Delimiting *Cladosporium* from morphologically similar genera

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**Abstract:** The genus *Cladosporium* is restricted to dematiaceous hyphomycetes with a coronate scar type, and *Davidiella* teleomorphs. In the present study numerous cladosporium-like taxa are treated, and allocated to different genera based on their morphology and DNA phylogeny derived from the LSU nrRNA gene. Several species are introduced in new genera such as *Hyalodendriella*, *Ochrocladosporium*, *Rachicladosporium*, *Rhizocladosporium*, *Toxicocladosporium* and *Verrucocladosporium*. A further new taxon is described in *Devriesia* (*Teratosphaeriaceae*). Furthermore, *Cladosporium castellanii*, the etiological agent of tinea nigra in humans, is confirmed as synonym of *Stenella araguata*, while the type species of *Stenella* is shown to be linked to the *Teratosphaeriaceae* (Capnodiales), and not the *Mycosphaerellaceae* as formerly presumed.

**Taxonomic novelties:** *Devriesia americana* Crous & Dugan, sp. nov., *Hyalodendriella Crous, gen. nov.*, *Hyalodendriella betulae Crous sp. nov.*, *Ochrocladosporium Crous & U. Braun, gen. nov.*, *Ochrocladosporidium Crous et al*, *Rachicladosporium luciae Crous, U. Braun & Hill, sp. nov.*, *Rhizocladosporium Crous & U. Braun, gen. nov.*, *Rhizocladosporium argillaceum* (Minoura) Crous & U. Braun, comb. nov., *Toxicocladosporium Crous & U. Braun, gen. nov.*, *Toxicocladosporium irritans* Crous & U. Braun, sp. nov., *Verrucocladosporium K. Schub., Aptroot & Crous, gen. nov.*, *Verrucocladosporidium dinitae K. Schub., Aptroot & Crous, sp. nov.*

**Key words:** Cladosporium, Davidiella, food spoilage, hyphomycetes, indoor air, LSU phylogeny, taxonomy.

**INTRODUCTION**

Cladosporioid hyphomycetes are common, widespread fungi. The genus *Cladosporium* Link is based on the type species, *Cladosporium herbarum* (Pers. : Fr.) Link, which in turn has been linked to *Davidiella Crous & U. Braun* teleomorphs (Braun et al. 2003, Schubert et al. 2007b – this volume). *Cladosporium* is one of the largest, most heterogeneous genera of hyphomycetes, comprising more than 772 names (Dugan et al. 2004), and including endophytic, fungicolous, human pathogenic, phytopathogenic and saprobic species. Species of this genus affect daily human life in various ways. The common saprobic members of *Cladosporium* occur on all kinds of senescing and dead leaves and stems of herbaceous and woody plants, as secondary invaders on necrotic leaf lesions caused by other fungi, are frequently isolated from air, soil, food stuffs, paint, textiles and other organic materials, are also known to be common endophytes (Riesen & Sieber 1985, Brown et al. 1998, El-Morsy 2000, De Jager et al. 2001, Inacio et al. 2002, Stohr & Dighton 2004, Leviš & Dorsey 2006). Furthermore, some *Cladosporium* species are known to be potential agents of medical relevance. *Cladosporium herbarum* is, for instance, a common contaminant in clinical laboratories and causes allergic lung mycoses (de Hoog et al. 2000, Schubert et al. 2007b – this volume).

In spite of the enormous relevance of this genus, there is no comprehensive modern revision of *Cladosporium*, but some attempts to revise and monograph parts of it have been initiated during the last decade (David 1997, Partridge & Morgan-Jones 2002, Wirsel et al. 2002, Braun et al. 2003, Dugan et al. 2004, Park et al. 2004, Seifert et al. 2004, Schubert & Braun 2004, 2005a, b, 2007, Heuchert et al. 2005, Schubert 2005a, b, Schubert et al. 2006). Previous molecular studies employing rDNA ITS sequence data (Crous et al. 2001) have shown *Cladosporium* spp. to cluster adjacent to the main monophyletic *Mycosphaerella* Johansson cluster, suggesting a position apart from the latter genus. Braun et al. (2003) carried out more comprehensive sequence analyses, based on ITS (ITS-1, 5.8S and ITS-2) and 18S rDNA data, providing further evidence that *Cladosporium* s. str. represents a sister clade of *Mycosphaerella*.

Various authors discussed the taxonomy and circumscription of *Cladosporium* (von Arx 1981, 1983, McKemy & Morgan-Jones 1990, Braun 1995), reaching different conclusions. However, a first decisive revision of *Cladosporium*, leading to a more natural concept of this genus, was published by David (1997), who carried out comprehensive scanning electron microscopic examinations of the scar and hilum structure in *Cladosporium* and *Heterosporium* Klotzsch ex Cook. The first Scanning Electron Micrograph (SEM) studies of these structures, published by Roquebert (1981), indicated that the conidigenous loci and conidial hilum in *Cladosporium* are characterised by having a unique structure. David (1997) confirmed these observations, based on a wide range of *Cladosporium* and *Heterosporium* species, and demonstrated that the structures of the conidigenous loci and hilum in the latter genus fully agree with those of *Cladosporium*, proving that *Heterosporium* was indeed a synonym of *Cladosporium* s. str. He introduced the term “coronate” for the *Cladosporium* scar type, which is characterised by having a central convex part (dome), surrounded by a raised periclinal rim (David 1997), and showed that this type is confined to anamorphs, as far as experimentally proven, connected with telemorphs belonging in “Mycosphaerella” s. lat. These results were confirmed in a later phylogenetic study by Braun et al. (2003). *Cladosporium* s. str. was shown to be a sister clade to *Mycosphaerella* s. str., for which the new teleomorph genus *Davidiella* was proposed. Although no clear morphological differences were reported between *Davidiella* and *Mycosphaerella*, a further study by Aptroot (2006) found ascospores of *Davidiella* to have characteristic irregular cellular inclusions (lumina), which are absent in species of *Mycosphaerella*, along with periphyssoids and pseudoparaphyses (Schubert et al. 2007b – this volume). Furthermore, a higher order phylogeny study by Schoch et al. (2006), which employed DNA sequence data of four loci (SSU nrDNA, LSU nrDNA, EF-1α, RPB2), revealed species of *Davidiella* to cluster in a separate family (*Davidiellaceae*) from species of *Mycosphaerella* (*Mycosphaerellaceae*), with both families residing in the *Capnodiales* (*Dothideomycetes*), and not *Dothideales* as always presumed.
| Anamorph | Teleomorph | Accession number | Host | Collector | Country | Host country collector | GenBank numbers |
|----------|------------|------------------|------|-----------|---------|------------------------|----------------|
| Cladoriella eucalypti | Coniothyrium palmarum | GS 11897: CPC 10984, CBS 118976, DAOM 23217 | Eucalyptus sp. | P.W. Crous | South Africa | South Africa | EU040224, EU040225 |
| Cladoriella acerispora | Cladoriella shelfordii | GS 118976: CPC 10984, CBS 118976 | Acer | N. Nickerson | U.S.A. | Canada | EU040226, EU040227 |
| Cladoriella thermodurans | Cladoriella shelfordii | GS 118978: CPC 10984 | Soil | N. Nickerson | Canada | Canada | EU040228, EU040229 |
| Cladoriella shelfordii | Cladoriella shelfordii | GS 118976: CPC 10984, CBS 118976 | Soil | N. Nickerson | Canada | Canada | EU040226, EU040227 |
| Cladoriella shelfordii | Cladoriella shelfordii | GS 118976: CPC 10984, CBS 118976 | Soil | N. Nickerson | Canada | Canada | EU040226, EU040227 |
| Cladoriella shelfordii | Cladoriella shelfordii | GS 118976: CPC 10984, CBS 118976 | Soil | N. Nickerson | Canada | Canada | EU040226, EU040227 |
| Cladoriella shelfordii | Cladoriella shelfordii | GS 118976: CPC 10984, CBS 118976 | Soil | N. Nickerson | Canada | Canada | EU040226, EU040227 |
| Cladoriella shelfordii | Cladoriella shelfordii | GS 118976: CPC 10984, CBS 118976 | Soil | N. Nickerson | Canada | Canada | EU040226, EU040227 |
| Cladoriella shelfordii | Cladoriella shelfordii | GS 118976: CPC 10984, CBS 118976 | Soil | N. Nickerson | Canada | Canada | EU040226, EU040227 |
| Cladoriella shelfordii | Cladoriella shelfordii | GS 118976: CPC 10984, CBS 118976 | Soil | N. Nickerson | Canada | Canada | EU040226, EU040227 |
| Cladoriella shelfordii | Cladoriella shelfordii | GS 118976: CPC 10984, CBS 118976 | Soil | N. Nickerson | Canada | Canada | EU040226, EU040227 |
| Cladoriella shelfordii | Cladoriella shelfordii | GS 118976: CPC 10984, CBS 118976 | Soil | N. Nickerson | Canada | Canada | EU040226, EU040227 |
| Cladoriella shelfordii | Cladoriella shelfordii | GS 118976: CPC 10984, CBS 118976 | Soil | N. Nickerson | Canada | Canada | EU040226, EU040227 |
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| Cladoriella shelfordii | Cladoriella shelfordii | GS 118976: CPC 10984, CBS 118976 | Soil | N. Nickerson | Canada | Canada | EU040226, EU040227 |
| Cladoriella shelfordii | Cladoriella shelfordii | GS 118976: CPC 10984, CBS 118976 | Soil | N. Nickerson | Canada | Canada | EU040226, EU040227 |
| Cladoriella shelfordii | Cladoriella shelfordii | GS 118976: CPC 10984, CBS 118976 | Soil | N. Nickerson | Canada | Canada | EU040226, EU040227 |
| Cladoriella shelfordii | Cladoriella shelfordii | GS 118976: CPC 10984, CBS 118976 | Soil | N. Nickerson | Canada | Canada | EU040226, EU040227 |
| Cladoriella shelfordii | Cladoriella shelfordii | GS 118976: CPC 10984, CBS 118976 | Soil | N. Nickerson | Canada | Canada | EU040226, EU040227 |
| Cladoriella shelfordii | Cladoriella shelfordii | GS 118976: CPC 10984, CBS 118976 | Soil | N. Nickerson | Canada | Canada | EU040226, EU040227 |

1 ATCC: American Type Culture Collection, Virginia, U.S.A.; ATHUM: Culture Collection of Fungi, University of Athens, Department of Biology, Athens, Greece; CBS: Centraalbureau voor Schimmelcultures, Utrecht, The Netherlands; CMW: Culture Collection of Mike Wingfield, Rabat, Morocco; CPC: Culture Collection of Pedro Crous, Utrecht, The Netherlands; DAOM: Plant Research Institute, Department of Agriculture, Ottawa, Canada; INIFAT: Alexander Humboldt Institute for Basic Research in Tropical Agriculture, Havana, Cuba; IMI: International Mycological Institute, CABI-Bioscience, Egham, U.K.; MUCL: Mycotheque de l' Université Catholique de Louvain, Louvain-la-Neuve, Belgium; OUT: Department of Fermentation Technology, Osaka University, Japan; W: W. Gams; H: H. Evans; M: M. Schol-Schwarz; a: A. Aptroot; G: G. Gams; F: F. Melin; E: E. Melin; B: B. Ahlert; O: O. Oberwinkler; A: A. Acosta; K: K. Todaie; R: R. F. Castañeda; P: P. Crous; T: T. Hijwegen; F: F. Hill; L: L. B. Sparrius; F: F. Hill; S: S. A. S. Sparrius; G: G. Gams; H: H. Evans; M: M. Schol-Schwarz; D: D. Davis; J: J. Yoshida.

2 ITIS: internal transcription spacer region and 5.8S rRNA gene. L: partial LSU rRNA gene.
The current circumscription of Cladosporium emend. can be summarised as follows: Dematiaceous hyphomycetes; Davidiella anamorphs; mycelium internal and external; hyphae branched, septate, pigmented; stromata lacking or occasionally present; conidiophores mononematous, solitary or fasciculate, cylindrical, geniculate-sinuous to nodulose, simple to branched, subhyaline to usually distinctly pigmented, continuous to septate, smooth to verruculose; conidigenous cells integrated, terminal and intercalary, usually sympodial, with a single to several scars; conidogenesis holoblastic; conidigenous loci coronate, i.e., more or less protuberant, composed of a central convex dome, surrounded by a raised periclinal rim, barely to distinctly darkened; conidia solitary or in short to long, simple to branched acropetal chains, amoero- to phragmosporous, subhyaline to usually distinctly pigmented, smooth, verruculose, verrucose, echinulate, cristate, hila coronate, more or less protuberant.

The new concept of Cladosporium s. str., supported by molecular data and typical coronate conidiogenous loci and conidial hila, rendered it possible to initiate a comprehensive revision of Cladosporium s. lat. The preparation of a general, annotated check-list of Cladosporium s. lat. was the first step in this direction (Dugan et al. 2004). The aim of the present study, therefore, was to delineate Cladosporium s. str. from other taxa that have in recent years been described in Cladosporium s. lat. To attain this goal isolates were studied under standardised conditions on a set of predescribed media (Schubert et al. 2007b – this volume), and subjected to DNA sequence analysis of the LSU nrRNA gene.

MATERIALS AND METHODS

Isolates
Isolates used were obtained from the Centraalbureau voor Schimmelcultures (CBS), or freshly isolated from various substrates (Table 1). Strains were cultured on 2 % malt extract plates (MEA; Gams et al. 2007), by obtaining single conidial colonies as explained in Crous (1998). Colonies were subcultured onto fresh MEA, oatmeal agar (OA), potato-dextrose agar (PDA) and synthetic nutrient-poor agar (SNA) (Gams et al. 2007), and incubated under near-ultraviolet light to study their morphology. Cultural characteristics were assessed after 2–4 wk on OA and PDA at 25 °C in the dark, using the colour charts of Rayner (1970). Nomenclatural novelties and descriptions were deposited in MycoBank (www.MycoBank.org).

DNA isolation, sequencing and phylogeny
Fungal colonies were established on agar plates, and genomic DNA was isolated following the CTAB-based protocol described in Gams et al. (2007). The primers V9G (de Hoog & Gerrits van den Ende 1998) and LR5 (Vilgalys & Hester 1990) were used to amplify part of the nuclear rDNA operon spanning the 3′ end of the 18S rRNA gene (SSU), the first internal transcribed spacer (ITS1), the 5.8S rRNA gene, the second ITS region and the 5′ end of the 28S rRNA gene (LSU). Four internal primers, namely ITS4 (White et al. 1990), LR0R (Rehner & Samuels 1994), LR3R (wwwbiology.duke.edu/fungi/mycolab/primers.htm), and LR16 (Moncalvo et al. 1993), were used for sequencing to ensure that good quality overlapping sequences are obtained. The PCR conditions, sequence alignment and subsequent phylogenetic analysis followed the methods of Crous et al. (2006d). The ITS1, ITS2 and 5.8S rRNA gene (ITS) were only sequenced for isolates of which these data were not available. The ITS data were not included in the analyses but deposited in GenBank where applicable. Gaps longer than 10 bases were coded as single events for the phylogenetic analyses; the remaining gaps were treated as missing data. Sequence data were deposited in GenBank (Table 1) and alignments in TreeBASE (www.treebase.org).

Morphology
Wherever possible, 30 measurements (∗ 1 000 magnification) were made of structures mounted in lactic acid or Shear’s solution (Gams et al. 2007), with the extremes of spore measurements given in parentheses. Microscopic observations were made from colonies cultivated for 7 d under continuous near-ultraviolet light at 25 °C on SNA as explained in Schubert et al. (2007b – this volume). Three classes of conidia are distinguished. Ramoconidia are defined as short apical branches (often conidiogenous cells) of a conidiophore which secede and function as conidia. They are characterised by having a truncate, undifferentiated base, i.e., they differ from true conidia by lacking characteristic basal hila caused by conidogenesis. Ramoconidia give rise to branched or unbranched conidia. Secondary ramoconidia are branched conidia with a narrowed base, bearing a true hilum, that can occur in chains, giving rise to conidia, which differ from secondary ramoconidia with regards to shape, size and septation. In previous literature on Cladosporium and allied genera, the true ramoconidia have often been classified as “ramoconidia s. str.” whereas the secondary ramoconidia have been named “ramoconidia s. lat.”

RESULTS

DNA extraction, amplification and phylogeny
Amplicons of approximately 1 700 bases were obtained for the isolates listed in Table 1. The newly generated sequences were used to obtain additional sequences from GenBank, which were added to the alignment. The manually adjusted LSU alignment contained 73 sequences (including the two outgroup sequences) and 996 characters including alignment gaps. Of the 849 characters used in the phylogenetic analysis, 336 were parsimony-informative, 77 were variable and parsimony-uninformative, and 436 were constant. Neighbour-joining analyses using three substitution models on the sequence data yielded trees with identical topologies to one another. The neighbour-joining trees support the same clades as obtained from the parsimony analysis, but with a different arrangement at the deeper nodes, which were poorly supported in the bootstrap analyses or not at all (for example, the Helotiales and Pleosporales are swapped around). Performing a parsimony analysis with gaps treated as new characters increases the number of equally parsimonious trees to 94; the same topology is observed but with less resolution for the taxa in the Helotiales (data not shown). Forty-four equally most parsimonious trees (TL = 1 572 steps; CI = 0.436; RI = 0.789; RC = 0.344), one of which is shown in Fig. 1, were obtained from the parsimony analysis of the LSU sequence data. The cladosporium-like taxa were found to belong to the Helotiales, Pleosporales, Sordariales and as sister taxa to the Davidiellaceae in the Capnodiales.

The LSU alignment used for parsimony and distance analysis was supplemented with sequences for Parapleurotheciospora inaequiseptata (Matsush.) P.M. Kirk and Subramaniomyces fusiaprophyticus (Matsush.) P.M. Kirk, as well as related sequences
Fig. 1. One of 44 equally most parsimonious trees obtained from a heuristic search with 100 random taxon additions of the LSU sequence alignment using PAUP v. 4.0b10. The scale bar shows 10 changes, and bootstrap support values from 1000 replicates are shown at the nodes. Thickened lines indicate the strict consensus branches and ex-type sequences are printed in bold face. The tree was rooted to two sequences obtained from GenBank (Athelia epiphylla AY586633 and Paullicorticium anseratum AY586693).
Consensus phylogram (50% majority rule) of 800 trees resulting from a Bayesian analysis of the LSU sequence alignment using MrBayes v. 3.1.2. Bayesian posterior probabilities are indicated at the nodes. Ex-type sequences are printed in bold face. The tree was rooted to two sequences obtained from GenBank (Athelia epiphylla AY586633 and Paullicorticium anatum AY586693).

Fig. 2.
from GenBank. This alignment was subjected to a Bayesian analysis using a general time-reversible (GTR) substitution model with inverse gamma rates and dirichlet base frequencies and the temp value set to 0.5. The Markov Chain Monte Carlo (MCMC) analysis of 4 chains started from a random tree topology and lasted 1 000 000 generations. Trees were saved each 1 000 generations, resulting in 1 000 trees. Burn-in was set at 200 000 generations after which the likelihood values were stationary, leaving 800 trees from which the consensus tree (Fig. 2) and posterior probabilities (PP’s) were calculated. The average standard deviation of split frequencies was 0.018459 at the end of the run. The same overall topology as that observed using parsimony was obtained, with the main exception that the Helotiales and Pleosporales swapped around, as observed with the distance analysis.

**Taxonomy**

The present study has delineated several cladosporium-like genera which are phylogenetically unrelated to, and morphologically distinct from Cladosporium s. str. (Davidiellaceae, Capnodiales). These are treated below:

**Capnodiales, incertae sedis**

*Rachicladosporium* Crous, U. Braun & C.F. Hill, gen. nov. MycoBank MB504430.

*Etymology:* Named after the apical rachis on conidiophores, and its cladosporium-like appearance.

Differnt a Cladosporio conidiophoris cum rachibus terminalibus, locis conidiogenis inconspicuis vel subconspicuis, margine leviter incrassatis, non fuscatis et non refractivis, hilis inconspicuis.

*Mycelium* consisting of branched, septate, smooth, hyaline to pale brown, thin-walled hyphae. *Conidiophores* erect, solitary, macroonematous, arising from superficial hyphae, subcylindrical, straight to somewhat geniculate-sinuous, medium brown, finely verruculose; basal foot cell without swelling or rhizoids. *Conidiogenous cells* integrated, terminal, subcylindrical or tips slightly swollen, forming an apical rachis, multilocal, loci terminal and lateral, without evident sympodial proliferation (non-geniculate); conidiogenous loci inconspicuous or subconspicuous by being very slightly thickened along the rim, but neither darkened nor refractive, giving rise to simple or branched chains or solitary conidia. *Ramoconidia* medium brown, finely verruculose, 0–1-septate, subcylindrical to narrowly ellipsoid; conidia ellipsoid, pale brown, 0(–1)-septate, smooth to finely verruculose; hila inconspicuous; secession schizolytic.

*Type species:* *Rachicladosporium luculiae* Crous, U. Braun & C.F. Hill, sp. nov.

![Fig. 3. Rachicladosporium luculiae (type material). A–F. Conidiophores with conidial chains, and conidiogenous loci aggregated in the upper region. G. Conidia. Scale bar = 10 µm.](image-url)
Rachicladosporium luculiae Crous, U. Braun & C.F. Hill, sp. nov. MycoBank MB504431. Fig. 3.

Etymology: Named after its host genus, Luculia.

Mycelium ex hyphis ramosis, septatis, levibus, hyalinis vel pallide brunneis, 2–3 µm latis cultura compositum. Conidiophora erecta, solitaria, macronemata, ex hyphis superficialiis oriunda, subcylindrica, recta a geniculata-sinusoida, ad 60 µm longa et 6 µmata, 3–6-septata, modica brunnea, subtiliter verruculosa, non crassituicnata, ad basim non inflata et non rhizoidae. Cellulae conidiogenae integratae, terminales, 8–15 × 4–5 µm, subcylindricae, apiocem versus attenuatae, apice obtuso, racidi terminali, locis conidiabibus numerosis, 1–2 µm latis, margini leviter incrassatis, non fisculatis et non refractivis. Conidia catenata vel solitaria. Ramoconidia medio brunnea, subtile verruculosa, 0–1-septata, subcylindrica vel anguste ellipsoidae, 10–17 × 4–5 µm; conidia secundaria ellipsoidae, pallide brunnea, 0(–1)–septata, levia vel subtile verruculosa, interdum guttulata, (7–)9–12(–15) × 3(–4) µm; hila inconspicua.

Mycelium consisting of branched, septate, smooth, thin-walled, hyaline to pale brown, 2–3 µm wide hyphae. Conidiophores erect, solitary, macronematous, arising from superficial hyphae, subcylindric, straight to somewhat geniculato-sinusoides, up to 60 µm long, and 6 µm wide, 3–6-septate, medium brown, finely verruculose, thin-walled (≤ 1 µm), rarely with a single percurrent proliferation; basal foot cell without swelling or rhizoids. Conidiogenous cells integrated, terminal, 8–15 × 4–5 µm, subcylindrica, tapering to an obtuse apex, occasionally slightly swollen at the tip, without distinct sympodial proliferation (non-guniculata), forming a rachis, with several conidiogenous loci, terminal and lateral, 1–2 µm wide, non-protruberant, quite inconspicuous to subconspicuous, very slightly thickened along the rim, but not darkened and refractive; giving rise to simple or branched chains or solitary conidia, thin-walled (≥ 0.75 µm). Ramoconidia medium brown, finely verruculose, 0–1-septate, subcylindrical to narrowly ellipsoid, 10–17 × 4–5 µm; conidia ellipsoid, pale brown, 0(–1)-septate, smooth to finely verruculose, at times guttulata, (7–)9–12(–15) × 3(–4) µm; hila inconspicuous, neither thickened nor darkened-refractive.

Cultural characteristics: Colonies on PDA erumpent, spreading, with moderate aerial mycelium and smooth, even margins; iron-grey in the centre, olivaceous-grey in the outer region (surface); iron-grey underneath. Colonies reaching 4 cm diam after 1 mo at 25 °C in the dark.

Specimen examined: New Zealand, Auckland, isolated from leaf spots on Luculia sp. (Rubiaceae), 25 Jul. 2004, F. Hill 1059, holotype CBS H-19891, culture ex-type CBS 121620 = CPC 11407.

Notes: Rachicladosporium is morphologically quite distinct from Cladosporium s. str. and allied cladosporoid genera by having an apical conidioaphore rachis with inconspicuous to subconspicuous scars and unthickened, not darkened-refractive conidia hilum. Due to the structure of the conidiogenous cells, R. luculiae superficially resembles species of the tretic genus Diplococcium Grove (Ellis 1971, 1976; Goh & Hyde 1998). However, there is no evidence for a tretic conidiogenesis in R. luculiae. The conidia are formed holoblastically and separated by a thin septum. Furthermore, in Diplococcium the conidiogenous cells are terminal as well as intercalary, the conidiophores are often branched, and branched conidial chains are lacking or at least less common. Molecular sequence data about Diplococcium species are not yet available, though taxa that have been analysed show affinities to the Pleosporaceae and Helotiales (Wang et al., unpubl. data), whereas Rachicladosporium is allied with the Capnodiales. The ecology of R. luculiae is still unclear, although it has been isolated from lesions on Luculia sp. Fruitimg of this species in vivo has not yet been observed, and its pathogenicity remains unproven.

Toxicocladosporium Crous & U. Braun, gen. nov. MycoBank MB504426.

Etymology: Named after ample volatile metabolites produced in culture, and cladosporium-like morphology.

Differt a Cladosporio locis conidiogenis denthulicati, incrassatis et fisculae-refractivis, sed non coronatis, conidioforis et conidis cum septis incrassatis et atrofuscis, et culturis cum metabolitis volatilis toxicis.

Mycelium consisting of branched, septate, dark brown, finely verruculose hyphae. Conidiophores solitary, dimorphic, solitary, macronematous or micronematous, reduced to conidigenous cells. Macronematous conidiophores subcylindrical, straight to geniculato-sinusoides, or irregularly curved, unbranched or branched above, septate, dark brown, finely verruculose, walls thick, septa dark brown; micronematous conidiophores reduced to conidigenous cells. Macronematous conidiophores subcylindrical, straight to geniculato-sinusoides, or irregularly curved, unbranched or branched above, septate, dark brown, finely verruculose, walls thick, septa dark brown; micronematous conidiophores reduced to conidigenous cells, erect, doliiform to subcylindrica, with slight taper towards the apex. Conidiogenous cells integrated, terminal or lateral, subcylindrica with slight taper towards apex; proliferating sympodially with apical loci protruding and denticile-like, thickened, darkened and refractive, but not coronate. Conidia catenulata in branched or unbranched chains, medium to dark brown, thick-walled, with dark, thick septa, smooth to finely verruculose; ramoconidia septate, prominently constricted at septe, broadly ellipsoid to subcylindrica; conidia ellipsoid to ovoid, pale to medium brown, 0(–1)-septate; hila not coronate, but protruding, thickened, darkened and refractive in ramoconidia, but less obvious in young conidia.

Type species: Toxicocladosporium irritans Crous & U. Braun, sp. nov.

Toxicocladosporium irritans Crous & U. Braun, sp. nov. MycoBank MB504427. Fig. 4.

Etymology: Named after the skin irritation resulting from exposure to the fungus.

Mycelium (in PDA) ex hyphis ramosis, septatis, atro-brunnise, minune verruculosis, (2–)3–4 µm latis, ultimo crassituicnatis et crassisepales. Conidiophora solitaria, dimorphosa, macronemata et solitaria vel micronemata. Conidiophora macronemata ex hyphis modice brunnis lateralel orienda, erecta, subcylindrica, recta, geniculata-sinusoida vel irregulariter curvata, non ramosa vel ad apicom ramosa, 1–2-septata, atro-brunnia, leviter verruculosa, crassituicnata, septa atro-brunnia, 30–60 × 4–6 µm; conidiophora micromaterna saepe non septe, rara 1–2-septata, erecta, doliformes vel subcylindrica, apicem versus leviter attenuata, 10–30 × 2.5–4 µm. Cellulae conidiogenae integratae terminales vel laterales, subcylindricae, apicem versus leviter attenuatae, 7–12 × 3–4 µm, symodiales, cum 1–3 locis conidiogenibus, dentlucatis, 1–1.5 µm lati, incrassatis, fisculae-refractivis. Conidia catenulata vel rami-catenulata, modice vel atro-brunnia, crassituicnata, septs incrassatis, fisculae, levia vel subtile verruculosa, ramoconidia (0–1)–(3–5)-septata, constricta, later ellipsoidae vel subcylindrica, 7–15 × 3–5 µm; conidia secundaria ellipsoidae vel ovoidae, palide vel modice brunnia, 0(–1)–septata, (5–)6–(8–)10 × (3–)4(–5) µm; hila protuberantes, 1–1.5 µm lata, hila ramoconidionum incrassata et fisculae-refractiva, vel hila conidionurum secondariumum 0.5–1 µm lata et subconspicua.

Mycelium on PDA consisting of branched, septate, dark brown, finely verruculose, (2–)3–4 µm wide hyphae; walls and septa becoming thickened and darkened with age. Conidiophores solitary, dimorphic, macronematous and solitary, or micronematous, reduced to conidigenous cells. Macronematous conidiophores subcylindrical, straight to geniculato-sinusoides, or irregularly curved, unbranched or branched above, 2–7-septate, dark brown, finely verruculose, walls thick, septa dark brown, 30–60 × 4–6 µm; medium brown hyphae giving rise to lateral, erect branches that become swollen, dark brown, and develop into macronematous conidiophores with thick-walled and dark septa; micronematous conidiophores
aseptate, reduced to conidiogenous cells (rarely 1–2-septate, i.e., with 1–2 supporting cells), erect, doliiform to subcylindrical, with slight taper towards the apex, 10–30 × 2.5–4 µm. Conidiogenous cells integrated, terminal or lateral, subcylindrical with slight taper towards apex, 7–12 × 3–4 µm; proliferating sympodially with 1–3 apical loci that can be slightly protruding and denticle-like, 1–1.5 µm wide, thickened, darkened and refractive. Conidia catenulate in branched or unbranched chains, medium to dark brown, thick-walled, with dark, thick septa, smooth to finely verruculose; ramoconidia (0–)1(–3)-septate, prominently constricted at septa, broadly ellipsoid to subcylindrical, 7–15 × 3–5 µm; conidia ellipsoid to ovoid, younger apical conidia pale to medium brown, 0(–1)-septate, (5–)8–(10) × (3–)4(–5) µm; hila protruding, 1–1.5 µm wide, thickened, darkened and refractive in ramoconidia, but less obvious in young conidia, where hila are 0.5–1 µm wide.

Cultural characteristics: Colonies on PDA erumpent, spreading, with dense aerial mycelium and smooth, even margins; surface olivaceous-black (centre), olivaceous-grey in outer region; reverse olivaceous-black. Colonies reaching 35 mm diam after 1 mo at 25 °C in the dark; colonies fertile.

Fig. 4. Toxicoacladosporium irritans (type material). A–B, F. Microconidiophores. C–E. Macroconidiophores. G–H. Ramoconidia and conidia. Scale bars = 10 µm.
was deposited as "distincte fuscata-refractiva."

pallide brunnea, tenuitunicata (≤ 0.5 µm), irregulariter verruculosa-rugosa, utrinque minusve recta, obovoidea, ellipsoidea, fusiformes vel subcylindricae, sed saepe ad basim late truncata, non attenuata, 2–2.5 µm lata, non incrassata, sed leviter cylindrica, 16–21 × (2–)2.5–3 µm, non septata, pallide brunnea, tenuitunicata, truncatis, 1–1.8(–2) µm latis, incrassatis et fuscatis-refractivis. Ramoconidia locis conidiogenibus 1–3, saepe ad apicem aggregatis, interdum protuberantibus, intercalares, cylindricae, angustae, 9–20 µm longae, holoblasticae, sympodiales, crassitunicata. Cellulae conidiogenae integratae, saepe terminales, interdum recta, interdum leviter flexuosa, anguste cylindrica vel filiformes, non geniculta, tenuitunicatae. Conidiophora ex hyphis repentibus lateraliter oriunda, erecta, Mycelium sparsiamentebranched; hyphae 1–3 µm wide, septate, not constricted at septa, hyaline, smooth to irregularly rough-walled, sometimes constricted toward the apex and base, hila truncate, (0.5–)0.8–1.5(–2) µm wide, barely to slightly thickened, but distinctly darkened-refractive. Ramoconidia cylindricae, aseptate, concolorous with conidiophores, thin-walled, irregularly rough-walled, verruculose to verruculose-rugose; hila unthickened but somewhat refractive. Conidia in long unbranched or loosely branched chains, more or less straight, obovoid, ellipsoid, fusiform to subcylindrical, with swollen and constricted parts, often appearing irregular in shape and outline, 0–1-septate, pale brown, thin-walled and irregularly rough-walled, verruculose-rugose; hila truncate, barely to slightly thickened, but distinctly darkened-refractive. Type species: Verrucocladosprium dirinae K. Schub., Aptroot & Crous, sp. nov.

Verrucocladosprium dirinae K. Schub., Aptroot & Crous, sp. nov.

Verrucocladosprium dirinae was deposited as Cladosporium arthoniae M. Christ. & D. Hawksw., but the name was misspelled. The latter species, described from antheridia of Arthonia impolita on Quercus from Sweden, does not possess clearly visible, distinct conidigenous loci and hila, and therefore has to be excluded from the genus Cladosporium s. str. and is also easily distinguishable from the newly introduced species above. Furthermore the conidiophores are apically frequently branched and the conatene, ellipsoid conidia are smaller and wider, 6–10 × 4–5 µm (Hawksworth 1979). Due to the conidiogenesis and the structure of the conidiogenous loci and conidia, C. arthoniae is rather close to lichenicolous Taeniella S. Hughes species. The unique feature of the new genus Verrucocladosprium is its unusual conidial and hyphal ornamentation. Furthermore, it differs from Cladosporium s. str. in having cylindrical-filiform conidiophores, which are neither geniculate nor nodulose, quite distinct, thickened and darkened, but non-corneate conidigenous loci and often irregularly shaped conidia. Phylogenetically, it is also distinct as a sister taxon to Cladosporium s. str. Concerning differences to other cladosporioid genera, see ‘key to the genera’. Verrucocladosprium dirinae has been isolated from the lichen species Dirina massiliensis, i.e., this species is probably lichenicolous, although its ecology is not quite clear. Fruiting of this species in vivo has not yet been observed. A second unnamed, taeniella-like, lichenicolous hyphomycete was also present on the thallus of this lichen.
Devriesia americana Crous & Dugan, sp. nov. MycoBank MB504434. Fig. 6.

*Etymology:* Named after the geographic location of its type strain, New York, U.S.A.

Differt a *D. shelburniensi* conidiophoris brevioribus (ad 30 µm longis), leviter latioribus (2–3 µm), ramoconidiis saepe nullis et conidiis 0–1-septatis.

*Mycelium* consisting of branched, septate, 1.5–3 µm wide hyphae, irregular in width, predominantly guttulate, smooth, forming hyphal strands and hyphal coils; hyphae frequently forming dark brown, thick-walled, intercalary, muriformly septate chlamydospores on PDA in culture. *Conidiophores* subcylindrical, medium brown, straight to irregularly curved, up to 7-septate and 30 µm tall, 2–3 µm wide, or reduced to conidiogenous cells. *Conidiogenous cells* terminal or lateral on hyphae, 5–12 × 2–3 µm, medium brown, smooth, guttulate, subcylindrical, mono- to polyblastic; scars somewhat darkened and thickened, but not refractive. *Conidia* medium brown, guttulate, smooth, in mostly unbranched chains, subcylindrical to narrowly ellipsoidal, tapering towards truncate ends, 0–1-septate, (7–)8–12(–16) × 2(–2.5) µm; hila darkened, somewhat thickened, not refractive, 1–1.5 µm wide.

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**Capnodiales, Teratosphaeriaceae**

*Devriesia americana* Crous & Dugan, sp. nov. MycoBank MB504434. Fig. 6.

*Etymology:* Named after the geographic location of its type strain, New York, U.S.A.

Differt a *D. shelburniensi* conidiophoris brevioribus (ad 30 µm longis), leviter latioribus (2–3 µm), ramoconidiis saepe nullis et conidiis 0–1-septatis.

*Mycelium* consisting of branched, septate, 1.5–3 µm wide hyphae, irregular in width, predominantly guttulate, smooth, forming hyphal strands and hyphal coils; hyphae frequently forming dark brown, thick-walled, intercalary, muriformly septate chlamydospores on PDA in culture. *Conidiophores* subcylindrical, medium brown, straight to irregularly curved, up to 7-septate and 30 µm tall, 2–3 µm wide, or reduced to conidiogenous cells. *Conidiogenous cells* terminal or lateral on hyphae, 5–12 × 2–3 µm, medium brown, smooth, guttulate, subcylindrical, mono- to polyblastic; scars somewhat darkened and thickened, but not refractive. *Conidia* medium brown, guttulate, smooth, in mostly unbranched chains, subcylindrical to narrowly ellipsoidal, tapering towards subtruncate ends, 0–1-septate, (7–)8–12(–16) × 2(–2.5) µm; hila darkened, somewhat thickened, not refractive, 1–1.5 µm wide.

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Fig. 5. *Verrucocladosporium dirinae* (type material). A. Colonies on MEA. B–C. Conidial chains. D–H. Ramoconidia and conidia. Scale bars = 10 µm.
Cultural characteristics: Colonies erumpent, with sparse aerial mycelium on PDA, and smooth, uneven, wide margins, submerged under the agar surface; greenish-black (surface); reverse olivaceous-black; on OA iron-grey (surface). Colonies reaching 6–15 mm diam on PDA after 14 d at 25 °C in the dark; colonies fertile, but sporulation sparse.

Specimen examined: U.S.A., New York, Long Island, isolated from air, F.M. Dugan, holotype CBS-H 19894, culture ex-type CBS 117726 = ATCC 96545 = CPC 5121.

Notes: Until recently, this species was treated as part of the “Phaeoramularia” hachijoensis species complex (Braun et al. 2003). The present strain has conidia that are smaller than those of “Phaeoramularia” hachijoensis, which has ramoconidia that are 1–3-septate, up to 30 µm long, and conidia that are predominantly 1-septate, 10–21 × 2–4 µm (Matsushima 1975). From the illustration provided by Matsushima, it appears that “Phaeoramularia” hachijoensis is indeed a species of Pseudocladosporium U. Braun, a finding which is in agreement with the name Pseudocladosporium hachijoense (Matsush.) U. Braun proposed by Braun (1998).

Devriesia americana is both morphologically and phylogenetically more allied to Teratosphaeria Syd. & P. Syd. than Venturia Sacc. Based on its pigmented conidiophores and catenulate conidia, and scars that are somewhat darkened and thickened, and the formation of chlamydothecia in culture, it is allocated to Devriesia Seifert & N.L. Nick. Species of the genus Devriesia are ecologically different, however (Seifert et al. 2004), being soil-borne and thermotolerant. It is possible, therefore, that further collections of this fungus may eventually indicate that it needs to be placed in a distinct genus within the Teratosphaeriaceae. Devriesia americana is the second species of Devriesia with muriform chlamydothecia, beside D. shelburniensis N.L. Nick. & Seifert, but the latter species is easily distinguishable by its long and narrow conidiophores (ca 100–200 × 1.5–2.5 µm) and abundant ramoconidia, up to 25.5 µm long, with 0–3 septa. Furthermore, D. shelburniensis is a thermotolerant soil-borne hyphomycete.

Stenella araguata Syd., Ann. Mycol. 28(1/2): 205. 1930. Figs 7–8. = Cladosporium araguatum (Syd.) Arx, Genera of Fungi Sporulating in pure Culture, Edn 2 (Vaduz): 224. 1974. = Cladosporium castellanii Borelli & Marcano, Castellania 1: 154. 1973.

Leaf spots hypophyllous, irregular to subcircular, up to 8 mm diam, indistinct, yellow to pale brown with indistinct margins on IMI 15728(a); on IMI 34905 (Fig. 7) lesions are amphigenous, and fascicles and sporodochia are rare, with superficial mycelium being predominant. Mycelium consisting of internal and external, medium brown, septeate, branched, verruculose, 3–4 µm wide hyphae. Caespituli fasciculate to sporodochial, hypophyllous, medium brown, up to 120 µm wide and 60 µm high. Conidiophores arising singly from superficial mycelium, or aggregated in loose to dense fascicles arising from the upper cells of a brown stroma up to 70 µm wide and 30 µm high; conidiophores medium brown, finely verruculose, 1–5-septate, subcylindrical, straight to geniculate-sinuous, unbranched.

Fig. 6. Devriesia americana (type material). A–B. Chlamydospore-like structures formed in culture. C–F. Conidiophores giving rise to conidial chains. G–H. Conidia. Scale bars = 10 µm
or branched, 20–40 × 3–4 µm. Conidiogenous cells terminal or lateral, unbranched, medium brown, finely verruculose, tapering to slightly or flat-tipped loci, proliferating sympodially, 5–20 × 3–4 µm; scars thickened, darkened and refractive. Conidia solitary or catenulate, in simple chains, medium brown, verruculose, subcylindrical to narrowly obclavate, apex obtuse, base bluntly rounded with truncate hilum, straight, 0–3-septate, (7–)13–20(–25) × 3(–3.5) µm; hila thickened, darkened, refractive, 1–1.5 µm wide.

Description based on CBS 105.75 (Fig. 8): Mycelium consisting of branched, septate, verruculose, medium brown, 2–4 µm wide hyphae. Conidiomata brown, superficial, sporodochial, up to 200 µm diam Conidiophores solitary, erect, micro- to macronematous, 1–12-septate, subcylindrical, straight to geniculate-sinuous or irregularly curved, 10–70 × 3–4 µm; frequently swollen and constricted at septa, thick-walled, medium brown, verruculose. Conidiogenous cells terminal and intercalary, subcylindrical, straight, but frequently branched laterally, 6–20 × 3–4 µm, with 1–3 flat-tipped loci that can be subdenticulate, 1.5–2 µm wide, somewhat darkened and thickened, not prominently refractive. Conidia medium brown, thick-walled, verruculose, septa becoming darkly pigmented, occurring in branched chains. Ramoconidia subcylindrical to narrowly ellipsoid, 12–25 × 3.5–4(–5) µm, 1(–4)-septate. Conidia occurring in short chains (–8), subcylindrical to narrowly ellipsoid, 0–1(–3)-septate, (7–)10–15(–20) × (2–)3–3.5(–4) µm; hila somewhat thickened, darkened but not refractive, 1.5–2(–2.5) µm wide.

Cultural characteristics: Colonies on OA erumpent, spreading, with moderate aerial mycelium and smooth, even margins; olivaceous-grey (surface); on PDA olivaceous-black (surface), margins feathery, uneven, with moderate aerial mycelium; reverse iron-grey. Colonies reaching 20 mm diam after 1 mo at 25°C in the dark on OA.

Specimens examined: Venezuela, Aragua, La Victoria, on leaf spots of Pithecellobium lanceolatum (Mimosaceae), Jan. 1928, H. Sydow, lectotype of S. araguata (selected here) IMI 15728(a); 3 Feb. 1928, syntype of S. araguata, IMI 34905. Venezuela, isolated from man with tinea nigra, 1973, D. Borelli, holotype of C. castellanii, IMI 183818, culture ex-type CBS 105.75.

Notes: Stenella araguata is a leaf spot pathogen of Pithecellobium in Venezuela, and represents the type species of the genus Stenella [Two collections were cited, viz. no. 407, 'La Victoria', and no. 370, 'inter La Victoria et Suata', both without any date, and without any specific type indication. Thus, the two collections have to be considered syntypes. The two IMI collections with different dates are parts of the syntypes, of which IMI 15728(a) is proposed here to serve as lectotype]. Stenella araguata was incorrectly seen as a species of Cladosporium by von Arx (1974), which has recently been morphologically circumscribed (Braun et al. 2003, Schubert et al. 2007b – this volume), and is linked to Davidiella teleomorphs.

In a study by McGinnis & Padhye (1978), Cladosporium castellanii (tinea nigra of human in Venezuela) was shown to be synonymous to Stenella araguata (leaf spots of Pithecellobium lanceolatum in Venezuela). In the present study we re-examined the ex-type strain of C. castellanii (CBS 105.75), and found conidia to be 0–1(–3)-septate, (7–)10–15(–20) × (2–)3–3.5(–4) µm, while those of the type specimen of S. araguata were similar, namely 0–3-septate, (7–)13–20(–25) × (3–3.5) µm. Furthermore, both collections have verruculose hyphae, which is the primary feature distinguishing Stenella from Passalora Fr. (Crous & Braun 2003).
Stenella has always been used for anamorphs of Mycosphaerella (Crous et al. 2004, 2006c), and the fact that it belongs to Teratosphaeria (Teratosphaeriaceae), and not Mycosphaerella (Mycosphaerellaceae), raised the question of how to treat stenella-like anamorphs in Mycosphaerella. Due to insufficient availability of cultures (Crous et al. 2000, 2001), the status of Stenella was left unresolved (Crous & Braun 2003). Presently (Crous & Groenewald, unpubl. data), it is clear that the stenella-like morphology type is polyphyletic within the Mycosphaerellaceae, and paraphyletic within the Capnodiales. Several species are known that represent morphological transitions between Stenella and Passalora. It seems logical, therefore, that future studies should favour using Passalora to also accommodate Mycosphaerella anamorphs with superficial, verruculose hyphae, which have traditionally been placed in Stenella. This is in spite of the fact that there are other generic names available within the Mycosphaerellaceae for taxa with a stenella-like morphology (pigmented structures, darkened, thickened, refractive scars, and superficial, verruculose mycelium), namely Zasmidium Fr. (1849) (see Arzanlou et al. 2007 – this volume), and Verrucisporota D.E. Shaw & Alcorn (1993). Based on the phylogenetic position of the type species, Stenella s. str. is an anamorph of Teratosphaeria (Teratosphaeriaceae). Using the generic concept as employed in this volume of the Studies in Mycology, however, the anamorph genus is accepted as being poly- and paraphyletic within the order Capnodiales.
**Helotiales, incertae sedis**

**Hyalodendriella** Crous, gen. nov. MycoBank MB504435.

**Etymology:** Morphologically similar to *Hyalodendron* Diddens.

Differs from *Hyalodendron* and *Retroconis*, but distinct in that it has morphic conidiophores, conidia that turn brown with age, and have thickened scars. *Microconidiophores* forming as lateral branches on hyphae, subcylindrical, subhyaline to pale brown, smooth, septate, with terminal conidigenous cells. *Macroconidiophores* septate, subcylindrical, straight to curved, subhyaline to pale brown, smooth, with an apical rachis that is pale brown, smooth, subcylindrical, with numerous, aggregated loci. *Conidia* limoniform to ellipsoid, aseptate, smooth, pale brown, in short chains, tapering towards ends that are prominently apiculate, prominently thickened and darkened, but not refractive.

**Type species:** *Hyalodendriella betulicola* Crous, sp. nov.

**Hyalodendriella betulicola** Crous sp. nov. MycoBank MB504436. Fig. 9.

*Mycelium* ex hyphis ramosis, septatis, 1.5–2 µm latis, levibus, hyalinis vel pallide brunnei compositum. *Conidiophora* dimorphica: (A) *Conidiophora* ex hyphis lateraliter orunda, subcylindrica, subhyalina vel pallide brunnea, levia, 1–6-septata, ad 40 µm longa et 2–3 µm lata. Cellulae conidiogenae terminales, 5–15 × 2–3 µm, laco conidiogeno singulare et terminale, cellula ellipsoidea (conido ?), persistente, interdum cellulis catenulis (ad 6), pallide brunneo, apice subacuto rotundato, basi truncata, 5–7 × 3–4 µm. (B) Conidiophora 10–20 × 2–3 µm, 1–2-septata, subcylindraceae, rectis vel curvatis, subhyalina vel pallide brunnea, levibus. Cellulae conidiogenae pallide brunneo, levia, subcylindraceae, locis numerosis, aggregatis, inconspicuis vel subdenteculatis, leviter protruberantibus, 0.5 µm diam, incrassatis et fusatis. Conidio catenulato (2–3), (4–5)–6(–7) × 2.5–3 µm, limoniformes vel ellipsoideae, non septata, levia, pallide brunnea, utrinque attenuata, apiculata, 0.5–1.0 × 0.5 µm, incrassata et fusata, non refractiva.

**Mycelium** consisting of branched, septate, 1.5–2 µm wide hyphae, smooth, hyaline to pale brown. *Conidiophores* dimorphic. Type A: *Conidiophores* forming as lateral branches on hyphae, subcylindrical, subhyaline to pale brown, smooth, 1–6-septate, up to 40 µm long, and 2–3 µm wide. *Conidiogenous cells* terminal, 5–15 × 2–3 µm, with a single, apical locus, giving rise to an ellipsoidal cell (conidium?) which mostly remains attached, pale brown, with a subacutely rounded apex and truncate base, 5–7 × 3–4 µm, at times forming chains of up to 6 such cells. Type B: *Conidiophores* 10–20 × 2–3 µm, 1–2-septate, subcylindrical, straight to curved, subhyaline to pale brown, smooth. *Conidiogenous cells* pale brown, smooth, subcylindrical with numerous, aggregated loci, inconspicuous to subdenticulate and somewhat protruding, 0.5 µm wide, somewhat thickened and darkened. *Conidia* in chains of 2–3, limoniform to ellipsoid, widest in the middle, aseptate, smooth, pale brown, tapering towards ends that are prominently apiculate, 0.5–1 µm long, 0.5 µm wide, prominently thickened and darkened, but not refractive.

**Cultural characteristics:** Colonies on PDA slimy, spreading, somewhat erumpent in the centre, with even, catenulate margins, lacking aerial mycelium; surface fuscous-black to olivaceous-black, with patches of cream; reverse fuscous-black with patches of cream. Colonies reaching 25 mm diam on PDA after 1 mo at 25 °C in the dark; colonies fertile with profuse sporulation on SNA.

**Notes:** Morphologically *Hyalodendriella* resembles the genera *Hyalodendron* and *Retroconis* de Hoog & Bat. Vegte (de Hoog & Batenburg van der Vegte 1989). It is distinct, however, in its pigmentation, dimorphic conidiophores and conidia. Furthermore, a strain of *Retroconis fusiformis* (S.M. Reddy & Bilgrami) de Hoog & Bat. Vegte (CBS 330.81) clusters apart from *Hyalodendriella*, namely in the Chaetomiaceae, Sordariales.

**Pleosporales, incertae sedis**

**Ochrocladosporium** Crous & U. Braun, gen. nov. MycoBank MB504437.

**Etymology:** Named after its pale brown, cladosporium-like conidia.

Differs a *Cladosporium* et generis cladosporioidibus diversis conidiophoris cum cellulis basaliis T-formibus et vel cicatricibus non incrassatis, non vel leviter fuscatis-refractivis.

*Mycelium* consisting of branched, septate hyphae, subhyaline to pale brown, smooth, giving rise to two types of conidiophores. *Macronematous conidiophores* solitary, erect, arising from superficial hyphae, composed of a subcylindrical stipe, without a swollen or lobed base or rhizoids, with or without a T-shaped foot cell, pale to dark brown; apical conidiogenous apparatus with or without additional branches, branched part, if present, with short branchlets composed of conidigenous cells and ramoconidia, continuous to septate, wall thin or slightly thickened, pale brown. *Conidiogenous cells* integrated, terminal or intercalary, subcylindrical to doliform, pale brown, thin-walled, smooth; unicolar or multilocular, determinate to sympodial, loci conically truncate, subdenticulate, neither thickened, nor darkened-refractive or only slightly darkened-refractive. *Micronematous conidiophores* integrated in hyphae, reduced to a lateral peg-like locus or erect, frequently reduced to conidigenous cells, pale brown, smooth, subcylindrical. *Conidia* occurring in branched chains, fusiform, ellipsoid-ovoid to subcylindrical, 0(–1)–septate, ramoconidia present, pale brown, thin-walled, smooth to finely verruculose, ends attenuated, hila obconically truncate to almost pointed, neither thickened nor darkened-refractive.

**Type species:** *Ochrocladosporium elatum* (Harz) Crous & U. Braun, comb. nov.

**Ochrocladosporium elatum** (Harz) Crous & U. Braun, comb. nov. MycoBank MB504438. Fig. 10.

**Basionym:** Hormodendrum elatum Harz, Bull. Soc. Imp. Naturalistes Moscou 44: 140. 1871.

Differs from *Cladosporium* et generis cladosporioidibus diversis conidiophoris cum cellulis basaliis T-formibus et vel cicatricibus non incrassatis, non vel leviter fuscatis-refractivis.

*Mycelium* consisting of branched, septate, smooth, hyaline, 2–4 µm wide, thin-walled, hyphae, becoming darker brown in places, giving rise to erect conidiophores. *Conidiophores* either reduced to conidigenous cells, or well-differentiated, terminal and lateral on hyphae, erect, highly variable, arising from superficial and submerged hyphae, reduced to subdenticulate loci, 1–1.5 µm wide, or well-differentiated, up to 60 µm long, 1–3-septate, 3–4 µm wide, hyaline to medium brown, smooth, thin-walled (< 1 µm). *Conidigenous cells* integrated as lateral peg-like loci on hyphal cells, or erect, subcylindrical, up to 25 µm long, 2.5–4 µm wide, with 1–3 terminal loci, occasionally also lateral, 1–1.5 µm wide, not thickened and darkened, but frequently somewhat refractive (mounted in Shear’s solution, not lactic acid). *Ramoconidia*
subcylindrical to ellipsoid, hyaline to pale brown, smooth to finely verruculose, 10–40 × 3–5 µm, 0(–1)-septate, giving rise to branched chains of conidia (up to 20 per chain) that are subcylindrical to ellipsoid, aseptate, (7–)8–10(–14) × (3–)4(–4.5) µm, smooth to finely verruculose, olivaceous-brown, thin-walled (up to 0.5 µm), hila 0.5–1 µm wide, neither thickened nor, or barely, darkened refractive.

Cultural characteristics: Colonies erumpent, spreading, fast growing, covering the plate within 1 mo at 25 °C; aerial mycelium abundant, margins smooth on PDA; surface isabelline in centre, umber in outer region; olivaceous-black in reverse.

Specimen examined: Sweden, Iggesund, isolated from wood pulp, Jan. 1976, E. Melin, specimen CBS-H 19896, culture CBS 146.33.

Notes: “Hormodendrum” elatum was originally described from a wooden stump in Germany. The culture examined here was deposited by Melin in 1933 as culture 389:14, isolated from wood chips in Sweden, and described by Nannfeldt, and has since been accepted as authentic for the species. Earlier publications (de Vries 1952, Ho et al. 1999, de Hoog et al. 2000), clearly state that this species does not belong in Cladosporium s. str., and this statement is supported by the phylogenetic analysis placing it in the Pleosporales.

**Ochrocladosporium frigidarii** Crous & U. Braun, sp. nov. MycoBank MB504439. Fig. 11.

Etymology: Named after it collection site, within a cooled incubation room.

Differt a O. elato conidiophoris distincte dimorphis, macroconidiophoris majoribus, ad 600 × 5–7 µm, septis incrassates, cellulis basalibus T-formibus et conidiis leniter brevioribus et lationibus, (6–)7–8(–10) × (4–)5.5(–6) µm.

Mycelium consisting of branched, septate, 2–7 µm wide hyphae, occasionally constricted at septa with hyphal swellings, subhyaline to pale brown, smooth, thin-walled, giving rise to two types of conidiophores. Macronematous conidiophores solitary, erect, arising from superficial hyphae, up to 600 µm long, composed of a subcylindrical stipe, 5–7 µm wide, 10–15(–20)-septate, without a swollen or lobed base or rhizoids, but with a T-shaped foot cell, wall ≤ 1 µm wide, guttulate, with thick septa, dark brown, finely verruculose, apical 1–2 cells at times medium brown, giving rise to 1–2 primary branches, 0–1-septate, subcylindrical, thin-walled, pale brown, smooth to finely verruculose, 10–20 × 4–6 µm, giving rise to (1–)2–4 secondary branches, 0–1-septate, subcylindrical, 8–13(–20) × 4–5 µm, or giving rise directly to conidiogenous cells. Conidiogenous cells subcylindrical to doliform, pale brown, smooth, 8–15 × 3–4 µm, loci somewhat protruding 1–2 µm wide, neither...
Micronematous conidiophores erect, pale brown, smooth, subcylindrical, reduced to conidiogenous cells, or up to 4-septate, 15–90 × 2–3.5 µm, mostly unbranched, rarely branched below; conidiogenous cells subcylindrical, pale brown, smooth to finely verruculose, tapering at apex and sometimes at base, proliferating sympodially via 1(–3) loci, 1–1.5 µm wide, denticle-like, which can appear somewhat darkened; micronematous conidiophores frequently occurring at the base of macronematous conidiophores. Ramoconidia, if present, up to 30 µm long, 0–1-septate. Conidia and ramoconidia ellipsoid to ovoid, aseptate, pale brown, thin-walled (≤ 0.75 µm), finely verruculose, occurring in branched chains; conidia (6–)7–8(–10) × (4–)4.5–5(–6) µm; hila 0.5–1 µm wide, not darkened, thickened or refractive.

Cultural characteristics: Colonies on PDA erumpent, spreading, with profuse sporulation and moderate aerial mycelium, even margins, olivaceous-grey (surface); reverse olivaceous-black. Colonies covering the dish after 1 mo at 25 °C in the dark.

Specimen examined: Germany, Hannover, isolated from a cooled room, Jan. 1981, B. Ahlert, holotype CBS-H 19897, culture ex-type CBS 103.81.

Notes: Ochrocladosporium frigidarii is characterised by its dimorphic fruiting, and inconspicuous scars and conidial hila, which
are distinct from *Cladosporium s. str*. The phylogenetic analysis of its LSU sequence places it in the *Pleosporales*, together with *O. elatum*.

The dimorphic conidiophores seen in *O. frigidarii* (CBS 103.81) are less obvious in *O. elatum* (CBS 146.33), but the scars and hila are similar. The macronematous conidiophores of *O. frigidarii* are much longer and wider and the conidia are shorter and slightly wider, (6–)7–8(–10) × (4–)4.5–5(–6) µm, than those of *O. elatum* which are (7–)8–10(–14) × (3–)4(–4.5) µm.
Incertae sedis

Rhizocladosporium Crous & U. Braun, gen. nov. MycoBank MB504440.

Etymology. Named after the presence of rhizoids on its conidiophores, and cladosporium-like conidia.

Differt a Cladosporio et generis cladosporioidibus diversis hyphis hyalinis, conidiophoris cum cellulis basalius lobatis vel rhizoidibus, cellulis conidiogenis monoblasticis, determinatis, locis margine leviter incrassatis et fuscatis, non refractivis, non coronatis, ramoconidii brunneis sed conidii hyalinis, hils non incrassati, non fusci-refractivi.

Mycelium consisting of branched, septate, smooth, hyaline hyphae. Conidiophores solitary, macronematous, subcylindrical, erect, arising from superficial mycelium, septate, pigmented, smooth; base somewhat inflated, lobed or with rhizoids. Conidiogenous cells integrated, terminal, monoblastic, determinate, subcylindrical, tapering towards a single flat-tipped locus, straight to once geniculate, occasionally with two loci, pigmented, smooth; locus flattened, undifferentiated to somewhat darkened and thickened along the rim, not refractive, giving rise to a single conidial chain or a single ramoconidium with several simple acropetal chains of secondary ramoconidia or conidia. Conidia occurring in branched chains; ramoconidia subcylindrical to narrowly ellipsoidal, straight to geniculate-sinuous, with apical and lateral conidial hila; ramoconidia with broadly truncate base medium brown; secondary ramoconidia with narrowed base subhyaline or hyaline, smooth; conidia aseptate, in chains, hyaline, guttulate, ellipsoidal with obtuse ends; hila inconspicuous, neither darkened nor refractive or thickened.

Type species: Rhizocladosporium argillaceum (Minoura) Crous & U. Braun, comb. nov.

Rhizocladosporium argillaceum (Minoura) Crous & U. Braun, comb. nov. MycoBank MB504441. Fig. 12.

Basionym: Cladosporium argillaceum Minoura, J. Ferment. Technol. 44: 140. 1966.

Mycelium consisting of branched, septate, smooth, hyaline, thin-walled, 1.5–2 μm wide hyphae. Conidiophores solitary, macronematous, erect, arising from superficial mycelium; base somewhat inflated, lobed or with rhizoids, up to 10 μm wide; conidiophore stipe subcylindrical, straight to curved, rarely geniculate-sinuous, wall up to 1 μm wide, medium brown, sometimes paler towards the tip, smooth, 1–6-septate, 35–160
μm tall, 4–6 μm wide. Conidiogenous cells terminal, straight, subcylindrical, tapering towards a flat-tipped locus, occasionally once geniculate, with two loci, medium brown, smooth, 15–35 × 4–6 μm; locus flattened, undifferentiated or very slightly darkened and thickened along the rim, not refractive, 1.5–2.5 μm wide. Conidia occurring in branched chains. Ramoconidia subcylindrical to narrowly ellipsoidal, straight to geniculate-sinuous, 17–35 × 4–5 μm, medium brown, smooth, thin-walled, frequently branching laterally, with apical and lateral subdenticulate conidial hila, 1.5–2.5 μm wide; secondary ramoconidia hyaline or subhyaline. Conidia aseptate, (10–)12–17–(20) × (3.5–)4(–4.5) μm, in branched chains (--6), hyaline or subhyaline, guttulate, ellipsoidal-fusiform, with obtuse ends, or tapering to obconically subtruncated ends with hila that are inconspicuous (either darkened or refractive or thickened), 0.5–1 μm wide.

Cultural characteristics: Colonies on PDA spreading, erumpent, with smooth, even margins and sparse to moderate aerial mycelium; hazel to fawn (surface); reverse hazel to fawn. Colonies reaching 35 mm diam after 1 mo at 25 °C in the dark; colonies fertile.

Specimen examined: Japan, Yoku Island, isolated from decayed myxomycete, 21 Oct. 1961, K. Tubaki No. 4262 holotype, culture ex-type CBS 241.67 = IFO 7055.

Notes: The lobed-rhizoid conidiophore base, and brown, disarticulating ramoconidia, with hyaline chains of conidia, are characteristic of Rhizocoladosporium. Although Minoura (1966) illustrated some conidiophores that were micronematous (reduced to conidiogenous cells on superficial mycelium), these were not observed in the present study. Metulocladosporiella Crous, Schroers, J.Z. Groenew., U. Braun & K. Schub. (Crous et al. 2006a) (Herpotrichiellaceae), comprising two banana leaf-spotting pathogens, is another cladosporioid hyphomycete genus having distinct rhizoid hyphae at the swollen base of conidiophores. It differs, however, in having conidiophores terminally branched in a metula-like manner and distinct conidiogenous loci and conidial hila. Pleurotheciopsis B. Sutton (Ellis 1976) is also characterised by having pigmented conidiophores and hyaline or pale, septate conidia formed in acrocastral chains, but the conidiophores proliferate percurrenty, the conidiogenous cells are polyblast and ramoconidia are lacking, i.e., the conidia are formed in unbranched chains. Parapleurotheciopsis P.M. Kirk (Kirk 1982) is very similar to Rhizocoladosporium. The conidiophores possess a single terminal unilocular conidiogenous cell giving rise to a single ramoconidium which forms several chains of acrocastral, aseptate, hyaline to pale olivaceous conidia. The base of the conidiophores is somewhat swollen and lobed [except for Parapleurotheciopsis coccolobae R.F. Castañeda & B. Kendr., Castañeda & Kendrick (1990), with at most slightly swollen, but unlobed base]. However, R. argillaceum occasionally has once-geniculate conidiogenous cells with two loci. Furthermore, it clusters in the Helotiales (Fig. 1), whereas a sequenced strain of Parapleurotheciopsis inaequiseptata (MUC 41089), belongs to the Xylariales (Fig. 2). The occasionally occurring conidiogenous cells with two loci and the aseptate conidia connect Rhizocoladosporium with Subramaniomyces Varghese & V.G. Rao (Varghese & Rao 1979, Kirk 1982) in which, however, terminal ramoconidia are lacking. Furthermore, the type species, S. fusiisaprophyticus (Matsush.) P.M. Kirk, frequently has branched conidiophores. Subramaniomyces simplex U. Braun & C.F. Hill (Braun & Hill 2002) is a species with unbranched conidiophores is, however, morphologically similar to R. argillaceum, but the genus Subramaniomyces is phylogenetically distinct and also belongs to the Xylariales (CBS 418.95, Fig. 2).

Key to Cladosporium and morphologically similar genera
(bearing simple or branched acrocastral chains of aemoro- to phragmosporous blastoconidia)

1. Conidiophores and conidia hyaline ............................................................................................................................................ 2
2. Conidiophores and conidia pigmented ................................................................................................................................... 6

3. Conidiogenous cells sympodial, with distinct conidiogenous loci (scars), thickened and darkened; conidia aseptate or euseptate; plant pathogenic, leaf-spotting fungi (Mycosphaerella anamorphs; Mycosphaerellaceae) ................................................................. Ramularia
4. Conidia distoseptate, in simple chains ...................................................................................................................................... 9
5. Conidia euseptate ......................................................................................................................................................................... 12
6. Conidia in simple chains .............................................................................................................................................................. 4
7. Conidia in branched chains ........................................................................................................................................................... 3
8. Conidia aseptate or euseptate ....................................................................................................................................................... 5
9. Conidiophores little differentiated, micronematous to semimacronematous; conidiogenous loci undifferentiated, truncate, neither distinctly thickened nor darkened or only very slightly so .......................................................................................................................... 6
10. Conidiophores well-differentiated, semimacronematous (but multilocular and/or conidiogenous loci well-differentiated) to macronematous ................................................................................................................................................. 12
11. Conidiophores and conidia delicate, thin-walled, in long, easily disarticulating chains .............................................................. 7
12. Conidiophores and conidia robust, wall thickened, dark, conidial chains often seceding with difficulty ......................................... 9

1. At least conidiophores pigmented .................................................................................................................................................. 6
2. Conidia in simple chains .............................................................................................................................................................. 4
3. Conidia distoseptate, in simple chains ...................................................................................................................................... 9
4. Conidia aseptate or euseptate ....................................................................................................................................................... 5
5. Conidiophores little differentiated, micronematous to semimacronematous; conidiogenous loci undifferentiated, truncate, neither distinctly thickened nor darkened or only very slightly so .......................................................................................................................... 6
6. Conidiophores well-differentiated, semimacronematous (but multilocular and/or conidiogenous loci well-differentiated) to macronematous ................................................................................................................................................. 12
7. Conidiophores and conidia delicate, narrow, 1–3 μm wide, hyaline to pale olivaceous ................................................................. Polyscytalum
8. Conidiophores and conidia hyaline ............................................................................................................................................ 2
9. Conidiophores and conidia pigmented ................................................................................................................................... 6
10. Conidiophores and conidia pigmented .................................................................................................................................. 6
11. Conidiophores and conidia pigmented .................................................................................................................................. 6
12. Conidiophores and conidia pigmented .................................................................................................................................. 6

Notes: The lobed-rhizoid conidiophore base, and brown, disarticulating ramoconidia, with hyaline chains of conidia, are characteristic of Rhizocoladosporium. Although Minoura (1966) illustrated some conidiophores that were micronematous (reduced to conidiogenous cells on superficial mycelium), these were not observed in the present study. Metulocladosporiella Crous, Schroers, J.Z. Groenew., U. Braun & K. Schub. (Crous et al. 2006a) (Herpotrichiellaceae), comprising two banana leaf-spotting pathogens, is another cladosporioid hyphomycete genus having distinct rhizoid hyphae at the swollen base of conidiophores. It differs, however, in having conidiophores terminally branched in a metula-like manner and distinct conidiogenous loci and conidial hila. Pleurotheciopsis B. Sutton (Ellis 1976) is also characterised by having pigmented conidiophores and hyaline or pale, septate conidia formed in acrocastral chains, but the conidiophores proliferate percurrenty, the conidiogenous cells are polyblast and ramoconidia are lacking, i.e., the conidia are formed in unbranched chains. Parapleurotheciopsis P.M. Kirk (Kirk 1982) is very similar to Rhizocoladosporium. The conidiophores possess a single terminal unilocular conidiogenous cell giving rise to a single ramoconidium which forms several chains of acrocastral, aseptate, hyaline to pale olivaceous conidia. The base of the conidiophores is somewhat swollen and lobed [except for Parapleurotheciopsis coccolobae R.F. Castañeda & B. Kendr., Castañeda & Kendrick (1990), with at most slightly swollen, but unlobed base]. However, R. argillaceum occasionally has once-geniculate conidiogenous cells with two loci. Furthermore, it clusters in the Helotiales (Fig. 1), whereas a sequenced strain of Parapleurotheciopsis inaequiseptata (MUC 41089), belongs to the Xylariales (Fig. 2). The occasionally occurring conidiogenous cells with two loci and the aseptate conidia connect Rhizocoladosporium with Subramaniomyces Varghese & V.G. Rao (Varghese & Rao 1979, Kirk 1982) in which, however, terminal ramoconidia are lacking. Furthermore, the type species, S. fusiisaprophyticus (Matsush.) P.M. Kirk, frequently has branched conidiophores. Subramaniomyces simplex U. Braun & C.F. Hill (Braun & Hill 2002), a species with unbranched conidiophores is, however, morphologically similar to R. argillaceum, but the genus Subramaniomyces is phylogenetically distinct and also belongs to the Xylariales (CBS 418.95, Fig. 2).
7. Conidiophores unbranched, micronematous or semimicronematous, integrated in ordinary hyphae, forming minute, lateral, monoblastic, determinate, peg-like protuberances to semimacronematous, forming short lateral branches (conidiophores) with several inconspicuous to denticle-like loci ................................................................. 8

8. Phialidic synanamorphs often present, but sometimes also lacking; saprobic, rarely plant pathogenic, often human pathogenic (Herpotrichiellaceae, Chaetothyriales) .................................................................................................. Cladophialophora

8. Without phialidic synanamorphs; saprobic or plant pathogenic (Venturina, Venturiaceae) .......................................................................................................................... Fuscidium s. lat. (incl. Pseudocladosporium)

9(6). Conidia aseptate, rarely 1-septate; lignonicolous, on dead wood .......................................................... Xylohypha

9. Conidia septate .................................................................................................................................................. 10

10. Conidia 1-septate, with a dark brown to blackish band at the septum; on dead wood ........................................ Bispora

10. Conidia at least partly 2- to pluriseptate and/or without dark brown to blackish band at the septum ................................................... 11

11. Conidia branched ............................................................................................................................................. 12

11. Conidia unbranched ......................................................................................................................................... Taeniola

12(5). Conidiogenous loci and conidial hila distinctly coronate, i.e., composed of a central convex dome surrounded by a periclinal raised rim, mostly at least somewhat protuberant (anamorphs of Davidiella, Davidiellaceae, Capnodiales) .............. Cladosporium s. str.

12. Conidiogenous loci non-coronate (either inconspicuous, thickened and darkened or denticle-like) .................. 13

13. Mycelium, conidiophores and conidia at first hyaline or subhyaline, later turning pale brown; conidiophores dimorphic, either conidiogenous cells with a single conidiogen loci, giving rise to an ellipsoid cell (conidium?) which mostly remains attached, base truncate, apex subacutely rounded, at times forming chains of such cells; or conidiophores with numerous aggregated loci, inconspicuous to subdenticulate; conidia in short chains, of mostly 2-3 (isolated from Alnus in Europe) ......................... Hyalodendriella

13. Fruiting different; at least conidiophores consistently pigmented or conidiophores uniform or loci distinct; conidia mostly in long, often branched chains ........................................................................................................ 14

14. Conidiophores with verruculose conidiogenous apices, otherwise smooth; conidia distinctly verruculose-verrucose; conidiogenous loci and conidial hila inconspicuous ...................................................................................................................... 15

14. Conidiophores either smooth throughout or verruculose below and smooth above or verruculose throughout; and/or conidiogenous loci conspicuous, i.e., thickened and darkened or denticle-like ...................................................................................................................... 16

15. Conidiophores macronematous, unbranched, base swollen, with percurrent regenerative proliferations, unrelated to conidiation; conidiogenous cells terminal, occasionally also subterminal; conidia terminally and laterally formed, aseptate (saprobic on leaves) .................................................................................. Castanedae

15. Conidiophores little differentiated, semimacronematous, unbranched or with short lateral branchlets, base indifferenitiated, without percurrent proliferations; conidiogenous cells terminal and occasionally intercalary-pleurogenous; conidia terminally and subterminally formed, 0–2-septate (lignonicolous, on decorticated wood) .................................................................................................................. Webstemonymes

16(14). Conidiophores unbranched, with a simple terminal conidiogenous cell, non-geniculate-sinuous, subcyllindrical to somewhat inflated at the tip; conidiogenous loci terminal and lateral, inconspicuous or subconspicuous, neither thickened nor darkened, non-protuberant; conidia attached with a very narrow, pointed hilum ............................................................................................................ 17

16. Conidiophores with a branched terminal conidiogenous apparatus, composed of conidiogenous cells and/or ramoconidia or conidiophores unbranched, with a single terminal conidiogenous cell or additional intercalary ones, but conidiogenous loci different, conspicuous, thickened and darkened or denticle-like .................................................................................................................. 18

17. Conidiophores with distinct rhizoid-digitate base; tips of the conidiogenous cells somewhat swollen, usually unilaterally swollen or somewhat curved; conidia solitary or only in very short unbranched chains; hyperparastic on rusts .......................................................... Digitopodium

17. Conidiophores without rhizoid-digitate base; tips of the conidiogenous cells subcyllindrical to somewhat swollen, but swellings not unilateral and not curved; conidia solitary and in simple or branched chains; associated with leaf spots ........................................ Rachicladosporium

18(16). Conidiophores in synnematous conidiomata .................................................................................................................. 19

18. Synnemata lacking .............................................................................................................................................. 20

19. Conidiogenous cells with a single or several truncate to subdenticulate, relatively broad conidiogenous loci; conidia with truncate, flat hila; on wood, resin ................................................................................................................................................. Sorocybe

19. Conidiogenous loci with few, mostly 1–2 conidiogenous loci formed as minute spicules; conidia with narrow hila (shallowly apiculate); plant pathogenic, causing bud blast and twig blight ................................................................................ Seifertia

20(18). Conidiophores unbranched or occasionally branched; conidiogenous cells distinctly inflated, ampulliform, doliform or clavate, non-denticulate; conidia at least partly globose, dark brown when mature; colonies effuse, dark; wood-inhabiting ................................ Phaeoblasterphora

52
20. Conidiogenous cells not inflated, if somewhat inflated, loci denticle-like or conidia non-globose ................................. 21

21. Conidiophores penicillate, i.e., with an unbranched stipe and distinct terminal branched “head” composed of branchlets, conidiogenous cells and/or ramoconidia ............................................................................................................ 22

21. Conidiophores non-penicillate, i.e., irregularly and loosely branched, branchings not confined to the apical portion, sometimes only with short lateral branchlets, or unbranched ................................................................. 27

22. Penicillate apex simple, only composed of a single terminal conidiogenous cells giving rise to several ramoconidias which form secondary ramoconidia and conidia ................................................................................................................. Penidiella p.p. [P. strumelloidea] 23

22. Penicillate apex more complex, composed of true branchlets and/or conidiogenous cells and ramoconidia ................................. 23

23. Conidiophores with a compact, dense, subglobose to broadly ovoid head; conidiogenous loci and conidial hila unthickened or almost so, but distinct by being darkened-refractive [fruiting dimorphic, periconidioblast conidiophores formed on overwintered stem of Paeonia spp., unbranched cladosporioid conidiophores on leaf spots, biotrophic] (belonging to the Capnodiales) ........................................................................................................... Dichocladosporiaceae 24

23. Penicillate apex loose, neither compact nor subglobose .................................................................................................................. 24

24. Branched apex composed of short branchlets and conidiogenous cells; ramoconidia lacking; conidiogenous cells subcylindrical to subclavate, non-geniculate; conidiogenous loci usually numerous and aggregated, terminal and lateral, non-protererant, flat, conspicuous, thickened and darkened, at least around the rim; conidia solitary or in short chains .................................................................................. Periconiella 25

24. Ramoconidia often present; conidiogenous cells distinct, sympodial, somewhat geniculate or subdenticulate; conidiogenous loci inconspicuous or somewhat protruding, denticle-like, unthickened or almost so, not or somewhat darkened-refractive; conidia in long, often branched chains .................................................................................................................... 25

25. Branched apex composed of short branchlets consisting of conidiogenous cells or ramoconidia, in pairs or whorls of 3–4, mostly distinctly constricted at the base; hyperparasitic on Asterina spp. .............................................................. Parapericoniella 26

25. Branched apex distinct, composed of branchlets, conidiogenous cells and/or ramoconidia, if true branchlets lacking conidiogenous cells and ramoconidia not in whorls and not distinctly constricted at the base; saprobic or biotrophic .......................................................... 26

26. Penicillate apex of the conidiophores loosely to densely branched, occasionally metula-like, base of the conidiophores simple, undifferentiated; saprobic or biotrophic (Teratosphaeriaceae, Capnodiales) ................................................................. Penidiella 27

26. Penicillate apex always dense, metula-like, base of the conidiophores swollen or lobed, often with rhizoid hyphae; plant pathogenic [on banana] (Chaetothyriales) ................................................................................................................ Metulocladosporiaceae 27

27(21). Conidiophores simple or branched; septa of the conidiophores and conidia becoming thick-walled and dark; conidiogenous loci subdenticulate, somewhat thickened and conspicuously darkened-refractive; cultures producing ample amounts of volatile metabolites causing skin irritation after exposure to the fungus; saprobic (isolated from mouldy paint) .................................................................................. Toxicocladosporiaceae 28

27. Without conspicuously thickened-darkened septa; cultures without irritant, volatile metabolites .............................................................................................................. 28

28. Conidiogenous loci conspicuous, distinctly thickened and darkened (visible as small dark circles when viewed upon the scar), sometimes on small shoulders formed by sympodial proliferation, but not distinctly denticulate (Capnodiales) .................................................................................................................. 29

28. Conidiogenous loci inconspicuous or conspicuous by being denticle-like, not or barely thickened, not darkened or at most upper truncate end very slightly thickened and somewhat darkened-refractive .............................................................................................................. 29

29. Mycelium smooth; conidiophores and conidia smooth or almost so, at most faintly rough-walled; conidiophores solitary, fasciculate, sporodochial to synnematous; biotrophic, usually leaf-spotting (Mycosphaerella anamorphs, Mycosphaerellaceae) .................................................................................................................. 30

29. At least mycelium distinctly verruculose ........................................................................................................................................... 30

30. Mycelium, conidiophores and conidia coarsely verruculose-verrucose; conidial shape variable, often irregular; isolated from a lichen (Dirina) ................................................................................................................................. Verrucocladosporiaceae 31

30. Mycelium verruculose; conidiophores mostly smooth, sometimes somewhat rough-walled, conidia smooth to distinctly verruculose; biotrophic, often leaf-spotting ................................................................................................................. Stenella 31

31(28). Conidiophores with swollen, often lobed base ............................................................................................................................... 32

31. Conidiophores without swollen base, at most slightly swollen, but not lobed ........................................................................ 35

32. Conidia septate .................................................................................................................................................................................. 33

32. Conidia aseptate .................................................................................................................................................................................. 34

33. Conidiophores with a single, terminal, monoblastic, determinate conidiogenous cell giving rise to a single ramoconidium that forms simple or branched chains of conidia .......................................................................................... Parapleurotheciaceae 34
33. Terminal conidiogenous cells polyblastic, with several denticle-like conidiogenous loci .................. Anungitea p.p. (e.g. A. longicatenata)

34(32). Conidiogenous cells terminal, monoblastic, with a single ramoconidium giving rise to conidial chains or occasionally with 2–3 denticle-like loci; base of the conidiophores often with rhizoid hyphae .................................................. Rhizocladosporium

34. Conidiogenous cells polyblastic, with two or several denticle-like loci; base of the conidiophores without rhizoid hyphae .......................................................... Subramaniomyces

35(31). Conidiophores unbranched, with a terminal monoblastic conidiogenous cell, determinate or percurrent ................................................................. 36

35. Conidiophores branched or unbranched, but conidiogenous cells at least partly polyblastic .................................................. 38

36. Conidiogenous cell giving rise to a single ramoconidium which forms simple or branched chains of 0–1-septate conidia .......................................................................................................................... Parapeurothecopsis p.p. (P. coccolobae)

36. Conidiogenous cells giving rise to simple conidial chains without ramoconidia; conidia septate .......................................................................................... 37

37. Conidiophores sometimes with percurrent proliferations; conidiophores and conidia with somewhat thickened, dark walls; conidia 1–10-septate, width usually exceeding 4 µm ......................................................................... Heterocononium

37. Percurrent proliferations lacking; conidiophores and conidia delicate, thin-walled and paler; conidia usually 0–1–3-septate and narrow, usually below 4 µm wide (Chaetothyriales) .......................................................................................... Cladophilophora p.p. (e.g. C. chaetospira)

[Similar anamorphs of the Venturiaeae, see Fuscidium (incl. Pseudocladosporium)]

38(35). Conidiophores often branched; conidiogenous loci distinctly denticle-like or subdenticulate; conidia asceptate; lignicolous, on dead wood, resin or isolated from hydrocarbone-rich substrates (jet-fuel, cosmetics, etc.) .................................................. 39

38. Either with unbranched conidiophores or conidiogenous loci not distinctly denticle-like, or conidia septate, or on other substrates .......................................................................................................................... 42

39. Conidiogenous cells distinctly denticulate; conidia rather broad, approx. 7–13 µm ......................................................................................................... Haplotrichum

39. Conidiogenous cells non-denticulate or at most subdenticulate; conidia narrower, approx. 3–6 µm ........................................................................................................... 40

40. Colonies effuse, dense, but felted, black, brittle and appearing carbonaceous when dry; conidiophores solitary, brown; conidiogenous cells terminal and pleurogenous; conidia pale to dark brown, lateral walls conspicuously thicker than the hila; on conifer resin .............................................................................................................................................................................. Sorocybe (mononematous form, Hormodendrum resinum)

40. Colonies effuse, dense, resupinate, hypochnoid, powdery, chocolate-brown and/or conidiophores lightly pigmented; conidia subhyaline to lightly pigmented and/or lateral walls not thicker than poles; on dead wood or isolated from hydrocarbone-rich substrates (jet-fuel, cosmetics, etc.) .............................................................................................................................................................................. Parahaplotrichum

41. Colonies effuse, dense, resupinate, hypochnoid, powdery, chocolate-brown; conidiophores smooth; conidia subhyaline to very pale yellowish, hila very thin; on dead wood ................................................................................................................................................................................ Parahaplotrichum

41. Colonies neither resupinate nor hypochnoid; conidiophores warty; lateral walls of the conidia not thicker than the hila; isolated from hydrocarbone-rich substrates (jet-fuel, cosmetics, etc.) ...................................................................................................................................................................................................................... Hormonennis

42(38). Conidiophores simple or branched; conidiogenous cells monoblastic or occasionally polyblastic; conidiogenous loci subdenticulate, neither thickened nor darkened, forming simple or branched chains of regular conidia, uniform in shape, size and septation ........................................................................................................................................................................... Septonema

42. Conidia not uniform in shape, size and septation; conidiogenous loci flat-tipped, subdenticulate, unthickened or slightly so, not to somewhat thickened-refractive .................................................................................................................. 43

43. Conidiophores simple or branched; in culture forming abundant chlamydospores; mostly soil-borne and heat-resistant (Teratosphaeraceae, Capnodiales) ................................................................. Devriesia

43. Without chlamydospores in culture; phylogenetically distinct ............................................................................................................................... 44

44. Conidiophores dimorphic; conidia mostly aseptate, hila inconspicuous, neither thickened nor darkened (Pleosporales) .............................................................................................................................................................................. Ochrocladosporium

44. Conidiophores either uniform or conidia at least partly septate or hila more conspicuous by being slightly thickened or at least somewhat darkened or refractive; phylogenetically distinct .......................................................................................................................... 45

45. Phialidic synanamorphs often present, but sometimes also lacking; saprobic, rarely plant pathogenic, often human pathogenic (Herpotrichiellaceae, Chaetothyriales) .......................................................................................................................... Cladophilophora

45. Without phialidic synanamorphs; saprobic or plant pathogenic; phylogenetically distinct ......................................................................................................................... 46

46. Conidiophores usually unbranched (Venturia, Venturiaceae) .......................................................................................................................... Fuscidium s. lat. (incl. Pseudocladosporium)

[similar, barely distinguishable taxa, also clustering in the Venturiaeae, but apart from the Venturia clade are tentatively referred to as Anungitea until this genus will be resolved by sequences of its type species]
DISCUSSION

Phylogenetic studies conducted on species of Cladosporium s. lat. proved the genus to be highly heterogeneous (Braun et al. 2003). It could be demonstrated that various anamorphs, previously referred to as Cladosporium, e.g. Cladosporium fulvum Cooke [= Passalora fulva (Cooke) U. Braun & Crous], have to be excluded since they clustered in the Mycosphaerella clade (Mycosphaerellaceae). Previous re-examinations and reassessments of human pathogenic Cladosporium species, including morphology, biology/ecology, physiology and molecular data (Masclaux et al. 1995, Untereiner 1997, Gerrits van den Ende & de Hoog 1999, Untereiner & Naveau 1999, Untereiner et al. 1999; de Hoog et al. 2000), could also be confirmed. In all phylogenetic analyses, it could be shown that the human pathogenic fungi concerned formed a clade belonging to the Herpotrichiellaceae (Capronia Sacc./Cladophilalophora Borellii) and Venturia anamorphs with catenate conidia, previously often assigned to Cladosporium s. lat., clustered together with other anamorphs of the Venturiaceae, and formed a monophyletic clade (Braun et al. 2003, Schubert et al. 2003, Beck et al. 2005). Venturia has now also been shown to accommodate less well-known anamorph genera such as Pseudocladosporium, which represent an additional synonym of Fuscidicladium Bonord. (Crous et al. 2007 – this volume).

Seifert et al. (2004) examined morphological, ecological and molecular characters of Cladosporium staurophorum (W.B. Kendr.) M.B. Ellis and three allied heat-resistant species and placed them in the new genus Devriesia, which formed a monophyletic group apart from the Cladosporium clade. Crous et al. (2006b) erected the genus Cladoriella Crous for a saprobiic species (incertae sedis) characterised by having narrowly ellipsoidal to cylindrical or fusoid, 0–1-septate, medium brown, thick-walled, finely verruculose conidia arranged in simple or branched chains, with thickened, darkened, refractive hila, with a minute central pore. Cladosporium musae E.W. Mason, the causal agent of banana speckle disease, has recently been shown to be allied to the Chaetothyriales (Crous et al. 2006a), and was placed in a new genus, Metulocladospiorlla with C. musae as type species. Digitopodium U. Braun, Heuchert & K. Schub. (type species: Cladosporium hemelae Steyaert) and Parapericoniella U. Braun, Heuchert & K. Schub. (type species: Cladosporium asterinae Deighton) represent two new genera of hyperparasitic hyphomycetes, introduced due to unique morphological features and striking differences to Cladosporium s. str. (Heuchert et al. 2005), but have as yet been excluded from DNA-based studies due to the absence of cultures. Schubert et al. (2007a – this volume) introduced a new genus, Dichocladosporium K. Schub., U. Braun & Crous (allied to the Davidiellaceae, Capnodiales) to accommodate a fungus with dimorphic fruiting that is pathogenic to Paenonia spp. The present study introduced yet several additional cladosporium-like genera, which could be distinguished based on their morphology and distinct DNA phylogeny, namely Ochrocladosporum (Pleosporales), Rhizocladosporum (incertae sedis), Rachicladospiorum, Toxicocladosporium and Verrucocladosporum (Capnodiales).

Although all these genera are cladosporium-like, and many have in the past been confused with Cladosporium s. str., the unique coronate scar type of Cladosporium s. str. allows a critical revision of cladosporoid hyphomycetes, based on reliable, distinctive morphological characters. In all cases where cladosporium-like (Cladosporium s. lat.) hyphomycetes clearly clustered apart from Cladosporium s. str. in the phylogenetic analyses, it could be demonstrated that the fungal groups concerned were also morphologically unambiguously distinguished, above all with regard to the structure of the conidiogenous hila. Hence, the excluded groups of species, belonging in other genera, sometimes even in new genera, are genetically as well as morphologically clearly distinct from Cladosporium s. str.

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REFERENCES

Aptroot A (2006). Mycosphaerella and its anamorphs: 2. Conspicuous of Mycosphaerella. CBS Biodiversity Series 5: 1–231.
Arzaniou M, Groenewald JZ, Gams W, Braun U, Shin H-J, Crous PW (2007). Phylogenetic and morphotaxonomic revision of Ramichloridium and allied genera. Studies in Mycology 58: 57–93.
An J.A van (1974). The Genera of Fungi Sporulating in Pure Culture. 2nd edn. J. Cramer, Vaduz.
An J.A van (1981). The Genera of Fungi Sporulating in Pure Culture. 3rd edn. J. Cramer, Vaduz.
An J.A van (1983). Mycosphaerella and its anamorphs. Proceedings of the Koninklijke Nederlandse Akademie van Wetenschappen, Ser. C 86(1): 15–54.
Beck A, Ritschel A, Schubert K, Braun U, Triebel D (2005). Phylogenetic relationship of the anamorphic genus Fuscidiaulum s. lat. as inferred by ITS data. Mycological Progress 4: 111–116.
Braun U (1995). A monograph of Cercosporaella, Ramularia and allied genera (phytopathogenic hyphomycetes) Vol. 1. IHV-Verlag, Eching.
Braun U (1996). Taxonomic notes on some species of the Cercospora complex (IV). Sydowia 48: 205–217.
Braun U (1998). A monograph of Cercosporaella, Ramularia and allied genera (phytopathogenic hyphomycetes) Vol. 2. IHV-Verlag, Eching.
Brown K.B, Hyde KD, Guest DI (1998). Preliminary studies on endophytic fungal communities of Musa acuminata species complex in Hong Kong and Australia. Fungal Diversity 1: 27–51.
Castañeda RF, Kendrick B (1990). Conidial fungi from Cuba I. University of Waterloo Biological Series 33: 1–61.
Crous PW, Aptroot A, Castañeda RF and W. Gams for providing collections and cultures of Cladosporium and cladosporium-like species over the past few years, without which this study would not have been possible. A research visit of K. Schubert to CBS was supported by a Synthesys grant (No. 2559), and the Odo van Vloten Stichting. We thank M. Vermaas for preparing the graphical plates, and A. van Ieperen for preparing all the fungal cultures for examination. H.-J. Schroers is thanked for generating some of the sequence data used in this paper. A.J.L. Phillips is thanked for providing comments on an earlier draft of the paper.

REFERENCES

Aptroot A (2006). Mycosphaerella and its anamorphs: 2. Conspicuous of Mycosphaerella. CBS Biodiversity Series 5: 1–231.
Arzaniou M, Groenewald JZ, Gams W, Braun U, Shin H-J, Crous PW (2007). Phylogenetic and morphotaxonomic revision of Ramichloridium and allied genera. Studies in Mycology 58: 57–93.
An J.A van (1974). The Genera of Fungi Sporulating in Pure Culture. 2nd edn. J. Cramer, Vaduz.
An J.A van (1981). The Genera of Fungi Sporulating in Pure Culture. 3rd edn. J. Cramer, Vaduz.
An J.A van (1983). Mycosphaerella and its anamorphs. Proceedings of the Koninklijke Nederlandse Akademie van Wetenschappen, Ser. C 86(1): 15–54.
Beck A, Ritschel A, Schubert K, Braun U, Triebel D (2005). Phylogenetic relationship of the anamorphic genus Fuscidiaulum s. lat. as inferred by ITS data. Mycological Progress 4: 111–116.
Braun U (1995). A monograph of Cercosporaella, Ramularia and allied genera (phytopathogenic hyphomycetes) Vol. 1. IHV-Verlag, Eching.
Braun U (1996). Taxonomic notes on some species of the Cercospora complex (IV). Sydowia 48: 205–217.
Braun U (1998). A monograph of Cercosporaella, Ramularia and allied genera (phytopathogenic hyphomycetes) Vol. 2. IHV-Verlag, Eching.
Brown K.B, Hyde KD, Guest DI (1998). Preliminary studies on endophytic fungal communities of Musa acuminata species complex in Hong Kong and Australia. Fungal Diversity 1: 27–51.
Castañeda RF, Kendrick B (1990). Conidial fungi from Cuba I. University of Waterloo Biological Series 33: 1–61.
Crous PW (1998). Mycosphaerella spp. and their anamorphs associated with leaf spot diseases of Eucalyptus, Mycologia Memoria 21: 1–170.
Crous PW, Aptroot A, Kang J-C, Braun U, Wingfield MJ (2000). The genus Mycosphaerella and its anamorphs. Studies in Mycology 45: 107–121.
Crous PW, Braun U (2003). Mycosphaerella and its anamorphs. 1. Names published in Cercospora and Passalora. CBS Biodiversity Series 1: 1–569.
Crous PW, Groenewald JZ, Mansilla JP, Hunter GC, Wingfield MJ (2004). Phylogenetic reassessment of Mycosphaerella spp. and their anamorphs occurring on Eucalyptus. Studies in Mycology 50: 195–214.
Crous PW, Kang JC, Braun U (2001). A phylogenetic redefinition of ascomycete genera in Mycosphaerella based on ITS rDNA sequences. Mycologia 93: 1081–1101.

Crous PW, Schroers HJ, Groenewald JZ, Braun U, Schubert K (2006a). Metulocladosporiella gen. nov. for the causal organism of Cladosporium aculeatum disease of mango. Mycological Research 110: 264–275.

Crous PW, Schubert K, Braun U, Hoog GS de, Hocking AD, Shin H-D, Groenewald JZ (2007). Opportunistic, human-pathogenic species in the Pseudocercospora. Mycological Research 111: 923–32.

Crous PW, Verkley GJM, Groenewald JZ (2006b). Eurypactus microfungi known from culture. 1. Cladorina and Fulvolvulam genera nova, with notes on some other poorly known taxa. Studies in Mycology 55: 53–63.

Crous PW, Wingfield MJ, Mansilla JP, Allenas AC, Groenewald JZ (2006c). Phylogenetic reassessment of Mycosphaerella spp. and their anamorphs occurring on Eucalyptus. II. Studies in Mycology 55: 99–131.

David JC (1997). A contribution to the systematics of Cladosporium. Revision of the fungi previously referred to Heterosporium. Mycological Papers 172: 1–157.

Dugan FM, Schubert K, Braun U (2004). Check-list of Cladosporium names. Schlechtendalia 11: 1–103.

Ellis MB (1971). Dematiaceous hyphomycetes. Commonwealth Mycological Institute, Kew.

Ellis MB (1976). More dematiaceous hyphomycetes. Commonwealth Mycological Institute, Kew.

El-Morsy EM (2000). Fungi isolated from the endohosphere of halophytic plants from the Red Sea Coast of Egypt. Fungal Diversity 5: 43–54.

Garne W, Verkley GJM, Crous PW (2007). CBS Course of Mycology, 5th ed. Centraalbureau voor Schimmelcultures, Utrecht.

Gerrits van den Ende AHG, Hoog GS de (1999). Variability and molecular diagnostics of the neurotropic species Cladophialophora bantiana. Studies in Mycology 43: 151–162.

Goh TK, Hyde KO (1998). A synopsis of and key to Diaporthaceae species, based on the literature, with a description of a new species. Fungal Diversity 1: 65–83.

Hawksworth DL (1979). The lichenicolous hyphomycetes. Academic Press, San Diego, California: 315–322.

Hawksworth DL (1982). New or interesting microfungi. IV. Dematiaceous hyphomycetes. Mycotaxon 13: 1–132.

Heuchert B, Braun U, Schubert K (2005). Morphotaxonomic revision of fungicolous cladosporium species. Schlechtendalia 14: 53–55.

Ho MH-M, Castañeda RF, Dugan FM, Jong, SC (1999). Cladosporium and Cladophialophora in culture: descriptions and a expanded key. Mycota 72: 115–157.

Hoog GS de, Batenburg van der Vegte WH (1989). Retroconis, a new genus of ascomycetous hyphomycetes. Studies in Mycology 31: 99–105.

Hoog GS de, Gerrits van den Ende AHG (1998). Molecular diagnostics of clinical strains of filamentous Basidiomycetes. Mycoses 41: 183–189.

Hoog GS de, Guarro, J, Gené J, Figueras MJ (2000). Asperisporium, Dischloridium, Fusicladium, and Metulocladosporiella genera in (hyphomycetes). Mycologia 43: 76–97.

Hoog GS de, Gerrits van den Ende AHG, Hoog GS de (1999). Nutritional conidiogenése chez quelques champignon microscopiques. Memoires du Museum d’Histoire Naturelle, Sér B, Botanique 28: 3–79.

Schoch C, Shoemaker RA, Seifert KA, Hambleton S, Spatafora JW, Crous PW (2006). A multigene phylogeny of the Dothideomycetes using four nuclear loci. Mycologia 98: 1041–1052.

Schubert K (2005a). Morphotaxonomic revision of fusicladium Cladosporium species (hyphomycetes). PhD thesis, Martin-Luther-University, Halle.

Schubert K (2005b). Taxonomic revision of the genus Cladosporium s. lat. 3. A revision of Cladosporium species described by J.J. Davis and H.C. Greene (WIS). Mycotaxon 92: 55–76.

Schubert K, Braun U (2004). Taxonomic revision of the genus Cladosporium s. lat. 2. Morphotaxonomic examination of Cladosporium species occurring on hosts of the families Bignoniaceae and Orchidaceae. Sydowia 56: 78–97.

Schubert K, Braun U (2005a). Taxonomic revision of the genus Cladosporium s. lat. 1. Species reallocated to Fusidium, Parastenella, Passalora, Pseudocercospora and Stenella. Mycological Progress 4: 101–109.

Schubert K, Braun U (2005b). Taxonomic revision of the genus Cladosporium s. lat. 4. Species reallocated to Aspéricosporium, Dischloridium, Fusidium, Passalora, Pseudasperidium and Stenella. Fungal Diversity 20: 187–208.

Schubert K, Braun U (2007). Taxonomic revision of the genus Cladosporium s. lat. 5. New species, reallocations to and synonyms of Cercoascospora, Fusidium, Passalora, Septornema and Stenella. Nova Hedwigia 84: 189–208.

Schubert K, Braun U, Groenewald JZ, Crous PW (2007a). Cladosporium leaf-blotch and stem rot of Paeonia spp. caused by Dichocladosprium chlorocephalum gen. nov. Studies in Mycology 58: 95–104.

Schubert K, Braun U, Mulenko W (2008). Taxonomic revision of the genus Cladosporium s. lat. 5. Validations and descriptions of new species. Schlechtendalia 14: 53–55.

Schubert K, Groenewold JZ, Braun U, Dijkstra J, Stankir M, Hill CF, Zalar P, Hoog GS de, Crous PW (2007b). Biodiversity in the Cladosporium herbarum complex (Davidiellaceae, Capnodiales), with standardisation of methods for Cladosporium taxonomy and diagnostics. Studies in Mycology 58: 105–156.

Schubert K, Ritchael A, Braun U (2003). A monograph of Fusidium s. lat. (hyphomycetes). Schlechtendalia 8: 1–132.

Seifert K, Nickerson NL, Cortlett M, Jackson ED, Lois-Seize G, Davies RJ (2004). Devriesia, a new hyphomycete genus to accommodate heat-resistant, cladosporium-like fungi. Canadian Journal of Botany 82: 914–926.

Storhn SN, Dighton J (2004). Effects of species diversity on establishment and coexistence: A phylloplane fungal community model system. Microbial Ecology 47: 431–438.

Unterreiner WA (1997). Taxonomy of selected members of the ascomycete genus Capronia with notes on anamorph-teleomorph connections. Mycologia 89: 120–131.

Unterreiner WA, Gerrits van den Ende AHG, Hoog GS de (1999). Nutritional physiology of species of Capronia. Studies in Mycology 43: 98–106.

Unterreiner WA, Naveau FA (1999). Molecular systematics of the Herpotrichiellaceae with an assessment of the phylogenetic positions of Exopiha dermatidis and Philophila americana. Mycologia 91: 67–83.

Varghese KIM, Rao VG (1979). Forest microfungi – I. Subramaniomyces, a new genus of Hyphomycetes. Kavakova 7: 83–85.

Vilgalys R, Hester M (1990). Rapid genetic identification and mapping of enzymatically amplified ribosomal DNA from several Cryptococcus species. Journal of Bacteriology 172: 4239–4246.

Vries GA de (1952). Contribution to the Knowledge of the Genus Cladosporium Link ex Fr. Centraalbureau voor Schimmelcultures, Baarn.

White TJ, Bruns T, Lee S, Taylor J (1990). Amplification and direct sequencing of fungal ribosomal RNA genes for phylogenetics. In: PCR Protocols: a guide to methods and applications (Innis MA, Gelfand DH, Sninsky JI, White TJ, eds). Academic Press, San Diego, California: 315–322.

Witsell SGR, Runge-Frobose C, Ahn DG, Kemen E, Oliver RP, Mendgen KW (2002). Four or more species of Cladosporium sympatoically colonize Phragmites australis. Fungal Genetics and Biology 35: 99–113.

Partridge EC, Morgan-Jones G (2002). Notes on hyphomycetes, LXXXVIII. New genera in which to classify Alsidium resinae and Pycnostyssurus azaleae, with a consideration of Sorocoryce. Mycotaxon 83: 335–352.

Rayner RW (1970). A mycological colour chart. CMI and British Mycological Society. Iowa.

Rahn RA, Samuels GJ (1944). Taxonomy and phylogeny of Glociocladium analysed from nuclear large subunit ribosomal DNA sequences. Mycological Research 98: 625–634.

Riesen T, Sieber T (1985). Endophytic fungi in winter wheat (Triticum aestivum L.). Swiss Federal Institute of Technology, Zürich.

Roquebert MF (1981). Analyse des phenanomes panaux au cours de la conidiogene se chez quelques champignon microscopiques. Mémoires du Museum d’Histoire Naturelle, Sér B, Botanique 28: 3–79.