17B, 27.

**Etymology:** Named after the country of origin, Japan.

*Veronaea compactae* similis, sed cellulis inflatis, aggregatis, crassitunicatis, fuscis *in vitro* formatis distinguenda.

*In vitro:* Submerged hyphae subhyaline, smooth, thin-walled, 1.5–3  $\mu$ m wide; aerial hyphae slightly narrower, pale brown; hyphal cells later becoming swollen, thick-walled, dark brown, often aggregated. Conidiophores slightly differentiated from aerial vegetative hyphae, lateral, or terminal, often wider than the supporting hypha, 2–3  $\mu$ m wide, up to 65  $\mu$ m long, unbranched or occasionally branched,



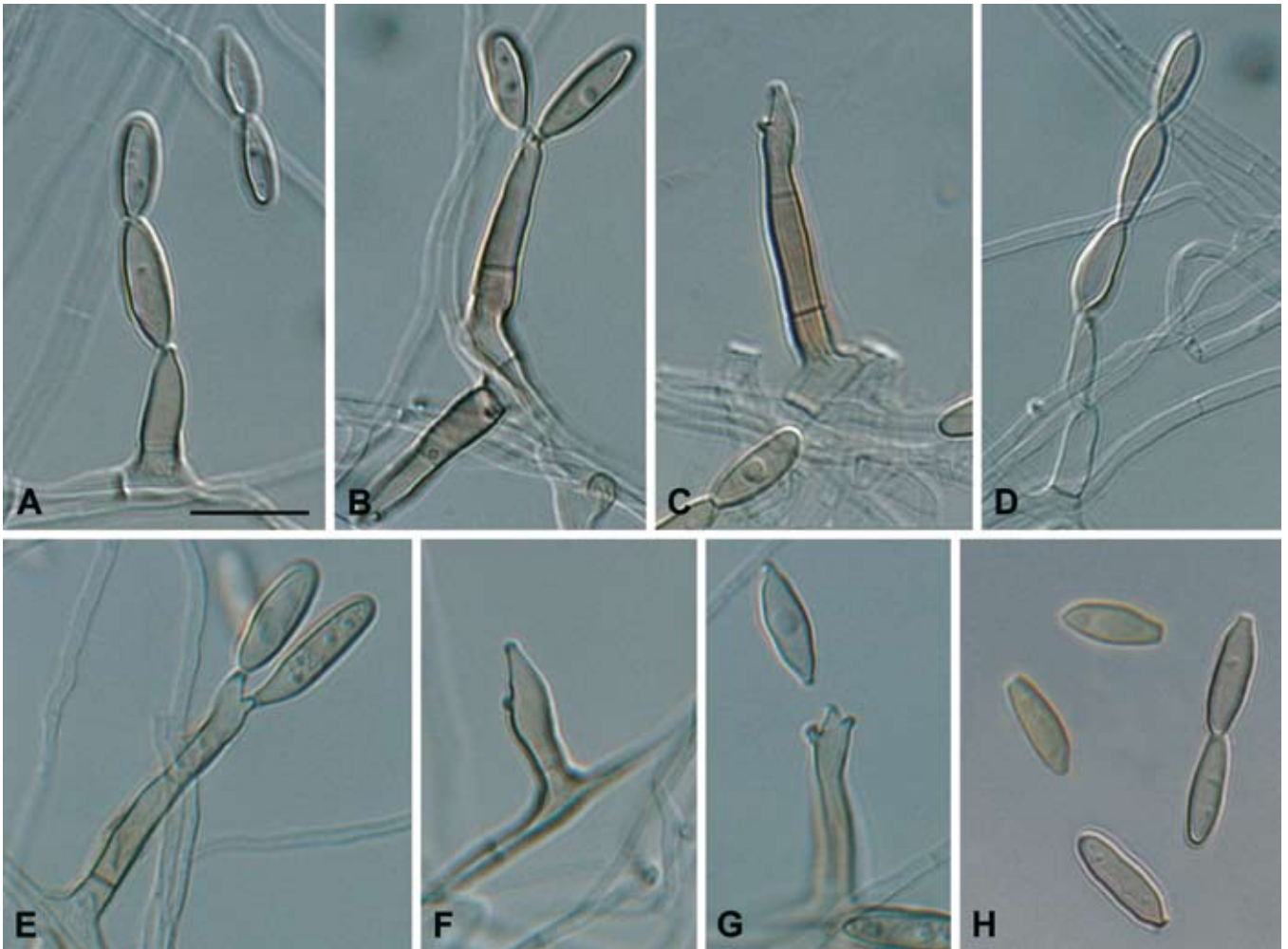


Fig. 28. *Pleurothecium obovoideum* (CBS 209.95). A–C. Conidial apparatus consisting of conidiophores with sympodially proliferating conidiogenous cells as seen in slide cultures of ca. 14 d. D. Short chain of conidia. E–G. Sympodially proliferating conidiogenous cells, resulting in a short rachis with subcylindrical to cylindrical denticles. H. Conidia. Scale bar = 10  $\mu\text{m}$ .

pale brown, thin-walled, smooth, with 1–3 additional septa. *Conidiogenous cells* terminal, occasionally intercalary, variable in length, up to 15  $\mu\text{m}$  long, pale brown, cylindrical to clavate, with hardly prominent denticles; scars flat, slightly pigmented, not thickened, about 0.5  $\mu\text{m}$  diam. *Conidia* solitary, pale brown, smooth, thin-walled, ellipsoidal to ovoid, (0–)1-septate, often constricted at the septum, (6–)7–8(–10)  $\times$  2–2.5(–4)  $\mu\text{m}$ , with a round apex and truncate base; hilum unthickened but slightly darkened, about 1  $\mu\text{m}$  diam.

**Cultural characteristics:** Colonies rather slow growing, reaching 7.5 mm diam on MEA after 14 d at 24  $^{\circ}\text{C}$ ; surface velvety to lanose, slightly raised in the centre, olivaceous-brown, with entire margin; reverse dark-olivaceous.

**Specimen examined:** Japan, Kyoto, Daitokuji Temple, Kyoto, inside dead bamboo culm, Dec. 1983, W. Gams, **holotype** CBS-H 3490, ex-type culture CBS 776.83.

**Note:** This species is morphologically similar to *V. compacta* (Papendorf 1976), but can be distinguished based on the presence of dark brown, swollen hyphal cells in culture, which are absent in *V. compacta*.

### *Pleurothecium obovoideum* clade (*Chaetosphaeriales*)

*Ramichloridium obovoideum* was regarded as similar to “*Ramichloridium*” (*Rhinochadiella*) *mackenziei* by some authors, and subsequently reduced to synonymy (Ur-Rahman *et al.* 1988). However, *R. obovoideum* clusters with *Carpoligna pleurothecii*, the teleomorph of *Pleurothecium* Höhn. Because it is also morphologically similar to other species of *Pleurothecium*, we herewith combine it into that genus.

***Pleurothecium obovoideum* (Matsush.) Arzanlou & Crous, comb. nov.** MycoBank MB504558. Fig. 28.

**Basionym:** *Rhinochadiella obovoidea* Matsush., *Icones Microfung. Mats. lect.*: 123. 1975.

$\equiv$  *Ramichloridium obovoideum* (Matsush.) de Hoog, *Stud. Mycol.* 15: 73. 1977.

**In vitro:** *Submerged hyphae* smooth, hyaline, thin-walled, 1–2  $\mu\text{m}$  wide; *aerial hyphae* hyaline to subhyaline, smooth. *Conidiophores* arising vertically from creeping hyphae, ascending hyphae thick-walled and dark brown; conidiophores 10–35  $\mu\text{m}$  long, 1–2-septate, often reduced to a conidiogenous cell, unbranched, thick-walled, smooth, tapering towards the apex, pale brown. *Conidiogenous cells* integrated, cylindrical to ampulliform, 5–20  $\mu\text{m}$  long, pale brown, elongating sympodially, with a short rachis giving rise to denticles, 1  $\mu\text{m}$  long, slightly pigmented. *Conidia* aseptate, solitary or in short chains of up to 3, smooth, pale brown, ellipsoidal to obovate, (9–)11–12(–14.5)  $\times$  (3–)4(–5)  $\mu\text{m}$ , smooth, thin-walled, with a more or less rounded apex, a truncate base and a slightly darkened, unthickened hilum, 1.5  $\mu\text{m}$  diam.

**Cultural characteristics:** Colonies slow-growing, reaching 15 diam after 14 d at 24 °C, with entire, smooth margin; surface rather compact, mycelium mainly flat, submerged, some floccose to lanose aerial mycelium in the centre, buff; reverse honey.

**Specimen examined:** Japan, Kobe Municipal Arboretum, T. Matsushima, from dead leaf of *Pasania edulis*, CBS 209.95 = MFC 12477.

## Incertae sedis (Sordariomycetes)

### *Ramichloridium schulzeri* clade

*Ramichloridium schulzeri*, including its varieties, clusters near *Thyridium* Nitschke and the *Magnaporthaceae*, and is phylogenetically as well as morphologically distinct from the other genera in the *Ramichloridium* complex. To accommodate these taxa, a new genus is introduced below.

***Myrmecridium*** Arzanlou, W. Gams & Crous, **gen. nov.** MycoBank MB504559.

**Etymology:** (Greek) *myrmekia* = wart, referring to the wart-like denticles on the rachis, suffix *-ridium* from *Chloridium*.

Genus ab allis generibus *Ramichloridii* similibus rachide recta longa, subhyalina, denticulis distantibus, verruciformibus praedita distinguendum.

**In vitro:** Colonies moderately fast-growing, flat, with mainly submerged mycelium, and entire margin, later becoming powdery to velvety, pale orange to orange. Mycelium rather compact, mainly submerged, in the centre velvety with fertile bundles of hyphae. *Conidiophores* arising vertically and clearly distinct from creeping hyphae, unbranched, straight or flexuose, brown, thick-walled. *Conidiogenous cells* terminally integrated, polyblastic, cylindrical, straight or flexuose, pale brown, sometimes secondarily septate, fertile part subhyaline, as wide as the basal part, with scattered pimple-shaped, apically pointed, unpigmented, conidium-bearing denticles. *Conidia* solitary, subhyaline, smooth or finely verrucose, rather thin-walled, with a wing-like gelatinous sheath, obovoidal or fusiform, tapering towards a narrowly truncate base with a slightly prominent, unpigmented hilum; conidial secession schizolytic.

**Type species:** *Myrmecridium schulzeri* (Sacc.) Arzanlou, W. Gams & Crous, **comb. nov.**

**Notes:** *Myrmecridium schulzeri* was fully described as *Acrotheca acuta* Grove by Hughes (1951). The author discussed several genera, none of which is suitable for the present fungus for various reasons as analysed by de Hoog (1977). Only *Gomphinaria* Preuss is not yet sufficiently documented. Our examination of *G. amoena* Preuss (B!) showed that this is an entirely different fungus, of which no fresh material is available to ascertain its position.

*Myrmecridium* can be distinguished from other ramichloridium-like fungi by having entirely hyaline vegetative hyphae, and widely scattered, pimple-shaped denticles on the long hyaline rachis. The conidial sheath is visible in lactic acid mounts with bright-field microscopy. The *Myrmecridium* clade consists of several subclusters, which are insufficiently resolved based on the ITS sequence data. However, two morphologically distinct varieties of *Myrmecridium* are treated here. The status of the other isolates in this clade will be dealt with in a future study incorporating more strains, and using a multi-gene phylogenetic approach.

***Myrmecridium schulzeri*** (Sacc.) Arzanlou, W. Gams & Crous, **comb. nov.** MycoBank MB504560. var. ***schulzeri*** Figs 7B, 29.

**Basionym:** *Psilobotrys schulzeri* Sacc., *Hedwigia* 23: 126. 1884.

≡ *Chloridium schulzerii* (Sacc.) Sacc., *Syll. Fung.* 4: 322. 1886.

≡ *Rhinochloidiella schulzeri* (Sacc.) Matsush., *Icon. Microfung. Mats. lect.* (Kobe): 124. 1975.

≡ *Ramichloridium schulzeri* (Sacc.) de Hoog, *Stud. Mycol.* 15: 64. 1977 var. *schulzeri*.

= *Acrotheca acuta* Grove, *J. Bot., Lond.* 54: 222. 1916.

≡ *Pleurophragmium acutum* (Grove) M.B. Ellis in Ellis, *More Dematiaceous Hyphomycetes*: 165. 1976.

= *Rhinotrichum multisporum* Doguet, *Rev. Mycol., Suppl. Colon.* 17: 78. 1953 (nom. inval. Art. 36) [non *Acrotheca multispora* (Preuss) Sacc., *Syll. Fung.* 4: 277. 1886].

[non *Acrothecium* (?) *multisporum* G. Arnaud, *Bull. Trimestriell. Soc. Mycol. France* 69: 288. 1953 (nom. inval. Art. 36)].

[non *Acrothecium multisporum* G. Arnaud *sensu* Tubaki, *J. Hattori Bot. Lab.* 20: 145. 1958].

**In vitro:** Submerged hyphae hyaline, thin-walled, 1–2 µm wide; aerial hyphae, if present, pale olivaceous-brown. *Conidiophores* arising vertically from creeping aerial hyphae, unbranched, straight, reddish brown, thick-walled, septate, up to 250 µm tall, 2.5–3.5 µm wide, with 2–7 additional septa, basal cell often inflated, 3.5–5 µm wide. *Conidiogenous cells* integrated, cylindrical, variable in length, 15–110 µm long, subhyaline to pale brown, later becoming inconspicuously septate, fertile part subhyaline, as wide as the basal part, forming a straight rachis with scattered, pimple-shaped denticles less than 1 µm long and approx. 0.5 µm wide, apically pointed, unpigmented, slightly thickened scars. *Conidia* solitary, subhyaline, thin-walled, smooth or finely verrucose, surrounded by a wing-like, gelatinous conidial sheath, up to 0.5 µm thick, ellipsoid, obovoid or fusiform, (6–)9–10(–12) × 3–4 µm, tapering to a subtruncate base; hilum unpigmented, inconspicuous.

**Cultural characteristics:** Colonies reaching 29 mm diam after 14 d at 24 °C, pale orange to orange, with entire margin; mycelium flat, rather compact, later becoming farinose or powdery due to sporulation, which occurs in concentric zones when incubated on the laboratory bench.

**Specimens examined:** Germany, Kiel-Kitzeberg, from wheat-field soil, W. Gams, CBS 134.68 = ATCC 16310. The Netherlands, isolated from a man, bronchial secretion, A. Visser, CBS 156.63 = MUCL 1079; Lienden, isolated from *Triticum aestivum* root, C.L. de Graaff, CBS 325.74 = JCM 7234.

***Myrmecridium schulzeri* var. *tritici*** (M.B. Ellis) Arzanlou, W. Gams & Crous, **comb. nov.** MycoBank MB504562.

**Basionym:** *Pleurophragmium tritici* M.B. Ellis, in Ellis, *More Dematiaceous Hyphomycetes*: 165. 1976.

≡ *Ramichloridium schulzeri* var. *tritici* (M.B. Ellis) de Hoog, *Stud. Mycol.* 15: 68. 1977.

**Specimen examined:** Ireland, Dublin, on wheat stem, Oct. 1960, J.J. Brady, **holotype** IMI 83291.

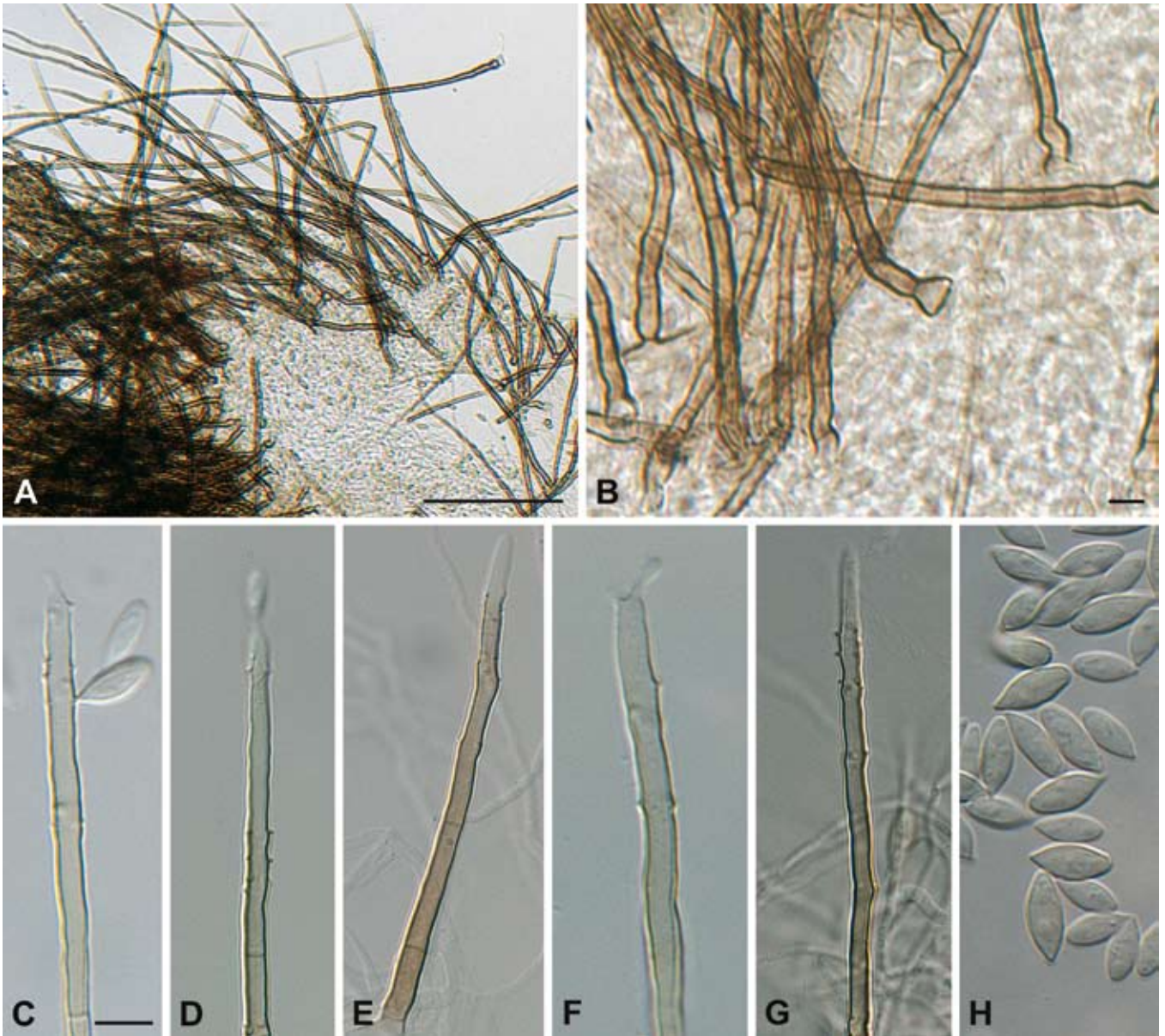
**Notes:** No reliable living culture is available of this variety. Based on a re-examination of the type specimen in this study, the variety appears sufficiently distinct from *Myrmecridium schulzeri* var. *schulzeri* based on the frequent production of septate conidia.

***Myrmecridium flexuosum*** (de Hoog) Arzanlou, W. Gams & Crous, **comb. et stat. nov.** MycoBank MB504563. Fig. 30.

**Basionym:** *Ramichloridium schulzeri* var. *flexuosum* de Hoog, *Stud. Mycol.* 15: 67. 1977.

**In vitro:** Submerged hyphae hyaline, thin-walled, 1–2 µm wide. *Conidiophores* unbranched, flexuose, arising from creeping aerial





**Fig. 29.** *Myrmecridium schulzeri* (CBS 325.74). A. Macronematous conidiophores. B. Inflated basal cells visible in some conidiophores. C–E. Conidial apparatus at different stages of development, resulting in macronematous conidiophores and sympodially proliferating conidiogenous cells. F–G. Rachis with scattered, pimple-shaped denticles. H. Conidia. Scale bars: A = 100  $\mu\text{m}$ , B–H = 10  $\mu\text{m}$ .

hyphae, pale brown, up to 250  $\mu\text{m}$  tall, 3–3.5  $\mu\text{m}$  wide, thick-walled, smooth, with up to 24 thin septa, delimiting 8–12  $\mu\text{m}$  long cells. *Conidiogenous cells* integrated, elongating sympodially, cylindrical, 20–150  $\mu\text{m}$  long, flexuose, brown at the base, subhyaline in the upper part, later becoming inconspicuously septate; rachis slightly flexuose, subhyaline, as wide as the basal part, thick-walled near the base, hyaline and thin-walled in the apical part, with scattered pimple-shaped, unpigmented, approx. 0.5  $\mu\text{m}$  long denticles. *Conidia* solitary, subhyaline, thin-walled, finely verrucose, with a wing-like gelatinous sheath, approx. 0.5  $\mu\text{m}$  wide, ellipsoid to obovoid, (5–)6–7(–9)  $\times$  3–4  $\mu\text{m}$ ; hilum slightly prominent, unpigmented, approx. 0.5  $\mu\text{m}$  diam.

**Cultural characteristics:** Colonies reaching 40 mm diam after 14 d at 24  $^{\circ}\text{C}$ ; mycelium submerged, flat, smooth; centrally orange, later becoming powdery to velvety and greyish brown due to sporulation, with sharp, smooth, entire margin; reverse yellowish orange.

**Specimen examined:** Surinam, isolated from soil, J.H. van Emden, ex-type culture CBS 398.76 = JCM 6968.

**Note:** This former variety is sufficiently distinguished from *M. schulzeri* s. str. by its flexuose conidiophores and conidia which lack an acuminate base, to be regarded as a separate species.

***Ramichloridium torvi*** (Ellis & Everh.) de Hoog, Stud. Mycol. 15: 79. 1977.

$\equiv$  *Ramularia torvi* Ellis & Everh., Rep. Missouri Bot. Gard. 9: 119. 1898.

$\equiv$  *Hansfordia torvi* (Ellis & Everh.) Deighton & Piroz., Mycol. Pap. 101: 39. 1965.

$\equiv$  *Acladium biophilum* Cif., Sydowia 10: 164. 1956.

$\equiv$  *Hansfordia biophila* (Cif.) M.B. Ellis, in Ellis, *More Dematiaceous Hyphomycetes*: 199. 1976.

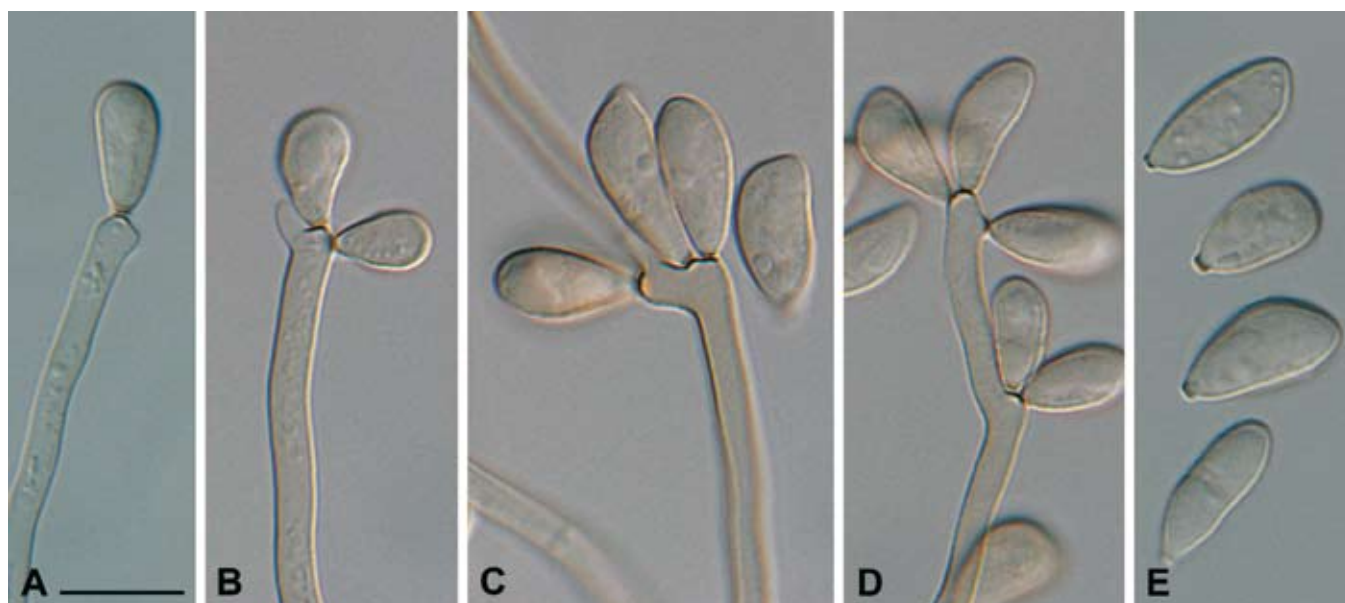
**Specimen:** Jamaica, Port Marant, Dec. 1890, on leaves of *Solanum torvum*, **holotype** of *Ramularia torvi* (NY) (specimen not examined).

**Notes:** According to the description and illustration of *R. torvi* provided by de Hoog (1977), this appears to be an additional species of *Myrmecridium*. Although it is morphologically similar to *M. flexuosum* in having a flexuose rachis, it differs from the other species of the genus by having smooth, clavate conidia. Fresh collections and cultures would be required to resolve its status.





**Fig. 30.** *Myrmecridium flexuosum* (CBS 398.76). A–C. Conidial apparatus at different stages of development, resulting in macronematous conidiophores with sympodially proliferating conidiogenous cells. D–H. Sympodially proliferating conidiogenous cells giving rise to a flexuose conidium-bearing rachis with pimple-shaped denticles. I. Conidia. Scale bar = 10  $\mu$ m.



**Fig. 31.** *Pseudovirgaria hyperparasitica* (CBS 121739). A–D. Conidial apparatus at different stages of development; conidiogenous cells with geniculate proliferation. E. Conidia. Scale bar = 10  $\mu$ m.

***Pseudovirgaria*** H.D. Shin, U. Braun, Arzanlou & Crous, **gen. nov.** MycoBank MB504564.

*Etymology*: Named after its morphological similarity to *Virgaria*.

*Hyphomycetes*. Uredinicola. Coloniae *in vivo* pallide vel modice brunneae, ferrugineae vel cinnamomeae, *in vitro* lentissime crescentes, murinae. Mycelium immersum et praecipue externum, ex hyphis ramosis et cellulis conidiogenis integratis compositum, conidiophoris ab hyphis vegetativis vix distinguendis. Hyphae ramosae, septatae, leves, tenuitunicatae, hyalinae vel pallide brunneae. Cellulae conidiogenae integratae in hyphis repentibus, terminales et intercalares, polyblasticae, sympodialiter proliferantes, subcylindricae vel geniculatae, cicatricibus conspicuis, solitariis vel numerosis, dispersis vel aggregatis, subdenticulatis, prominentibus, umbonatis vel apicem versus paulo attenuatis, non inspissatis, non vel parce fuscatis-refringentibus. Conidia solitaria, holoblastica, plus minusve obovoidea, recta vel leniter curvata, asymmetrica, continua, hyalina, subhyalina vel pallidissime olivaceo-brunnea, hilo subconspicuo vel conspicuo, truncato vel rotundato, non inspissato, non vel lenissime fuscato-refringente; secessio schizolytica.

Hyperparasitic on uredosori of rust fungi. Colonies *in vivo* pale to medium brown, rusty or cinnamon, *in vitro* slow-growing, pale to dark mouse-grey. Mycelium immersed and mainly aerial, composed of branched hyphae with integrated conidiogenous cells, differentiation between vegetative hyphae and conidiophores barely possible. Hyphae branched, septate, smooth, thin-walled, hyaline to pale brown. Conidiogenous cells similarly hyaline to pale brown, integrated in creeping threads (hyphae), terminal and intercalary, polyblastic, proliferation sympodial, rachis subcylindrical to geniculate, conidiogenous loci (scars) conspicuous, solitary to numerous, scattered to aggregated, subdenticulate, bulging out, umbonate or slightly attenuated towards a rounded apex, wall unthickened, not to slightly darkened-refractive. Conidia solitary, formation holoblastic, more or less obovoid, straight to somewhat curved, asymmetrical, aseptate, hyaline, subhyaline to very pale olivaceous-brown, with more or less conspicuous hilum, truncate to rounded, unthickened, not or slightly darkened-refractive; conidial secession schizolytic.

*Type species*: *Pseudovirgaria hyperparasitica* H.D. Shin, U. Braun, Arzanlou & Crous, sp. nov.

*Notes*: Other ramichloridium-like isolates from various rust species form another unique clade, sister to *Radulidium subulatum* (de Hoog) Arzanlou, W. Gams & Crous and *Ra. epichloës* (Ellis & Dearn.) Arzanlou, W. Gams & Crous in the *Sordariomycetidae*. Although *Pseudovirgaria* is morphologically similar to *Virgaria* Nees, it has hyaline to pale brown hyphae, conidia and conidiogenous cells. The conidiogenous cells are integrated in creeping threads (hyphae), terminal and intercalary, and the proliferation is distinctly sympodial. The subdenticulate conidiogenous loci are scattered, solitary, at small shoulders of geniculate conidiogenous cells, caused by sympodial proliferation, or aggregated, forming slight swellings of the rachis, i.e., a typical raduliform rachis as in *Virgaria* is lacking. Furthermore, the conidiogenous loci of *Pseudovirgaria* are bulging, convex, slightly attenuated towards the rounded apex, in contrast to more cylindrical denticles in *Virgaria* (Ellis 1971). The scar type of *Pseudovirgaria* is peculiar due to its convex, papilla-like shape and reminiscent of conidiogenous loci in plant-pathogenic genera like *Neoovularia* U. Braun and *Pseudodidymaria* U. Braun (Braun 1998). The superficially similar genus *Veronaea* is quite distinct from *Pseudovirgaria* by having erect conidiophores with a typical rachis and crowded conidiogenous loci which are flat or only slightly prominent and darkened. *Pseudovirgaria* is characterised by its mycelium which is composed of branched hyphae with integrated, terminal and intercalary conidiogenous cells. A differentiation between branched hyphae and “branched

conidiophores” is difficult and barely possible. It remains unclear if the “creeping threads” and terminal branches of hyphae are to be interpreted as “creeping conidiophores”. In any case, the mycelium forms complex fertile branched hyphal structures in which individual conidiophores are barely discernable. These structures and difficulties in discerning individual conidiophores remind one of some species of *Pseudocercospora* Speg. and other cercosporoid genera with abundant superficial mycelium *in vivo*.

***Pseudovirgaria hyperparasitica*** H.D. Shin, U. Braun, Arzanlou & Crous, **sp. nov.** MycoBank MB504565. Figs 6A, 31.

*Etymology*: Named after its hyperparasitic habit on rust fungi.

Hyphae 1.5–4 µm latae, tenuitunicatae, ≤ 0.5 µm crassae. Cellulae conidiogenae 15–50 × 2–5 µm, tenuitunicatae (≤ 0.5 µm), cicatricibus (0.5–)1.0(–1.5) µm diam, 0.5–1 µm altis. Conidia saepe obovoidea, interdum subclavata, 10–20 × 5–9 µm, apice rotundato vel paulo attenuato, basi truncata vel rotundata, hilo ca 1 µm diam.

*In vivo*: Colonies on rust sori, thin to moderately thick, loose, cobwebby, to dense, tomentose, pale to medium brown, rusty or cinnamon. Mycelium partly immersed in the sori, but mainly superficial, composed of a system of branched hyphae with integrated conidiogenous cells (fertile threads), distinction between conidiophores and vegetative hyphae difficult and barely possible. Hyphae 1.5–4 µm wide, hyaline, subhyaline to pale yellowish, greenish or very pale olivaceous, light brownish in mass, thin-walled (≤ 0.5 µm), smooth, pluriseptate, occasionally slightly constricted at the septa. Conidiogenous cells integrated in creeping fertile threads, terminal or intercalary, 15–50 µm long, 2–5 µm wide, subcylindrical to geniculate, subhyaline to very pale brownish, wall thin, ≤ 0.5 µm, smooth, proliferation sympodial, with a single to usually several conidiogenous loci per cell, often crowded, causing slight swellings, up to 6 µm wide, subdenticulate loci, formed by the slightly bulging wall, convex, slightly narrowed towards the rounded apex, (0.5–)1.0(–1.5) µm diam and 0.5–1 µm high, wall of the loci unthickened, not or slightly darkened-refractive, in surface view visible as minute circle (only rim visible and dark). Conidia solitary, obovoid, often slightly curved with ± unequal sides, 10–20 × 5–9 µm, aseptate, subhyaline, pale yellowish greenish to very pale olivaceous, wall ≤ 0.5 µm thick, smooth, apex slightly attenuated to usually broadly rounded, base rounded to somewhat attenuated towards a more or less conspicuous hilum, (0.5–)1(–1.5) µm diam, convex to truncate, unthickened, not to slightly darkened-refractive.

*In vitro*: Submerged hyphae hyaline to subhyaline, smooth; aerial hyphae smooth, subhyaline, up to 4 µm wide. Conidiogenous cells arising imperceptibly from aerial vegetative hyphae, terminal, occasionally intercalary, holoblastic, proliferating sympodially in a geniculate pattern, with more or less long intervals between groups of scars; loci slightly darkened, unthickened, approx. 0.5 µm diam. Conidia hyaline to subhyaline, aseptate, ovoid, often somewhat curved, (10–)13–15(–17) × (5–)6–7(–8) µm, with truncate base and acutely rounded apex; hila unthickened, slightly darkened-refractive.

*Cultural characteristics*: Colonies on MEA rather slow-growing, reaching 11 mm diam after 14 d at 24 °C, pale to dark mouse-grey, velvety, compacted, with colonies being up to 1 mm high.

*Specimens examined*: Korea, Seoul, on uredosori of *Frommeëlla* sp., on *Duchesnea chrysantha*, 17 Sep. 2003, H.D. Shin, **paratype**, 4/10, CPC 10702–10703 = CBS 121735–121736, HAL 2053 F; Chunchon, on *Phragmidium griseum* on *Rubus crataegifolius*, 20 Jul. 2004, H.D. Shin, **paratype**, 2/8, HAL 2057 F; Suwon,



**Fig. 32.** *Radulidium subulatum* (CBS 405.76). A–B. Macronematous conidiophores with symphyally proliferating conidiogenous cells, resulting in a conidium-bearing rachis. C–D. Rachis with crowded, blunt conidium-bearing denticles. E. Conidia. Scale bar = 10  $\mu$ m.



**Fig. 33.** *Radulidium epichloës* (CBS 361.63). A–C. Conidial apparatus at different stages of development, resulting in semi-micronematous conidiophores and symphyally proliferating conidiogenous cells. D. Rachis with crowded, blunt conidium-bearing denticles. E–F. Conidiophores with acute branches in the lower part. G. Conidia. Scale bar = 10  $\mu$ m.



on *Phragmidium pauciloculare* on *Rubus parvifolius*, 14 Oct. 2003, H.D. Shin, **paratype**, 23/10, HAL 2055 F; Hongchun, on *Phragmidium rosae-multiflorae* on *Rosa multiflora*, 11 Aug. 2004, H.D. Shin, **paratype**, 23/8, HAL 2056 F; Yangpyong, on *Phragmidium* sp. on *Rubus coreanus*, 30 Sep. 2003, H.D. Shin, **paratype**, 11/10-1, CPC 10704–10705 = CBS 121737–121738, HAL 2052 F, and the same locality, 23 Jul. 2004, HAL 2058 F; Chunchon, on *Pucciniastrum agrimoniae* on *Agrimonia pilosa*, 7 Oct. 2002, H.D. Shin, **holotype**, HAL 2054 F, culture ex-type CPC 10753–10755 = CBS 121739–121741.

### ***Radulidium subulatum* and *Ra. epichloës* clade**

*Ramichloridium subulatum* and *R. epichloës* form a distinct, well-supported clade with uncertain affinity. This clade is morphologically distinct and a new genus is introduced below to accommodate it.

***Radulidium* Arzanlou, W. Gams & Crous, gen. nov.** MycoBank MB504566.

*Etymology*: Latin *radula* = A flexible tongue-like organ in gastropods, referring to the radula-like denticles on the rachis.

Genus ab aliis generibus *Ramichloridii* similibus denticulis densissimis, prominentibus, hebetibus in rachide e cellula conidiogena aculeata orta distinguendum.

*Type species*: *Radulidium subulatum* (de Hoog) Arzanlou, W. Gams & Crous, comb. nov.

*In vitro*: Colonies fast-growing, velvety, floccose near the margin, centrally with fertile hyphal bundles up to 10 mm high, about 2 mm diam, with entire but vague margin; *mycelium* whitish, later becoming greyish brown. *Submerged hyphae* smooth, thin-walled. *Conidiophores* usually reduced to polyblastic conidiogenous cells arising from undifferentiated or slightly differentiated aerial hyphae, terminally integrated or lateral, rarely a branched conidiophore present, smooth, slightly thick-walled, pale brown, cylindrical to acicular, widest at the base and tapering towards the apex; apical part forming a pale brown, generally straight rachis, with crowded, prominent, blunt denticles, suggesting a gastropod radula; denticles 0.5–1 µm long, apically pale brown. *Conidia* solitary, subhyaline, thin- or slightly thick-walled, smooth or verrucose, obovoidal, fusiform to subcylindrical, base subtruncate and with a slightly prominent, conspicuously pigmented hilum; conidial secession schizolytic.

*Notes*: *Radulidium* can be distinguished from other ramichloridium-like fungi by its slightly differentiated conidiophores and prominent, blunt, very dense conidium-bearing denticles. Although the *Radulidium* clade consists of several subclusters that correlate with differences in morphology, the ITS sequence data appear insufficient to resolve this species complex. Therefore, only two species of *Radulidium* with clear morphological and molecular differences are treated here. The phylogenetic situation of other taxa in this clade will be treated in a further study employing a multi-gene approach.

***Radulidium subulatum* (de Hoog) Arzanlou, W. Gams & Crous, comb. nov.** MycoBank MB504567. Figs 10C, 32.

*Basionym*: *Ramichloridium subulatum* de Hoog, Stud. Mycol. 15: 83. 1977.

*Misapplied name*: *Rhinochlaeniella elatior* Mangenot *sensu* dal Vesco & B. Peyronel, Allionia 14: 38. 1968.

*In vitro*: *Submerged hyphae* hyaline, thin-walled, 1–2.5 µm wide; *aerial hyphae* brownish. *Conidiogenous cells* arising laterally from vegetative hyphae, pale brown, smooth, thick-walled, sometimes without a basal septum, cylindrical to aculeate, tapering gradually

towards the apex, widest at the base, 25–40 × 2–3 µm; proliferating sympodially, forming a pale brown rachis, with densely crowded, prominent, blunt conidium-bearing denticles, with pale brown apex. *Conidia* solitary, subhyaline, thin-walled, smooth, ellipsoidal to almost clavate, 5–7 × 1.5–2 µm, with a slightly pigmented, non-refractive hilum, about 1 µm diam.

*Cultural characteristics*: Colonies on MEA rather fast growing, reaching 50 mm diam after 14 d at 24 °C, with entire but vague margin, velvety, floccose near the margin, centrally with fertile hyphal bundles up to 10 mm high, about 2 mm diam; mycelium whitish, later becoming greyish brown; reverse grey, zonate.

*Specimens examined*: **Czech Republic**, on *Phragmites australis*, A. Samšínáková, **ex-type** culture CBS 405.76; Opatovický pond, from *Lasiptera arundinis* (gall midge) mycangia on *Phragmites australis*, M. Skuhřavá, CBS 101010.

***Radulidium epichloës* (Ellis & Dearn.) Arzanlou, W. Gams & Crous, comb. nov.** MycoBank MB504568. Fig. 33.

*Basionym*: *Botrytis epichloës* Ellis & Dearn., Canad. Record Sci. 9: 272. 1893.

= *Ramichloridium epichloës* (Ellis & Dearn.) de Hoog, Stud. Mycol. 15: 81. 1977.

*In vitro*: *Submerged hyphae* hyaline, thin-walled, 1–2.5 µm wide; *aerial hyphae* somewhat darker. *Conidiogenous cells* arising laterally or terminally from undifferentiated or slightly differentiated aerial hyphae, occasionally acutely branched in the lower part, smooth, thick-walled, pale brown, more or less cylindrical, later with thin septa, 25–47 µm long; proliferating sympodially, forming a rather short, pale brown, straight or somewhat geniculate rachis, with crowded, prominent, blunt denticles with pale brown apex. *Conidia* solitary, subhyaline, rather thin-walled, verrucose, obovoidal to fusiform, (4.5–)7–8(–11) × 2–3 µm, with a pigmented hilum, 1–1.5 µm diam.

*Cultural characteristics*: Colonies reaching 45 mm diam after 14 d at 24 °C, with smooth, rather vague, entire margin; velvety, centrally floccose and elevated up to 2 mm high; surface mycelium whitish, later becoming greyish brown; reverse pale ochraceous.

*Specimen examined*: **U.S.A.**, Cranberry Lake, Michigan, isolated from *Epichloë typhina* on *Glyceria striata*, G.L. Hennebert, CBS 361.63 = MUCL 3124; specimen in MUCL designated here as **epitype**.

### **Veronaea-like clade, allied to the *Annulatasceae***

A veronaea-like isolate from *Bertia moriformis* clusters near the *Annulatasceae*, and is morphologically distinct from other known anamorph genera in the *Ramichloridium* complex, and therefore a new genus is introduced to accommodate it.

***Rhodoveronaea* Arzanlou, W. Gams & Crous, gen. nov.** MycoBank MB504569.

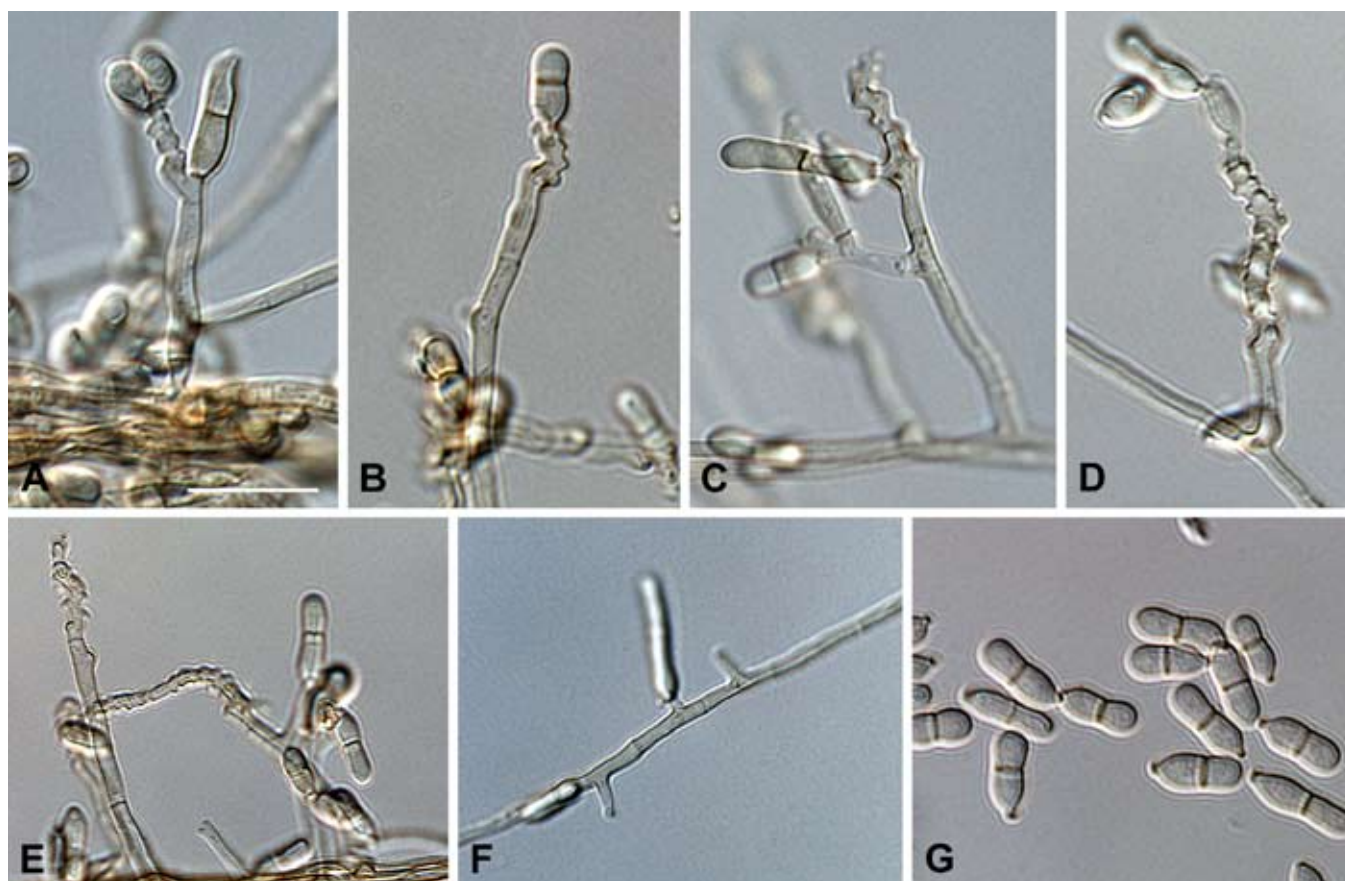
*Etymology*: (Greek) *rhodon* = the rose, referring to the red-brown conidiophores, suffix *-veronaea* from *Veronaea*.

Genus ab aliis generibus *Ramichloridii* similibus basi condiorum late truncata et marginata distinguenda.

*In vitro*: Colonies slow-growing, velvety, floccose; surface olivaceous-grey to dark olivaceous-green; reverse olivaceous-black. *Hyphae* smooth, thin-walled, pale olivaceous. *Conidiophores* arising vertically from creeping hyphae, straight or flexuose, simple, thick-walled, red-brown, with inflated basal cell. *Conidiogenous cells* terminally integrated, polyblastic, sympodial, smooth, thick-



**Fig. 34.** *Rhodoveronaea varioseptata* (CBS 431.88). A–D. Macronematous conidiophores with sympodially proliferating conidiogenous cells, resulting in conidium bearing rachis with slightly prominent conidium-bearing denticles. E–F. Conidia with minute marginal frill. Scale bar = 10  $\mu$ m.



**Fig. 35.** *Veronaeopsis simplex* (CBS 588.66). A–C. Conidial apparatus at different stages of development, resulting in semi-micronematous conidiophores and sympodially proliferating conidiogenous cells. D–E. Rachis with crowded, prominent denticles. F. Intercalary conidiogenous cells. G. Conidia. Scale bar = 10  $\mu$ m.

walled, pale brown, rachis straight, occasionally geniculate, with crowded, slightly prominent conidium-bearing denticles; denticles flat-tipped, slightly pigmented. *Conidia* solitary, pale brown, thin- or slightly thick-walled, smooth, ellipsoidal to obovoidal, 0–multi-septate, with a protruding base and a marginal basal frill; conidial secession schizolytic.

*Type species:* *Rhodoveronaea varioseptata* Arzanlou, W. Gams & Crous, sp. nov.

*Notes:* *Rhodoveronaea* differs from other ramichloridium-like fungi by the presence of a basal, marginal conidial frill, and variably septate conidia.

**Rhodoveronaea varioseptata** Arzanlou, W. Gams & Crous, **sp. nov.** MycoBank MB504570. Figs 10D, 34.

**Etymology:** Named for its variably septate conidia.

Hyphae 2–3 µm latae. Conidiophora ad 125 µm longa et 3–5 µm lata. Cellulae conidiogenae 30–70 µm longae et 3–5 µm latae. Conidia 0–2(–3)-septata, (8–)11–13(–15) × (2–)3–4(–6) µm.

**In vitro:** Submerged hyphae smooth, thin-walled, pale olivaceous, 2–3 µm wide; aerial hyphae smooth, brownish and slightly narrower. Conidiophores arising vertically from creeping hyphae, straight or flexuose, simple, smooth, thick-walled, red-brown, up to 125 µm long, 3–5 µm wide, often with inflated basal cell. Conidiogenous cells terminally integrated, smooth, thick-walled, pale brown at the base, paler towards the apex, straight, variable in length, 30–70 µm long and 3–5 µm wide, rachis straight, occasionally geniculate; slightly prominent conidium-bearing denticles, crowded, with slightly pigmented apex, about 1 µm diam. Conidia solitary, pale brown, thin- or slightly thick-walled, smooth, ellipsoid to obovoid, 0–2(–3)-septate, (8–)11–13(–15) × (2–)3–4(–6) µm with a protruding base, 1.5 µm wide, and marginal frill.

**Cultural characteristics:** Colonies reaching 12 mm diam after 14 d at 24 °C, velvety, floccose; surface olivaceous-grey to dark olivaceous-green; reverse olivaceous-black.

**Specimen examined:** Germany, Eifel, Berndorf, on *Bertia moriformis*, Sep. 1987, W. Gams, **holotype** CBS-H 19932, culture ex-type CBS 431.88.

### Venturiaceae (Pleosporales)

The ex-type strain of *Veronaea simplex* (Papendorf 1969) did not cluster with the genus *Veronaea* (*Herpotrichiellaceae*), but is allied to the *Venturiaceae*. *Veronaea simplex* is distinct from species of *Fusicladium* Bonord. by having a well-developed rachis with densely aggregated scars. A new genus is thus introduced to accommodate this taxon.

**Veronaeopsis** Arzanlou & Crous, **gen. nov.** MycoBank MB504571.

**Etymology:** The suffix *-opsis* refers to its similarity with *Veronaea*.

Genus *Veronaeae* simile sed conidiophoris brevioribus (ad 60 µm longis) et rachide dense denticulata distinguendum.

**In vitro:** Colonies moderately fast-growing; surface velvety, floccose, greyish sepia to hazel, with smooth margin; reverse mouse-grey to dark mouse-grey. Conidiophores arising vertically from aerial hyphae, lateral or intercalary, simple or branched, occasionally reduced to conidiogenous cells, pale brown. Conidiogenous cells terminally integrated on simple or branched conidiophores, polyblastic, smooth, thin-walled, pale brown; rachis commonly straight, geniculate, with densely crowded, prominent denticles, and slightly pigmented scars. Conidia solitary, subhyaline to pale brown, thin- or slightly thick-walled, smooth, oblong-ellipsoidal to subcylindrical, (0–)1-septate, with a slightly darkened, thickened, hilum; conidial secession schizolytic.

**Type species:** *Veronaeopsis simplex* (Papendorf) Arzanlou & Crous, **comb. nov.**

**Veronaeopsis simplex** (Papendorf) Arzanlou & Crous, **comb. nov.** MycoBank MB504572. Figs 17C, 35.

**Basionym:** *Veronaea simplex* Papendorf, *Trans. Brit. Mycol. Soc.* 52: 486. 1969.

**In vitro:** Submerged hyphae smooth, thin-walled, pale brown; aerial hyphae aggregated in bundles. Conidiophores arising vertically from aerial hyphae, lateral or intercalary, simple or branched, occasionally reduced to conidiogenous cells, pale brown, rather short, up to 60 µm long, 1.5–2 µm wide. Conidiogenous cells terminally integrated in the conidiophores, smooth, thin-walled, pale brown, variable in length, 5–25 µm long, rachis generally straight or irregularly geniculate, with crowded, prominent denticles, about 0.5 µm long, flat-tipped, with slightly pigmented apex. Conidia solitary, subhyaline to pale brown, thin- or slightly thick-walled, smooth, oblong-ellipsoidal to subcylindrical, (0–)1-septate, slightly constricted at the septum, (6–)10–12(–15) × (2–)2.5–3(–4) µm; hilum slightly darkened and thickened, not refractive, about 1 µm diam.

**Cultural characteristics:** Colonies reaching 25 mm diam after 14 d at 24 °C; surface velvety, floccose, greyish sepia to hazel, with smooth margin; reverse mouse-grey to dark mouse-grey.

**Specimen examined:** South Africa, Potchefstroom, on leaf litter of *Acacia karroo*, 1966, M.C. Papendorf, **holotype**, CBS H-7810; culture ex-type CBS 588.66 = IMI 203547.

**Notes:** The presence of 1-septate conidia in *Veronaeopsis* overlaps with *Veronaea*. However, *Veronaeopsis* differs from *Veronaea* based on its conidiophore and conidiogenous cell morphology. *Veronaea* has much longer, macronematous conidiophores than *Veronaeopsis*. Furthermore, *Veronaea* has a more or less straight rachis, whereas in *Veronaeopsis* the rachis is often geniculate. The conidiogenous loci in *Veronaea* are less prominent, i.e., less denticle-like.

## DISCUSSION

The present study was initiated chiefly to clarify the status of *Ramichloridium musae*, the causal organism of tropical speckle disease of banana (Jones 2000). Much confusion surrounded this name in the past, relating, respectively, to its validation, species and generic status. As was revealed in the present study, however, two species are involved in banana speckle disease, namely *R. musae* and *R. biverticillatum*. Even more surprising was the fact that *Ramichloridium* comprises anamorphs of *Mycosphaerella* Johanson (*Mycosphaerellaceae*), though no teleomorphs have thus far been conclusively linked to any species of *Ramichloridium*. By investigating the *Ramichloridium* generic complex as outlined by de Hoog (1977), another genus associated with leaf spots, namely *Periconiella*, was also shown to represent an anamorph of *Mycosphaerella*. Although no teleomorph connections have been proven for ramichloridium-like taxa, de Hoog *et al.* (1983) refer to the type specimen of *Wentomyces javanicus* Koord. (*Pseudoperisporiaceae*), on the type specimen of which (PC) some ramichloridium-like conidiophores were seen. Without fresh material and an anamorph-teleomorph connection proven in culture, however, this matter cannot be investigated further. It is interesting to note, however, that *Wentomyces* Koord. shows a strong resemblance to *Mycosphaerella*, except for the external perithecial appendages.

The genus *Mycosphaerella* is presently one of the largest genera of ascomycetes, containing close to 3 000 names (Aptroot 2006), to which approximately 30 anamorph genera have already been linked (Crous *et al.* 2006a, b, 2007). By adding two additional anamorph genera, the *Mycosphaerella* complex appears to be expanding



even further, though some taxa have been shown to reside in other families in the *Capnodiales*, such as *Davidiella* Crous & U. Braun (*Davidiellaceae*) and *Teratosphaeria* (*Teratosphaeriaceae*) (Braun *et al.* 2003, Crous *et al.* 2007, Schubert *et al.* 2007 – this volume).

Another family, which proved to accommodate several ramichloridium-like taxa, is the *Herpotrichiellaceae* (*Chaetothyriales*). Members of the *Chaetothyriales* are regularly encountered as causal agents of human mycoses (Haase *et al.* 1999, de Hoog *et al.* 2003), whereas species of the *Capnodiales* are common plant pathogens, or chiefly associated with plants. Species in the *Chaetothyriales* have consistently melanized thalli, which is a factor enabling them to invade humans, and cause a wide diversity of mycoses, such as chromoblastomycosis, mycetoma, brain infection and subcutaneous phaeohyphomycosis (de Hoog *et al.* 2003). The only known teleomorph connection in this genus is *Capronia* Sacc. (Untereiner & Naveau 1999).

*Rhinocladiella* and *Veronaea* were in the past frequently confused with the genus *Ramichloridium*. However, *Rhinocladiella*, as well as *Veronaea* and *Thysanoreia*, were shown to cluster in the *Chaetothyriales*, while *Ramichloridium* clusters in the *Capnodiales*. *Rhinocladiella mackenziei*, which causes severe cerebral phaeohyphomycosis in humans (Sutton *et al.* 1998), has in the past been confused with *Pleurothecium obovoideum* (Ur-Rahman *et al.* 1988). Data presented here reveal, however, that although morphologically similar, these species are phylogenetically separate, with *P. obovoideum* belonging to the *Sordariales*, where it clusters with sexual species of *Carpoligna* F.A. Fernández & Huhndorf that have *Pleurothecium* anamorphs (Fernández *et al.* 1999).

In addition to the genera clustering in the *Capnodiales* and *Chaetothyriales*, several ramichloridium-like genera are newly introduced to accommodate species that cluster elsewhere in the ascomycetes, namely *Pseudovirgaria*, *Radulidium* and *Myrmecridium*, *Veronaeopsis*, and *Rhodoveronaea*. Although the ecological role of these taxa is much less known than that of taxa in the *Capnodiales* and *Chaetothyriales*, some exhibit an interesting ecology. For instance, the fungicolous habit of *Pseudovirgaria*, as well as some species in *Radulidium*, which are found on various rust species, suggests that these genera should be screened further to establish if they have any potential biocontrol properties. Furthermore, these two genera share a common ancestor, and further work is required to determine whether speciation was shaped by co-evolution with the rusts. A further species of “*Veronaea*” that might belong to *Pseudovirgaria* is *Veronaea harunganae* (Hansf.) M.B. Ellis, which is known to occur on *Hemileia harunganae* Cummins on *Harungana* in Tanzania and Uganda (Ellis 1976). The latter species, however, is presently not known from culture, and needs to be recollected to facilitate further study.

The genera distinguished here represent homogeneous clades in the phylogenetic analysis. Only the species of *Rhinocladiella* are dispersed among others morphologically classified in *Exophiala* or other genera.

By integrating the phylogenetic data generated here with the various morphological data sets, we were able to resolve eight clades for taxa formerly regarded as representative of the *Ramichloridium* complex. According to the phylogeny inferred from 28S rDNA sequence data, the genera *Ramichloridium* and *Periconiella* were heterogeneous, requiring the introduction of several novel genera. Although the present 11 odd genera can still be distinguished based on their morphology, it is unlikely that morphological identifications without the supplement of molecular data would in the future be able to accurately identify all the novel

isolates that undoubtedly await description. The integration of morphology with phylogenetic data not only helps to resolve generic affinities, but it also assists in discriminating between the various cryptic species that surround many of these well-known names that are presently freely used in the literature. To that end it is interesting to note that for the majority of the taxa studied here, the ITS domain (Table 1) provided good species resolution. However, more genes will have to be screened in future studies aimed at characterising some of the species complexes where the ITS domain provided insufficient phylogenetic signal (data not shown) to resolve all of the observed morphological species.

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