Phylogenetic and morphotaxonomic revision of Ramichloridium and allied genera

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Abstract: The phylogeny of the genera Periconiella, Ramichloridium, Rhinocladiella 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 unclear 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 Streptizia, 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 Rhinocladiella (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 Venturiales (Pleosporales), and is placed in a new genus, Veronaea. The clade. Ramichloridium obovoideum clusters with Carpoglena pleurothecii (anamorph: Pleurothecium sp., Chaetothyriales), and a new combination is proposed in Pleurothecium. Other ramichloridium-like clades include R. subulatum and R. echinophloeus (incertae sedis, Sordariales), for which a new genus, Radulidium is erected. Ramichloridium schulzeri and its varieties are placed in a new genus, Mymecridium (incertae sedis, Sordariales). The genus Pseudovirgaria (incertae sedis) is introduced to accommodate ramichloridium-like isolates occurring on various species of rust fungi. A veronaea-like isolate from Berta moniliformis with mycogenetic affinity to the Annulatascaceae (Sordariales) 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. Trichiic (M.B. Ellis) Arzanlou, W. Gams & Crous, comb. nov., Periconiella araucata Arzanlou, S. Lee & Crous, sp. nov., Periconiella lewispora 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., exhibit branched conidiophores in culture, as did Stahel (1937) for Ramichloridium musae. De Hoog (1977) subsequently reintroduced 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 pigmentated 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 Rhinocladiella, Veronaea and Cladosporium Link. It was further noted that the main feature to distinguish Ramichloridium from Rhinocladiella, was the presence of exophiala-type budding cells in species of Rhinocladiella (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).

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 Rhinocladiella 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 reintroduced Ramichloridium, but typified it with R. apiculatum (J.H. de Hoog [1977], J.Z. Groenewald [1978], W. Gams [1983], U. Braun [1982] and P.W. Crous [1987].) Arzanlou & Crous, comb. nov., Gams & Crous, gen. nov., and Myrmecridium arsalalou M.B. Ellis. Arzanlou & Crous, nom. nov., Myrmecridium schulzeri (C.K. Campb. & Al-Hedaithy) Arzanlou & Crous, nom. nov., Myrmecridium brasilianum Arzanlou & Crous, sp. nov., Myrmecridium streptzie Arzanlou, W. Gams & Crous, sp. nov., Rhinocladiella bastiona (de Hoog) Arzanlou & Crous, comb. nov., Rhinocladiella fasciculata (V. Rao & de Hoog) Arzanlou & Crous, comb. nov., Rhinocladiella mackenziei (C.K. Campb. & Al-Hedaithy) Arzanlou & Crous, comb. nov., Radulidium Arzanlou, W. Gams & Crous, comb. nov., Radulidium subulatum (de Hoog) Arzanlou & Crous, comb. nov., Radulidium flexuosum (De Hoog) Arzanlou, W. Gams & Crous, comb. nov., Radulidium vittatum (de Hoog) Arzanlou, W. Gams & Crous, comb. nov., Radulidium fasciculatum Arzanlou & Crous, sp. nov., Radulidium obtusipila de Hoog & Crous, sp. nov., Radulidium obtusipila de Hoog & Crous, comb. nov., Rhinocladiella mackenziei (C.K. Campb. & Al-Hedaithy) Arzanlou & Crous, comb. nov., Radulidium Arzanlou, W. Gams & Crous, gen. nov., Radulidium obtusipila Arzanlou, W. Gams & Crous, sp. nov., Veronaea Arzanlou, W. Gams & Crous, gen. nov., Veronaea papuana (Aproux) Arzanlou, W. Gams & Crous, comb. nov., Veronaea japonica Arzanlou, W. Gams & Crous, sp. nov., Veronaea simplex (Papendorf) Arzanlou & Crous, comb.nov.

Key words: Capnodiales, Chaetothyriales, Mycosphaerellaceae, Periconiella, phylogeny, Rhinocladiella, Veronaea.
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-Heddahy is a serious human pathogen, causing cerebral phaeohyphomycosis (Al-Heddahy et al. 1988, Campbell & Al-Heddahy 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 morphological 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, Rhinocladiella 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 the large subunit 28S rRNA (LSU) gene was amplified with primers LR0R (Rehner & Samuels 1994) and LR5 (Vilgalys & Hester 1990). The ITS 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 MgCl₂, 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 Paullicorticium an satum Liberta 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).

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* | Source               | Origin                  | GenBank numbers (LSU, ITS) |
|----------------------------------|-------------------|----------------------|-------------------------|----------------------------|
| *Myrmecridium flexuosum*         | CBS 396.76*; IMI 203547 | Soil                 | Suriname                | EU041825, EU041768         |
| *Myrmecridium schulzeri*         | CBS 100.54; JCM 6974 | Soil                 | Zaire                   | EU041826, EU041769         |
|                                  | CBS 134.68; ATCC 16310 | Soil                 | Germany                 | EU041827, EU041770         |
|                                  | CBS 156.63         | Homo sapiens         | Netheands               | 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 | Triticum aestivum    | Netherlands             | EU041832, EU041775         |
|                                  | CBS 381.87         | —                    | Australia               | EU041833, EU041776         |
|                                  | CBS 642.76         | Malus sylvestris     | Switzerland             | EU041834, EU041777         |
|                                  | CBS 114996         | Cannomois virgata    | South Africa            | EU041835, EU041778         |
| Periconiella arcuata             | CBS 113477*        | Ischyrolepsis subverticellata | South Africa          | EU041836, EU041779         |
| Periconiella levispora           | CBS 873.73*        | Turpinia pomiicera    | Sri Lanka                | EU041837, EU041780         |
| Periconiella velutina            | CBS 101948*; CPC 2262 | Brabejum stellatitolum | South Africa           | EU041838, EU041781         |
|                                  | CBS 101949; CPC 2263 | Brabejum stellatitolum | South Africa           | EU041839, EU041782         |
|                                  | CBS 101950; CPC 2264 | Brabejum stellatitolum | South Africa           | EU041840, EU041783         |
| Pleurothecium obovoidum          | CBS 209.85*; MFC 12477 | Pasania edulis       | Japan                    | EU041841, EU041784         |
| Pseudovirgaria hyperparasitica   | CBS 121735; CPC 10702 | On Phragmidium sp. on Rubus coreanus | Korea            | EU041822, EU041765         |
|                                  | CBS 121738; CPC 10704 | On Phragmidium sp. on Rubus coreanus | Korea            | EU041823, EU041766         |
|                                  | CBS 121739*; CPC 10753 | On Pucciniastrum agrimoniae on Agrimonia pilosa | Korea            | EU041824, EU041767         |
| Radulidium epichloës             | CBS 361.63*; MUCL 3124 | Epichloë typhina     | U.S.A.                   | EU041842, EU041785         |
| Radulidium sp.                   | CBS 115704         | Poaceae              | Guyana                   | EU041843, EU041786         |
| Radulidium subulatum             | CBS 287.84         | Puccinia allii       | U.K.                     | EU041844, EU041787         |
|                                  | CBS 405.76*        | Phragmites australis | Czech Republic           | EU041845, EU041788         |
|                                  | CBS 912.96         | Incubator for cell cultures | Germany            | EU041846, EU041789         |
|                                  | CBS 101010         | Lasioptera arundinis | Czech Republic           | EU041847, EU041790         |
| Ramichloridium apiculatum        | 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         | Cucumis sativus      | South Africa             | EU041849, EU041792         |
|                                  | CBS 391.67; JCM 6966 | Aloe sp.             | South Africa             | EU041850, EU041793         |
|                                  | CBS 400.76; IM 088021 | Soil                 | Pakistan                 | EU041851, EU041794         |
| Ramichloridium australiense      | CBS 121710         | Musa banksii         | Australia                | EU041852, EU041795         |
| Ramichloridium bivericillatum    | CBS 335.36         | Musa sapientum       | —                        | EU041853, EU041796         |
| Ramichloridium brasilianum       | CBS 283.92*        | Forest soil          | Brazil                   | EU041854, EU041797         |
| Ramichloridium cerophilum        | CBS 103.59*        | Sasa sp.             | Japan                    | EU041855, EU041798         |
| Ramichloridium indicum           | CBS 171.96         | —                    | —                        | EU041856, EU041799         |
| Ramichloridium musae             | CBS 190.63; MUCL 9557 | Musa sapientum       | —                        | EU041857, EU041800         |
|                                  | CBS 365.36*; JCM 6973; MUCL 9556 | Musa sapientum       | —                        | EU041858, EU041801         |
| Ramichloridium pini              | CBS 461.82*; MUCL 28942 | Pinus contorta      | U.K.                     | EU041859, EU041802         |
| Ramichloridium strictitiae      | CBS 121711         | Streititia sp.       | South Africa             | EU041860, EU041803         |
| Rhinocladiella anceps           | CBS 157.54; ATCC 15680; MUCL 1081; MUCL 7992; MUCL 15756 | Fagus sylvatica       | France                    | EU041861, EU041804         |
|                                  | CBS 181.65*; ATCC 18655; DAOM 84422; IM 134453; MUCL 8233; OAC 10215 | Soil                 | Canada                    | EU041862, EU041805         |
| Rhinocladiella basilota         | CBS 101460*; IFM 47593 | Homo sapiens        | Japan                    | EU041863, EU041806         |
| Rhinocladiella fascicularata     | CBS 132.96*        | Decayed wood         | India                    | EU041864, EU041807         |
| Rhinocladiella mackenziei       | CBS 367.92; NCPF 2738; UTMB 3169 | Homo sapiens        | Israel                   | EU041865, EU041808         |
Table 1. (Continued).

| Species                          | Accession number1 | Source                  | Origin             | GenBank numbers (LSU, ITS) |
|----------------------------------|-------------------|-------------------------|--------------------|---------------------------|
| CBS 368.92; UTMB 3170             | Homo sapiens      | Israel                  |                    | EU041866, EU041809        |
| CBS 102590; NCPF 2853             | Homo sapiens      | United Arab Emirates    |                    | EU041867, EU041810        |
| Rhinocladiella phaeophora         | CBS 496.78*; IMI 297527 | Soil                    | Colombia           | EU041868, EU041811        |
| Rhinocladiella sp.                | CBS 264.99; MUCL 9904 | Honey                   | France             | EU041869, EU041812        |
| Rhodoveronaea vaniceptata         | CBS 431.88*       | Bertiia moriformis      | Germany            | EU041870, EU041813        |
| Thysanorea papuana                | CBS 212.96*       | Papua New Guinea        |                    | EU041871, EU041814        |
| Veronaea botyrosa                 | CBS 121.92        | Xanthorrhoea preissi    | Australia          | EU041872, EU041815        |
| Veronaea compacta                 | CBS 254.57*; IMI 070233; MUCL 9821 | —                       | Italy              | EU041873, EU041816        |
| Veronaea japonica                 | CBS 350.65; IMI 115127; MUCL 7972 | Goat dung               | India              | EU041874, EU041817        |
| Veronaea simplex                   | CBS 268.75*       | —                       | South Africa       | EU041876, EU041819        |
| Veronaea japonica                 | CBS 776.83*       | On dead bamboo culm     | Japan              | EU041875, EU041818        |
| Veronaea simplex                   | CBS 588.66*; IMI 203547 | Acacia karroo           | South Africa       | EU041877, EU041820        |
| Zasmidium cellare                 | CBS 146.36        | Wine cellar             |                    | EU041878, EU041821        |

1ATCC: 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 Toxins, 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.

2Ex-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 every 1 000 generations, resulting in 2 000 trees. Burn-in was set at 1500 trees from which the consensus tree (Fig. 1) 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 (Tabuki) de Hoog, R. indicum (Subram.) de Hoog, R. pilosum and three new species respectively isolated from Musa banksii, Strelitzia nicolaii, 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 Rhinocladiella in the Herpotrichiellaceae. The third clade (in the Sordariomycetes clade) includes R. obvoideum (Matsush.) de Hoog, which in a Blast search was found to have affinity with Carpoligia pleurotheci F.A. Fernández & Huhndorf (Chaetothyriales). The fourth clade (in the Sordariomycetes clade) includes a veronaea-like isolate from Bertiia moriformis, with phylogenetic affinity to the Anulatacaceae (Sordariomycetidae). The fifth clade (in the Sordariomycetes clade) includes R. schulzeri var. schulzerii and R. schulzeri var. flexuosum de Hoog, the closest relatives being Thyridium vestibum (Fr.) Fuckel in the Thyri diaceae and Magnaportae grisea (T.T. Hebert) M.E. Barr in the Magnaporthaceae. 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 botyrosa 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 ..................................................................................................................................................................................
   ![Image](https://www.studiesinmycology.org)

2. Conidiophores usually poorly differentiated from the vegetative hyphae; conidial apparatus often loosely branched; exophiala-like ................................................................. Pseudoveronaea

3. Conidiophores unbranched or, if branched, branches loose, irregular or dichotomous, but not distinctly separated into stalk and branched head ................................................................. Thysanorea

4. Conidiophores composed of a well-developed erect stalk and a terminal branched head ..........................................................................................................................................................................................................................

5. Conidia predominantly aseptate ..........................................................................................................................................................................................................................

6. Conidiophores monomorphic; branched head with fewer branches and looser; conidiogenous loci usually flat, non-prominent, less denticle-like; conidia aseptic to pluriseptate [anamorphs of Capnodiales] ..................................................................................................................................................

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] ..................................................................................................................................................

8. Vegetative mycelium entirely hyaline; rachis long, hyaline, with widely scattered pimple-shaped, terminally pointed, unpigmented denticles ..........................................................................................................................................................................................................................

9. Rachis with denticles 1–1.5 µm long, denticles almost cylindrical; conidia at least partly in short chains ............................................ Pleurothecium

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] ..................................................................................................................................................

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 Arzaniou & 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, Streitizia 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 subverticillata in South Africa. Zasmidium cellare (Pers.) Fr., the type species of Zasmidium (Pers.) Fr., is also shown to cluster within the Mycosphaerellaceae.
**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.
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.
**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.

**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 stellatilfodium, P. MacOwan, herb. G. Winter (B), *lectotype selected here*; Cape Town, on leaves of *Brabejum stellatilfodium* (= *B. stellatum*), P. Mac-Owan, PAD, F42165, F462166, *isolateotypes*; Stellenbosch, Jonkershoek Nature Reserve, on *Brabejum stellatum*, 24 Jan. 1999, J.E. Taylor, *epitope designated here* CBS H-15612, cultures ex-epitope CBS 101948–101950.

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

Etymology: Named after its curved conidia.

Ab allis speciebus Periconiellae conidias 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. Conidigenous 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, microcyclic conidiation observed in culture.

0.1 expected changes per site.
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 µm.

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 µm.
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 µm.

Fig. 6. A. *Pseudovirgaria hyperparasitica* (CBS 121739 = CPC 10753). B. *Periconiella levispora* (CBS 873.73). Scale bar = 10 µm.
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 Arzaniou, W. Gams & Crous, sp. nov. MycoBank MB504546. Figs 5–6B.

Eymology: (Latin) levis = smooth.

A simili Periconiella velutina conidii 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, 2–3.5 µm.

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 subblending 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 Rhinocladiella apiculata Matsush., in Matsushima, Icon. Microfung. Mats. lect.: 122. 1975.]
≡ Rhinocladiella 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–)5–6.5(–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-oxoquinoline 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. Penicilliella arcuata (CBS 113477). B. Mymicriadium schulzeri (CBS 325.74). C. Thysanorea papuana (CBS 212.96). Scale bars = 10 µm.
Ramichloridium australiense Arzaniou & Crous, sp. nov. MycoBank MB504548. Figs 9–10A.

Etymology: Named after its country of origin, Australia.

Ab alis speciebus Ramichloridi conidiophoris ex hyphis verrucosis, crassitunicatis ortis distinguendum.

In vitro: Submerged hyphae hyaline, smooth, thin-walled, 1–2 µm wide; aerial hyphae pale brown, warted. Conidiophores arising vertically and clearly differentiated from creeping aerial hyphae, up to 400 µm tall, with several additional thin septa; intercalary cells, 8–40 × 2–5 µm, 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 µm long, proliferating sympodially, giving rise to a short rachis with conspicuous conidiogenous loci; scars slightly thickened and darkened, about 1 µm diam. Conidia solitary, aseptate, thin-walled, smooth, subhyaline, subcylindrical to obclavate, (10–)12–15(–23) × 2.5–3 µm, with a truncate base and a slightly darkened and thickened hilum, 1.5–2 µm diam, rarely fusing at the basal part.

Cultural characteristics: Colonies on MEA rather slow growing, reaching 8 mm diam after 14 d at 24 °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°34'47.2" S, 145°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. Rhodoveronaea varioseptata (CBS 431.88). Scale bar = 10 μm.

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 μm.
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 µm.

Fig. 13. *Ramichloridium brasiliianum* (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 µm.

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 µm.
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. [≡ Cladosporium 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 2689; from Musa sapientum, J. Brun, CBS 190.63 = MUC 9557. Surinam, Paramaribo, from Musa sapientum leaf, G. Stahel, CBS 365.36 = JCM 6973 = MUC 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, dacryloid to pyriform, (2–3–4–6) × (1.5–2–2.5) µm, smooth, thin-walled, with an inconspicuous hilum.

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 103.99, ex-type.

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 similar Ramichloridio cerophiloo conidii minorii, ad 8 µm longis, et conidii 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, obvoid 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, Parelhe, 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: Acrorhachia cerophila Tubaki, J. Hattori Bot. Lab. 20: 143. 1958. [≡ Cladosporium cerophilum (Tubaki) Matsush., in Matsushima, Icon. Microfung. Matsu. 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, black gelatinous exudate droplets on OA.
Fig. 15. Ramichloridium indicum (CBS 171.96). A–B. Macronematous conidiophores. C–E. Sympodially proliferating conidiogenous cells, resulting in a conidium-bearing rachis with pigmented and thickened scars. F. Conidia. Scale bar = 10 µm.

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

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 Rhinocladiella 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 µm wide, with thin septa; aerial hyphae coarsely verrucose, olivaceous-green, rather thick-walled, 2–2.5 µm 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 µm long, 2–4 µm wide, often with inflated basal cells. Conidiogenous cells terminally integrated, up to 165 µm long, smooth, dark brown, sympodially proliferating, rachis straight or flexuose, geniculate or nodose, subhyaline; scars thickened and darkened, clustered at nodes, approx. 0.5 µm 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) × (4–)6–6.5(–9) µm, with truncate base; hilum conspicuous, slightly darkened, not thickened, about 1 µm 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

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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.
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, De Matoiaceous 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 *R. 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 aniceps*, *R. mackenziei*, *R. fasciculatum* and *R. basitonum*.
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, subhyaline, aseptate, thin-walled, smooth, subglobose, with a slightly pigmented hilum; conidial secession schizolytic.

Type species: Rh. atrovirens Nannf., Svenska Skogsvårdsfören. Tidsskr. 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 to 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.
**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 µm 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 µm wide. *Conidiogenous cells* terminal, variable in length, 10–100 µm long, pale brown, straight or geniculate, proliferating sympodially, giving rise to a long, 2–2.5 µm 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) × 1–2 µm, hilum conspicuous, slightly darkened and thickened, less than 0.5 µm diam.

*Cultural characteristics*: Colonies on MEA reaching 19 mm diam after 14 d at 24 °C, with entire, smooth, sharp margin; mycelium rather flat and slightly elevated in the centre, pale olivaceous-grey to olivaceous-black; 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 µm 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 µm long and 2–3 µm wide, with 0–5 thin additional septa. *Conidiogenous cells* terminal, cylindrical, 30–100 µm long, thin-walled, smooth, pale brown, fertile part as wide as the basal part, up to 2 µm wide, proliferating sympodially, giving rise to a rachis with hardly prominent, slightly pigmented, not thickened scars, less than 0.5 µm diam. *Conidia* solitary, smooth, thick-walled, subhyaline, ellipsoidal, (2.5–)4–5(–6) × 2–3 µm, with truncate, slightly pigmented hilum, about 0.5 µm 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 µm long, 1–1.5 µm wide. *Conidia* smooth, thin-walled, aseptate, subhyaline, globose, 2–2.5 µm diam.

*Cultural characteristics*: Colonies on MEA reaching 8 mm diam after 14 d at 24 °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 µm.
Fig. 23. 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 µm.

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 µm.
Rhinocladiella mackenziei (C.K. Campb. & Al-Hedailh) Arzanlou & Crous, comb. nov. MycoBank MB504554. Fig. 22. Basionym: Ramichloridium mackenziei C.K. Campb. & Al-Hedailh, 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 365.92 = UTMB 3170; human brain abscess, E. Leffer, CBS 367.92 = NCPF 2738 = UTMB 3169. **Saudi Arabia:** from phaeohyphomycosis of the brain, S.S.A. Al-Hedailh, ex-type strain, CBS 650.93 = MUCL 40057 = NCPF 2808; from brain abscess, Pakistani male who travelled to Saudi Arabia, CBS 102292 = 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 form 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, 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)–(4) µm, with a truncate base and darkened hilum, 1 µm diam. *Macroconidium* 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)–(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 layers 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–(6)–(6) × (2–)3–(4)–(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 schizoletic.

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.

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

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

*Veronaea* species similes sed conidiophoris partim *Periconia* similibus dense ramosis distinguenda.

**Thysanorea** Arzanlou, W. Gams & Crous, comb. nov. MycoBank MB504556. Fig. 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, 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)–(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 schizoletic.

Type species: *Veronaea botryosa* Cif. & Montemart., Atti Ist. Bot. Lab. Crittog. Univ. Pavia, sér. 5, 15: 68. 1957.
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 µm wide and up to 200 µm long. Conidiogenous cells terminal, occasionally intercalary, cylindrical, 10–100 µm 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) × (1.5–)2–2.5(–3) µm, rounded at the apex and truncate at the base, pale brown, 1(–2)-septate, with a faintly darkened, unthickened hilum, about 0.5 µm diam.

Cultural characteristics: Colonies on MEA reaching 30 mm diam after 14 d at 24 °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 µm 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 µm wide, unbranched or branched at acute angles, with 1–3 additional septa, cells often inflated and flask-shaped, pale-brown, up to 60 µm long. Conidiogenous cells terminal, occasionally intercalary, variable in length, up to 10 µm long, pale brown, cylindrical to doliform or flask-shaped, with hardly prominent denticles; scars flat, slightly pigmented, not thickened, about 0.5 µm diam. Conidia solitary, pale brown, smooth, thin-walled, ellipsoidal to ovoid, 0–1(–2)-septate, often constricted at the septa, (4–)6–7–9 × 2–3 µm, with a round apex and truncate base; hilum prominent, slightly darkened, unthickened, about 0.5 µm diam.

Cultural characteristics: Colonies rather slow growing, reaching 15 mm diam on MEA after 14 d at 24 °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.
Veronaea japonica Arzanlou, W. Gams & Crous, sp. nov. MycoBank MB504557. Figs 17B, 27.

Etymology: Named after the country of origin, Japan.

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

In vitro: Submerged hyphae subhyaline, smooth, thin-walled, 1.5–3 µm 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 µm wide, up to 65 µm long, unbranched or occasionally branched.
pale brown, thin-walled, smooth, with 1–3 additional septa. 

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

Cultural characteristics: Colonies rather slow growing, reaching 7.5 mm diam on MEA after 14 d at 24 °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” (Rhinocladiella) mackenziei by some authors, and subsequently reduced to synonymy (Ur-Rahman et al. 1988). However, R. obovoideum clusters with Carpogina 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: Rhinocladiella obovoidea Matsush., Icones Microfung. Mats. lec.: 123. 1975.

≡ Ramichloridium obovoideum (Matsush.) de Hoog, Stud. Mycol. 15: 73. 1977.

In vitro: Submerged hyphae smooth, hyaline, thin-walled, 1–2 µm wide; aerial hyphae hyaline to subhyaline, smooth. Conidiophores arising vertically from creeping hyphae, ascending hyphae thick-walled and dark brown; conidiophores 10–35 µm 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 µm long, pale brown, elongating sympodially, with a short rachis giving rise to denticles, 1 µm 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) × (3–)4(–5) µm, smooth, thin-walled, with a more or less rounded apex, a truncate base and a slightly darkened, unthickened hilum, 1.5 µm 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 -ridum from Chloridium.

Genus ab allis generibus Ramichloridii similibus rachide recta longa, subhyalina, denticulis distantis, 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 terminal, integrated, polyblastic, cylindrical, straight or flexuose, pale brown, occasionally secondarily septate, fertile part subhyaline, as wide as the basal part, 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, obvoidal 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 (B1) 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 schulzeri (Sacc.) Sacc., Syll. Fung. 4: 322. 1886. = Rhinocladiella schulzeri (Sacc.) Matsush., Icon. Microfung. Mus. lect. (Kobe): 124. 1975. = Ramichloridium schulzeri (Sacc.) de Hoog, Stud. Mycol. 15: 64. 1977 var. schulzeri.

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, septe, 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 septe, 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, obvoid 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-Klitzeberg, from wheat-field soil, W. Gams, CBS 134.68 = ATCC 16310. The Netherlands, isolated from a man, bronchial secretion, V. Visser, CBS 156.63 = MUL 1079; Lienden, isolated from Triticum aestivum root, C.L. de Graaff, CBS 325.74 = JCM 7234.

Myrmecridium schulzeri var. triticici (M.B. Ellis) Arzanlou, W. Gams & Crous, comb. nov. MycoBank MB504562. Basionym: Pleurophragmium tritici M.B. Ellis, in Ellis, More Dematiaceous Hyphomycetes: 165. 1976.

In vitro: Submerged hyphae hyaline, thin-walled, 1–2 µm wide. Conidiophores unbranched, flexuose, arising from creeping aerial...
hyphae, pale brown, up to 250 µm tall, 3–3.5 µm wide, thick-walled, smooth, with up to 24 thin septa, delimiting 8–12 µm long cells. **Conidiogenous cells** integrated, elongating sympodially, cylindrical, 20–150 µm 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 µm long denticles. **Conidia** solitary, subhyaline, thin-walled, finely verrucose, with a wing-like gelatinous sheath, approx. 0.5 µm wide, ellipsoid to ovoid, (5–)6–7(–9) × 3–4 µm; hilum slightly prominent, unpigmented, approx. 0.5 µm diam.

**Cultural characteristics**: Colonies reaching 40 mm diam after 14 d at 24 °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.
≡ *Ramularia torvi* Ellis & Everh., Rep. Missouri Bot. Gard. 9: 119. 1898.
≡ *Hansfordia torvi* (Ellis & Everh.) Deighton & Piroz., Mycol. Pap. 101: 39. 1965.
≡ *Acladium biophilum* Cif., Sydowia 10: 164. 1956.
≡ *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 µm.

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 µm.
**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 brunneo, fertugineae vel cinnamomeae, in vitro lentissime crescentes, murinae. Mycelium immersum et praeципue externum, ex hyphis ramosis et cellulis conidiogenis integratis compositis, conidiophoris ab hyphis vegetativis vix distinguishis. Hyphae ramosae, septatae, levae, tenunticulatae, hyalinae vel pallide brunnaeae. Cellulae conidiogenae integratae in hyphis repentibus, terminales et intercalares, polyblasticae, sympodiales proliferantes, subcyclindicae 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 conidiogenae, holoblasticae, plus minusve obovoviae, recta vel leniter curvata, asymmetrica, continua, hyalina, subhyalina vel patidissime 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 cinnamom, *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 obovate, 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 & Deam.) Arzanlou, W. Gams & Crous in the *Sordariomycetidae*. Although *Pseudovirgaria* is morphologically similar to *Virgaria* Nees, it has hyaline to pale brown hyphal-, 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 *Neovolvaria* U. Braun and *Psuedodidymaria* 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 wide, hyaline, subhyaline to pale yellowish, light brownish in mass, thin-walled (*≤ 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, obovate, often slightly curved with ± unequal sides, 10–20 × 5–9 μm, aseptate, subhyaline, pale yellowish 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–)1.0–1.5 μm diam, convex to truncate, unthickened, not to slightly darkened-refractive.

**In vivo:** Colonies on rust sori, thin to moderately thick, loose, cobwebby, to dense, tomentose, pale to medium brown, rusty or cinnamom. Mycelium partly immersed in the sorus, 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, obovate, often slightly curved with ± unequal sides, 10–20 × 5–9 μm, aseptate, subhyaline, pale yellowish 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–)1.0(–1.5) μm diam, convex to truncate, unthickened, not to 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 Frommellia sp., on Duchesnea chrysanthha, 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 sympodially proliferating conidiogenous cells, resulting in a conidium-bearing rachis. C–D. Rachis with crowded, blunt conidium-bearing denticles. E. Conidia. Scale bar = 10 µm.

Fig. 33. *Radulidium epichloës* (CBS 361.63). A–C. Conidial apparatus at different stages of development, resulting in semi-micronematous conidiophores and sympodially 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 µm.
on Phragmidium pauciloculare on Rubus parvifolius, 14 Oct. 2003, H.D. Shin, paratype, 23/10, HAL 2055 F; Hongchon, 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:** Rhinocladiella eliator 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 aculate, 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. Samišťákova, ex-type culture CBS 405.76; Opatovicky pond, from Lasioptera arundinis (gall midge) mycangia on Phragmites australis, M. Skuhravá, 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, verruculose, 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 Glycera striata, G.L. Hennebert, CBS 361.63 = MUCL 3124; specimen in MUCL designated here as epitype.

**Veronaeae-like clade, allied to the Annulatascaceae**

A veronaeae-like isolate from Bertia mariforium clusters near the Annulatascaceae, 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 conidiorum late truncata et marginae 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 verticically from creeping hyphae, straight or flexuose, simple, thick-walled, red-brown, with inflated basal cell. **Conidiogenous cells** terminally integrated, polyblastic, sympodial, smooth, thick-
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 seporate conidia.
Rhodoveronaea varioseptata Arzanlou, W. Gams & Crous, sp. nov. MycoBank MB504570. Figs 10D, 34.

Etymology: Named for its variably septate conidia.

Colonies reaching 25 mm diam after 14 d at 24 °C; surface velvety, floccose; surface olivaceous-grey to dark olivaceous-green; reverse olivaceous-black.

Specimen examined: Germany, Effel, Berndorf, on Berlia moniformis, Sep. 1987, W. Gams, holotype CBS-H 19932, culture ex-type CBS 431.88.

Veronaeopsis (Pleosporales)

The ex-type strain of Veronaea simplex (Papendorf 1969) did not cluster with the genus Veronaea (Herpotrichiellaceae), but is allied to the Veronaeaceae. Veronaea simplex is distinct from species of Fusciadium 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.

Veronaeopsis differs from MycoBank comb. (1983) is distinct from species of Mycosphaerellaceae, 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 Wentiomyces 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 Wentiomyces 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), of 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 (Daviidiellaceae) 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 hosts, 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 Thysanorea, 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 Carpoigina 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, Radulidum and Mymaromixin, Veronaeaopsis, 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 Radulidum, 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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