

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., *Ochrocladosporium elatum* (Harz) Crous & U. Braun, comb. nov., *Ochrocladosporium frigidarii* Crous & U. Braun, sp. nov., *Rachicladosporium* Crous, U. Braun & Hill, gen. nov., *Rachicladosporium luciliae* 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., *Verrucocladosporium dirinae* 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 matters, are also known to be common endophytes (Riesen & Sieber 1985, Brown *et al.* 1998, El-Morsy 2000) as well as phylloplane fungi (Islam & Hasin 2000, De Jager *et al.* 2001, Inacio *et al.* 2002, Stohr & Dighton 2004, Levetin & 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, Wirsal *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* Johanson 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 conidiogenous loci and conidial hila 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 conidiogenous loci and hila 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 teleomorphs 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 periphysoids 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-1 α , 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.

Table 1. Isolates for which new sequences were generated.

Anamorph	Teleomorph	Accession number ¹	Host	Country	Collector	GenBank numbers ² (ITS, LSU)
<i>Cladonia eucaalypti</i>		CBS 115899*; CPC 10954	<i>Eucalyptus</i> sp.	South Africa	P.W. Crous	EU040224, EU040224
<i>Coniothyrium palmarum</i>		CBS 758.73; CMW 5283	<i>Phoenix dactylifera</i>	Israel	Y. Pinkas	DQ240000, EU040225
<i>Devriesia acadensis</i>		CBS 115874; DAOM 232211	Soil	Canada	N. Nickerson	AY692095, EU040226
<i>Devriesia americana</i>		CBS 117726; ATCC 96545; CPC 5121	Air	U.S.A.	F.M. Dugan	AY251068, EU040227
<i>Devriesia shelburniensis</i>		CBS 115876; DAOM 232217	Soil	Canada	N. Nickerson	AY692093, EU040228
<i>Devriesia thermoturans</i>		CBS 115878*; DAOM 225330	Soil	Canada	N. Nickerson	AY692087, EU040229
<i>Hormoconis resiniae</i>		CBS 365.86	–	–	–	EU040230, EU040230
		CBS 184.54; ATCC 11841; CPC 3692; IMI 089837; IFO 31706	Creosote-treated wooden pole	U.S.A.	–	AY251067, EU040231
<i>Hyalodendriella betulae</i>		CBS 261.82*	<i>Alnus glutinosa</i>	Netherlands	W. Gams	EU040232, EU040232
<i>Ochrocladosporium elatum</i>		CBS 146.33*; ATCC 11280; ATHUM 2862; IFO 6372; IMI 049629; MUCL 10094	Wood pulp	Sweden	E. Melin	EU040233, EU040233
<i>Ochrocladosporium frigidarii</i>		CBS 103.81*	Cooled room	Germany	B. Ahlert	EU040234, EU040234
<i>Parapleurotheciopsis inaequiseptata</i>		MUCL 41089; INIFAT C9830-1	Rotten leaf	Brazil	R.F. Castañeda	EU040235, EU040235
<i>Passalora daleae</i>		CBS 113031*	<i>Dalea spinosa</i>	Mexico	L.B. Sparrus	EU040236, EU040236
<i>Rachicladosporium luculiae</i>		CPC 11407*	<i>Luculia</i> sp.	New Zealand	F. Hill	EU040237, EU040237
<i>Ramularia aplospora</i>	<i>Mycosphaerella alchemillicola</i>	CBS 545.82*	Powdery mildew on <i>Alchemilla vulgaris</i>	Germany	T. Hijwegen	EU040238, EU040238
<i>Retroconis fusiformis</i>		CBS 330.81; IMI 170799	<i>Gossypium</i> sp.	Pakistan	–	EU040239, EU040239
<i>Rhizocladosporium argillaceum</i>		CBS 241.67*; ATCC 38103; IFO 7055; OUT 4262	Decayed myxomycete	Japan	K. Tubaki	EU040240, EU040240
<i>Subramaniomyces fusisaprophyticus</i>		CBS 418.95; INIFAT C94/134	Leaf litter	Cuba	R.F. Castañeda	EU040241, EU040241
<i>Theodonia ligustrina</i>		W1877	<i>Ligustrum</i> sp.	–	H. Evans	EU040242, EU040242
<i>Toxicocladosporium irritans</i>		CBS 185.58*	Mouldy paint	Suriname	M.B. Schol-Schwarz	EU040243, EU040243
<i>Verrucocladosporium dirinae</i>		CBS 112794*	<i>Dirina massiliensis</i>	U.K.	A. Aptroot	EU040244, EU040244

¹ATCC: American Type Culture Collection, Virginia, U.S.A.; ATHUM: Culture Collection of Fungi, University of Athens, Department of Biology, Section of Ecology and Systematics, Athens, Greece; CBS: Centraalbureau voor Schimmelcultures, Utrecht, The Netherlands; CMW: Culture collection of Mike Wingfield, housed at FABI, Pretoria, South Africa; CPC: Culture collection of Pedro Crous, housed at CBS; DAOM: Plant Research Institute, Department of Agriculture (Mycology), Ottawa, Canada; IFO: Institute For Fermentation, Osaka, Japan; IMI: International Mycological Institute, CAB International, Egham, Surrey, U.K.; INIFAT: Alexander Humboldt Institute for Basic Research in Tropical Agriculture, Ciudad de La Habana, Cuba; MUCL: Mycoltheque de l'Université Catholique de Louvain, Louvain-la-Neuve, Belgium; OUT: Department of Fermentation Technology, Faculty of Engineering, Osaka University, Yamadaue, Suita-shi, Osaka, Japan.

²ITS: internal transcribed spacer regions and 5.8S rRNA gene; LSU: partial 28S rRNA gene.

*Ex-type cultures.

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 to fasciculate, cylindrical, geniculate-sinuuous to nodulose, simple to branched, subhyaline to usually distinctly pigmented, continuous to septate, smooth to verruculose*; *conidiogenous cells integrated, terminal and intercalary, usually sympodial, with a single to several scars*; *conidiogenesis holoblastic*; *conidiogenous 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, amero- 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 (www.biology.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 ($\times 1\ 000$ 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 conidiogenesis. 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 *Parapleurotheciopsis inaequiseptata* (Matsush.) P.M. Kirk and *Subramaniomyces fusisaprophyticus* (Matsush.) P.M. Kirk, as well as related sequences

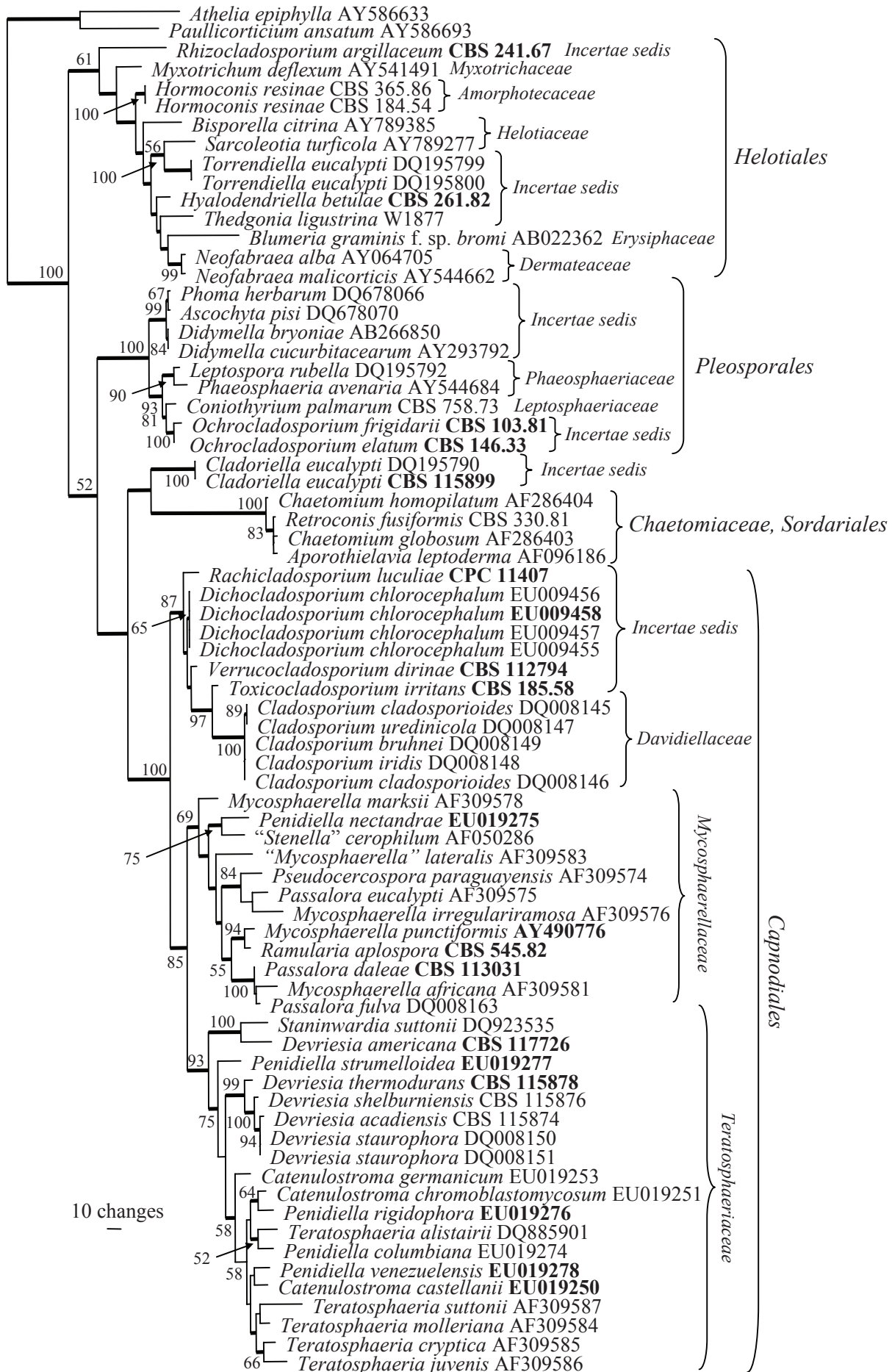


Fig. 1. One of 44 equally most parsimonious trees obtained from a heuristic search with 100 random taxon additions of the LSU sequence alignment using PAUP v. 4.0b10. The scale bar shows 10 changes, and bootstrap support values from 1 000 replicates are shown at the nodes. Thickened lines indicate the strict consensus branches and ex-type sequences are printed in bold face. The tree was rooted to two sequences obtained from GenBank (*Athelia epiphylla* AY586633 and *Paulliacorticium ansatum* AY586693).

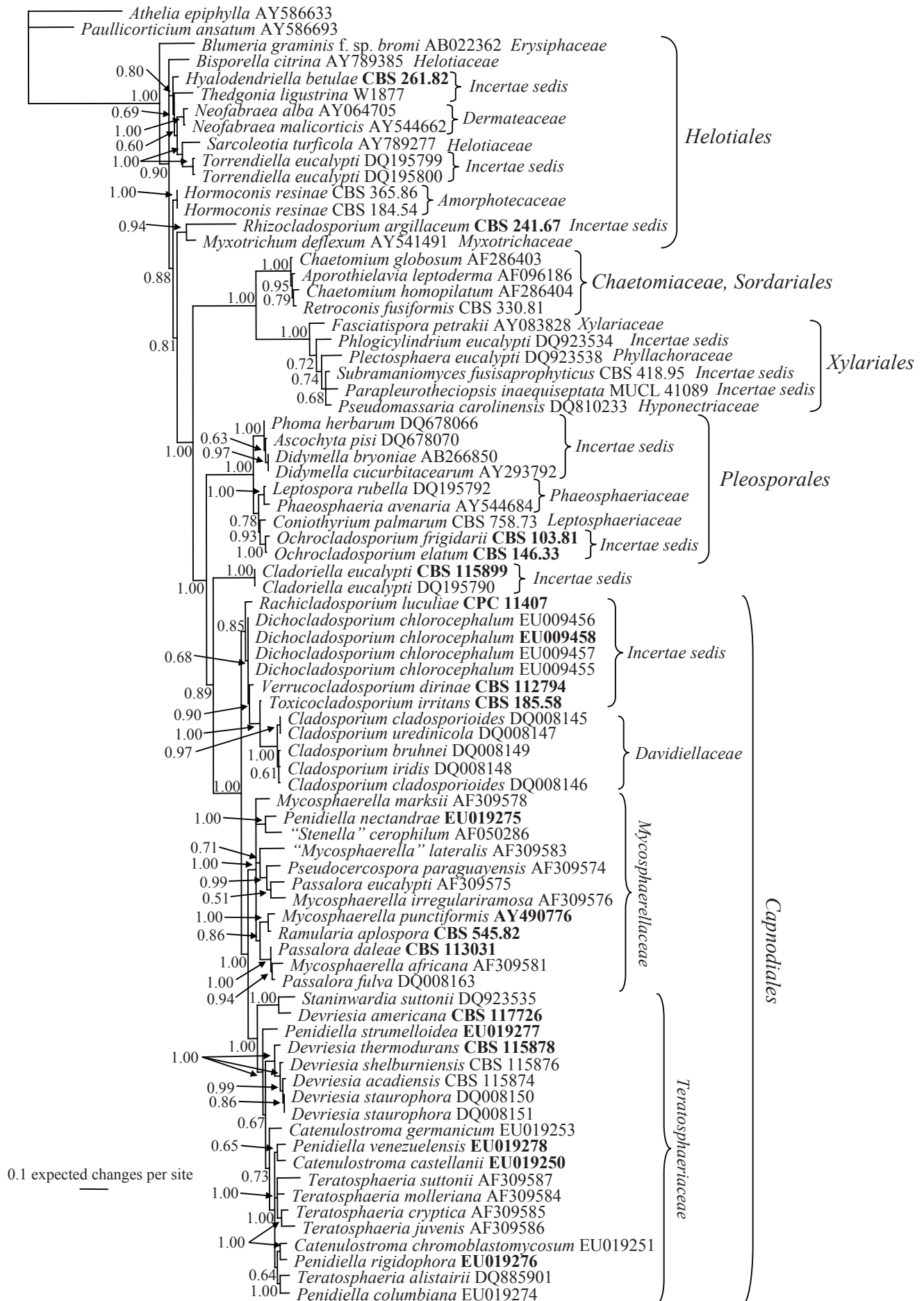


Fig. 2. Consensus phylogram (50 % majority rule) of 800 trees resulting from a Bayesian analysis of the LSU sequence alignment using MrBAYES v. 3.1.2. Bayesian posterior probabilities are indicated at the nodes. Ex-type sequences are printed in bold face. The tree was rooted to two sequences obtained from GenBank (*Athelia epiphylla* AY586633 and *Paullicorticium ansatum* AY586693).

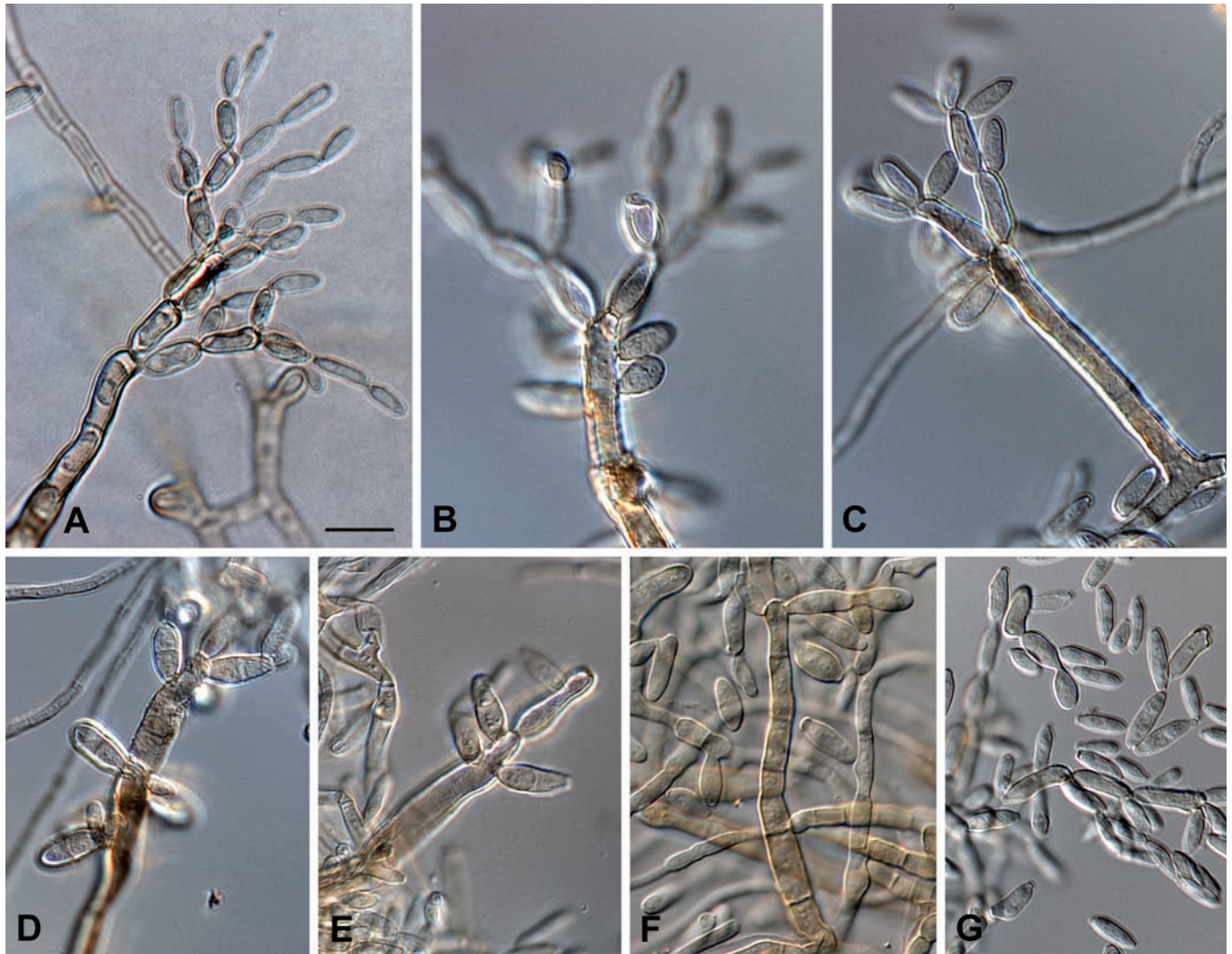


Fig. 3. *Rachicladosporium luculiae* (type material). A–F. Conidiophores with conidial chains, and conidiogenous loci aggregated in the upper region. G. Conidia. Scale bar = 10 μ m.

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.

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

Mycelium consisting of branched, septate, smooth, hyaline to pale brown, thin-walled hyphae. ***Conidiophores*** erect, solitary, macronematous, 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.

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 compositum. Conidiophora erecta, solitaria, macronemata, ex hyphis superficialibus oriunda, subcylindrica, recta to geniculata-sinuosa, ad 60 µm longa et 6 µm lata, 3–6-septata, modice brunnea, subtiliter verruculosa, non crassitunicata, ad basim non inflatae et non rhizoideae. Cellulae conidiogenae integratae, terminales, 8–15 × 4–5 µm, subcylindricae, apicem versus attenuatae, apice obtuso, rachidi terminali, locis conidialibus numerosis, 1–2 µm latis, margine leviter incrassatis, non fuscatis et non refractivis. Conidia catenata vel solitaria. Ramoconidia modice brunnea, subtile verruculosa, 0–1-septata, subcylindrica vel anguste ellipsoidea, 10–17 × 4–5 µm; conidia secundaria ellipsoidea, pallide brunnea, 0(–1)-septata, levia vel subtile verruculosa, interdum guttulate, (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, subcylindrical, straight to somewhat geniculate-sinuuous, 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, subcylindrical, tapering to an obtuse apex, occasionally slightly swollen at the tip, without distinct sympodial proliferation (non-geniculate), forming a rachis, with several conidiogenous loci, terminal and lateral, 1–2 µm wide, non-protuberant, 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 guttulate, (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 cladosporioid genera by having an apical conidiophore rachis with inconspicuous to subconspicuous scars and unthickened, not darkened-refractive conidial hila. Due to the structure of the conidiogenous cells, *R. luculiae* superficially resembles species of the tetric genus *Diplococcium* Grove (Ellis 1971, 1976; Goh & Hyde 1998). However, there is no evidence for a tetric 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. Fruiting 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 denticulatis, incrassatis et fuscatis-refractivis, sed non coronatis, conidiophoris et conidiis cum septis incrassatis et atrofuscis, et culturis cum metabolitis volaticis toxicis.

Mycelium consisting of branched, septate, dark brown, finely verruculose hyphae. *Conidiophores* solitary, dimorphic, solitary, macronematous or micronematous, reduced to conidiogenous cells. *Macronematous conidiophores* subcylindrical, straight to geniculate-sinuuous, or irregularly curved, unbranched or branched above, septate, dark brown, finely verruculose, walls thick, septa dark brown; *micronematous conidiophores* reduced to conidiogenous cells, erect, doliiform to subcylindrical, with slight taper towards the apex. *Conidiogenous cells* integrated, terminal or lateral, subcylindrical with slight taper towards apex; proliferating sympodially with apical loci protruding and denticle-like, thickened, darkened and refractive, but not coronate. *Conidia* catenulate in branched or unbranched chains, medium to dark brown, thick-walled, with dark, thick septa, smooth to finely verruculose; *ramoconidia* septate, prominently constricted at septa, broadly ellipsoid to subcylindrical; 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-brunneis, minute verruculosus, (2–)3–4 µm latis, ultimo crassitunicatis et crassiseptatis. Conidiophora solitaria, dimorphosa, macronemata et solitaria vel micronemata. Conidiophora macronemata ex hyphis modice brunneis lateraliter oriunda, erecta, subcylindrica, recta, geniculata-sinuosa vel irregulariter curvata, non ramosa vel ad apicem ramosa, 2–7-septata, atro-brunnea, leviter verruculosa, crassitunicata, septa atro-brunnea, 30–60 × 4–6 µm; conidiophora micronemata saepe non septata, raro 1–2-septata, erecta, doliiformes 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, sympodiales, cum 1–3 locis conidiogenibus, denticulatis, 1–1.5 µm latis, incrassatis, fuscatis-refractivis. Conidia catenulata vel rami-catenulata, modice vel atro-brunnea, crassitunicata, septis incrassatis, fuscatis, levia vel subtile verruculosa; ramoconidia (0–)1(–3)-septata, constricta, late ellipsoidea vel subcylindrica, 7–15 × 3–5 µm; conidia secundaria ellipsoidea vel ovoidea, pallide vel modice brunnea, 0(–1)-septata, (5–)6–8(–10) × (3–)4(–5) µm; hila protuberantes, 1–1.5 µm lata, hila ramoconidorum incrassata et fuscata-refractiva, vel hila conidorum secundariorum 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 conidiogenous cells. *Macronematous conidiophores* subcylindrical, straight to geniculate-sinuuous, 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*

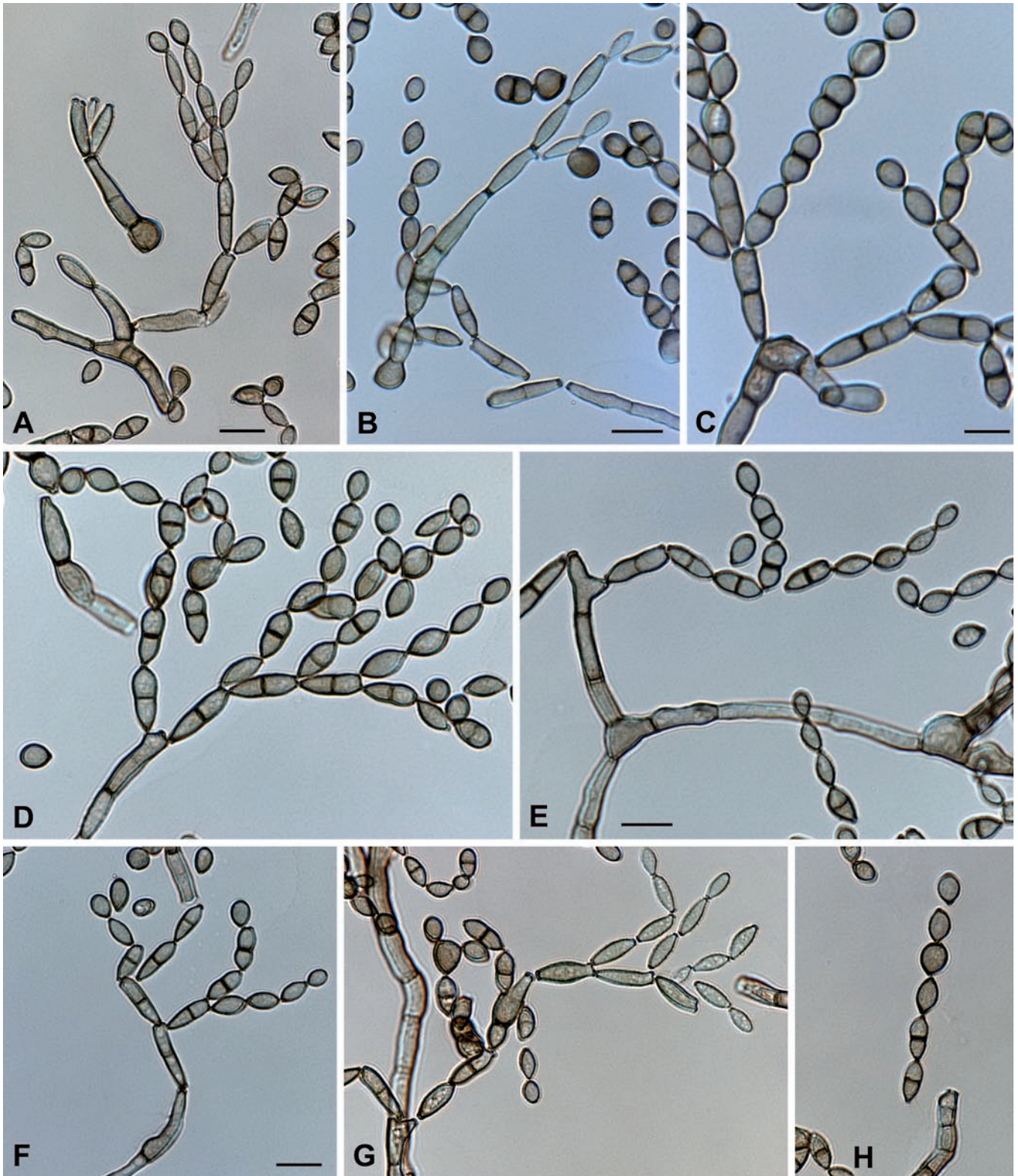


Fig. 4. *Toxicocladosporium irritans* (type material). A–B, F. Microconidiophores. C–E. Macroconidiophores. G–H. Ramoconidia and conidia. Scale bars = 10 µm.

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, $10\text{--}30 \times 2.5\text{--}4$ µm. *Conidiogenous cells* integrated, terminal or lateral, subcylindrical with slight taper towards apex, $7\text{--}12 \times 3\text{--}4$ 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, $7\text{--}15 \times 3\text{--}5$ µm; conidia ellipsoid to ovoid, younger apical conidia pale to medium brown, 0(–1)-septate, $(5\text{--})6\text{--}8\text{--}(10) \times (3\text{--})4\text{--}(5)$ 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.

Specimen examined: Suriname, Paramaribo, isolated from mouldy paint, Feb. 1958, M.B. Schol-Schwarz, **holotype** CBS-H 19892, culture ex-type CBS 185.58.

Notes: *Toxicocladosporium irritans* produces ample amounts of volatile metabolites, which cause a skin rash within minutes of opening an inoculated dish for microscopic examination. Morphologically and phylogenetically it is very similar to *Cladosporium s. str.*, and produces dimorphic conidiophores, which is also commonly observed in *Cladosporium*. It is distinct by having dark, thick-walled conidial and conidiophore septa, and lacking the typical coronate *Cladosporium* scar type (David 1997).

Verrucocladosporium K. Schub., Aptroot & Crous, **gen. nov.** MycoBank MB504432.

Etymology: Named after its frequently coarsely verrucose to warted hyphae, conidiophores and conidia, and cladosporium-like morphology.

Differt a *Cladosporio* hyphis saepe verrucosis, hyalinis, conidiophoris cylindraceis-filiformibus, rectis, non vel vix geniculatis, non nodulosis, locis conidiogenis leviter incrassatis, distincte fuscatis-refractivis, sed non coronatis, conidiis saepe valde variantibus, saepe irregulariter formatis, grosse verrucosis-rugosis.

Mycelium sparingly branched, hyphae septate, not constricted at septa, hyaline, almost smooth to irregularly rough-walled, coarsely verrucose to warted. *Conidiophores* arising laterally from creeping hyphae, erect, straight, or somewhat flexuous, narrowly cylindrical to filiform, neither geniculate nor nodulose, unbranched, septate, pale brown, thin-walled, smooth to often irregularly rough-walled or verrucose. *Conidiogenous cells* integrated, terminal or intercalary, cylindrical, polyblastic, with sympodial proliferation, with loci often crowded at the apex, truncate, barely to slightly thickened, but distinctly darkened-refractive. *Ramoconidia* cylindrical, aseptate, concolorous with conidiophores, thin-walled, irregularly rough-walled, coarsely verruculose to verrucose-rugose; hila unthickened but somewhat refractive. *Conidia* in long unbranched or loosely branched chains, 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: *Verrucocladosporium dirinae* K. Schub., Aptroot & Crous, sp. nov.

Verrucocladosporium dirinae K. Schub., Aptroot & Crous, **sp. nov.** MycoBank MB504433. Fig. 5.

Etymology: Named after its host, *Dirina massiliensis*.

Mycelium sparse ramosum. Hyphae 1–3 µm latae, septatae, non constrictae, hyalinae, leviae, vel irregulariter verruculosae, interdum verrucosae, tuberculatae, tenuitunicatae. Conidiophora ex hyphis repentibus lateraliter oriunda, erecta, recta, interdum leviter flexuosa, anguste cylindrica vel filiformes, non geniculata, non nodulosa, non ramosa, ad 85 µm longa, 2–3 µm lata, septata, tenuitunicata (≤ 0.75 µm), pallide brunnea, levia vel saepe irregulariter verrucosa, leviter crassitunicata. Cellulae conidiogenae integratae, saepe terminales, interdum intercalares, cylindricae, angustae, 9–20 µm longae, holoblasticae, sympodiales, locis conidiogenibus 1–3, saepe ad apicem aggregatis, interdum protuberantibus, truncatis, 1–1.8(–2) µm latis, incrassatis et fuscatis-refractivis. Ramoconidia cylindrica, 16–21 × (2–)2.5–3 µm, non septata, pallide brunnea, tenuitunicata, irregulariter verruculosa vel crosse verrucosa-rugosa, ad 4 hilis terminalibus, ad basim late truncata, non attenuata, 2–2.5 µm lata, non incrassata, sed leviter refractiva. Conidia catenata, in catenis longis, non ramosis vel laxe ramosis, plus minusve recta, obovoidea, ellipsoidea, fusiformes vel subcylindricae, sed saepe irregulares, 4–18(–23) × (2–)2.5–3.5 µm, 0–1-septata, ad septa interdum constricta, pallide brunnea, tenuitunicata (≤ 0.5 µm), irregulariter verruculosa-rugosa, utrinque leviter attenuata, hila truncata, (0.5–)0.8–1.5(–2) µm lata, vix vel leniter incrassata, sed distincte fuscata-refractiva.

Mycelium sparingly branched; hyphae 1–3 µm wide, septate, not constricted at septa, hyaline, smooth to irregularly rough-walled, sometimes coarsely verrucose, with small to large drop-like, tuberculate warts, walls unthickened. *Conidiophores* arising laterally from creeping hyphae, erect, straight, sometimes slightly flexuous, narrowly cylindrical to filiform, not geniculate, non nodulose, unbranched, up to 85 µm long, 2–3 µm wide, septate, thin-walled (≤ 0.75 µm), pale brown, smooth to often irregularly rough-walled, verrucose, walls slightly thickened. *Conidiogenous cells* integrated, mostly terminal, sometimes also intercalary, cylindrical, narrow, 9–20 µm long, conidiogenesis holoblastic, proliferation sympodial, with a single or up to three conidiogenous loci, often crowded at the apex, sometimes situated on small lateral prolongations, loci truncate, 1–1.8(–2) µm wide, thickened and darkened-refractive. *Ramoconidia* cylindrical, 16–21 × (2–)2.5–3 µm, aseptate, concolorous with conidiophores, thin-walled, irregularly rough-walled, verruculose to coarsely verrucose-rugose, apically with up to 4 hila, with a broadly truncate, non-attenuated base, 2–2.5 µm wide, unthickened but somewhat refractive. *Conidia* catenate, in long unbranched or loosely branched chains, more or less straight, obovoid, ellipsoid, fusiform to subcylindrical, but often appearing to form band-like structures, with swollen and constricted parts, accordion or fir tree-like and also due to ornamentation often appearing irregular in shape and outline, 4–18(–23) × (2–)2.5–3.5 µm, 0–1-septate, sometimes constricted at the more or less median septum, pale brown, thin-walled (≤ 0.5 µm), irregularly rough-walled, verruculose-rugose, somewhat attenuated towards apex and base, hila truncate, (0.5–)0.8–1.5(–2) µm wide, barely or slightly thickened, but distinctly darkened-refractive; microcyclic conidiogenesis not observed.

Cultural characteristics: Colonies erumpent, spreading, with catenate, feathery margins and moderate aerial mycelium on PDA. Surface grey-olivaceous, reverse iron-grey. Colonies reaching 25 mm after 1 mo at 25 °C.

Specimen examined: U.K., Somerset, Kingsbury Episcopi, isolated from the lichen *Dirina massiliensis* (Roccellaceae, Arthoniales), Mar. 2003, A. Aptroot, **holotype** CBS-H 19883, culture ex-type CBS 112794.

Notes: *Verrucocladosporium dirinae* was deposited as *Cladosporium arthoniae* M. Christ. & D. Hawksw., but the name was misapplied. The latter species, described from apothecia of *Arthonia impolita* on *Quercus* from Sweden, does not possess clearly visible, distinct conidiogenous 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 catenate, 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 *Taeniolella* S. Hughes species. The unique feature of the new genus *Verrucocladosporium* 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-coronate conidiogenous 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”. *Verrucocladosporium 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, taeniolella-like, lichenicolous hyphomycete was also present on the thallus of this lichen.

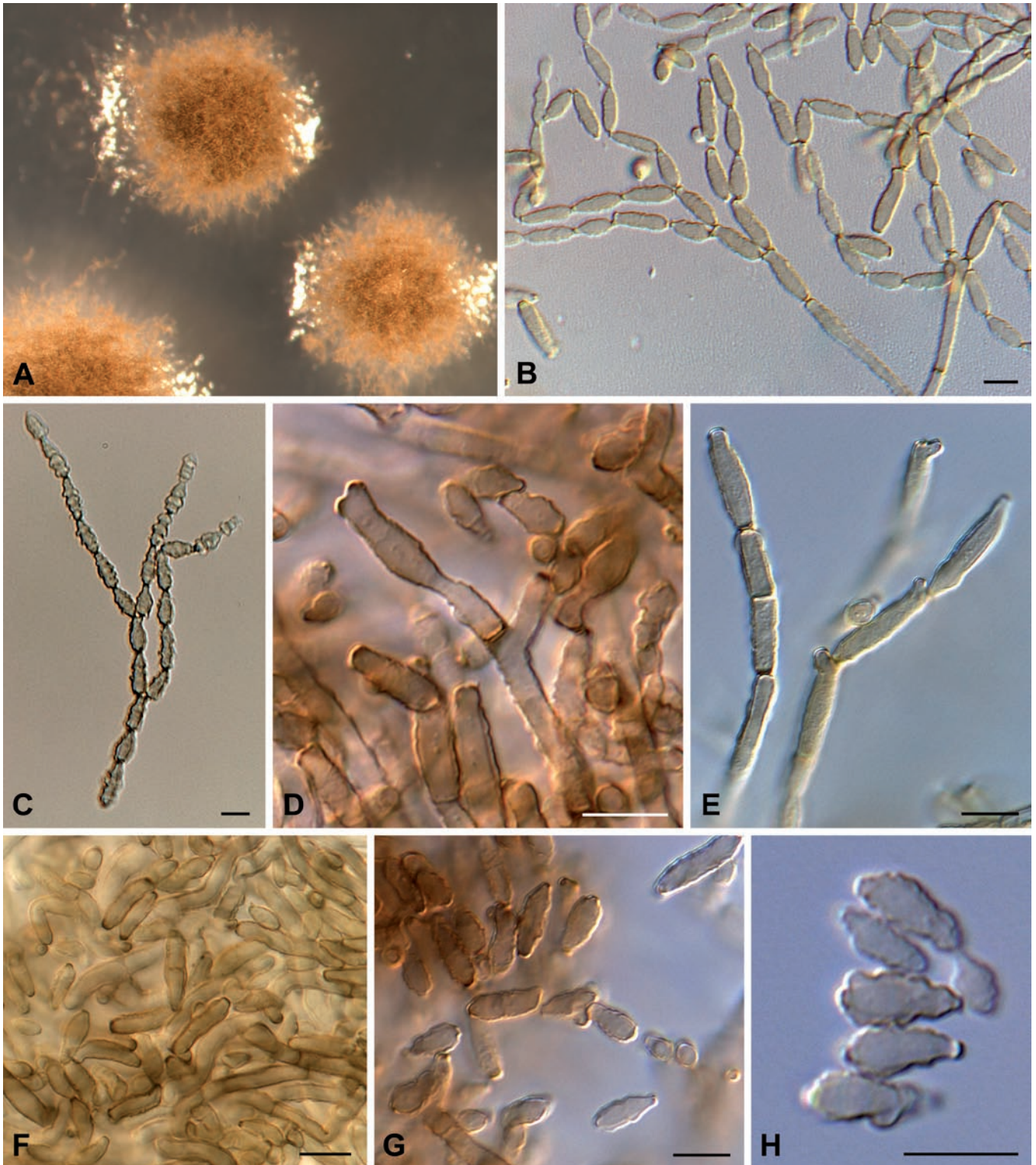


Fig. 5. *Verrucocladosporium dirinae* (type material). A. Colonies on MEA. B–C. Conidial chains. D–H. Ramoconidia and conidia. Scale bars = 10 µm.

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.

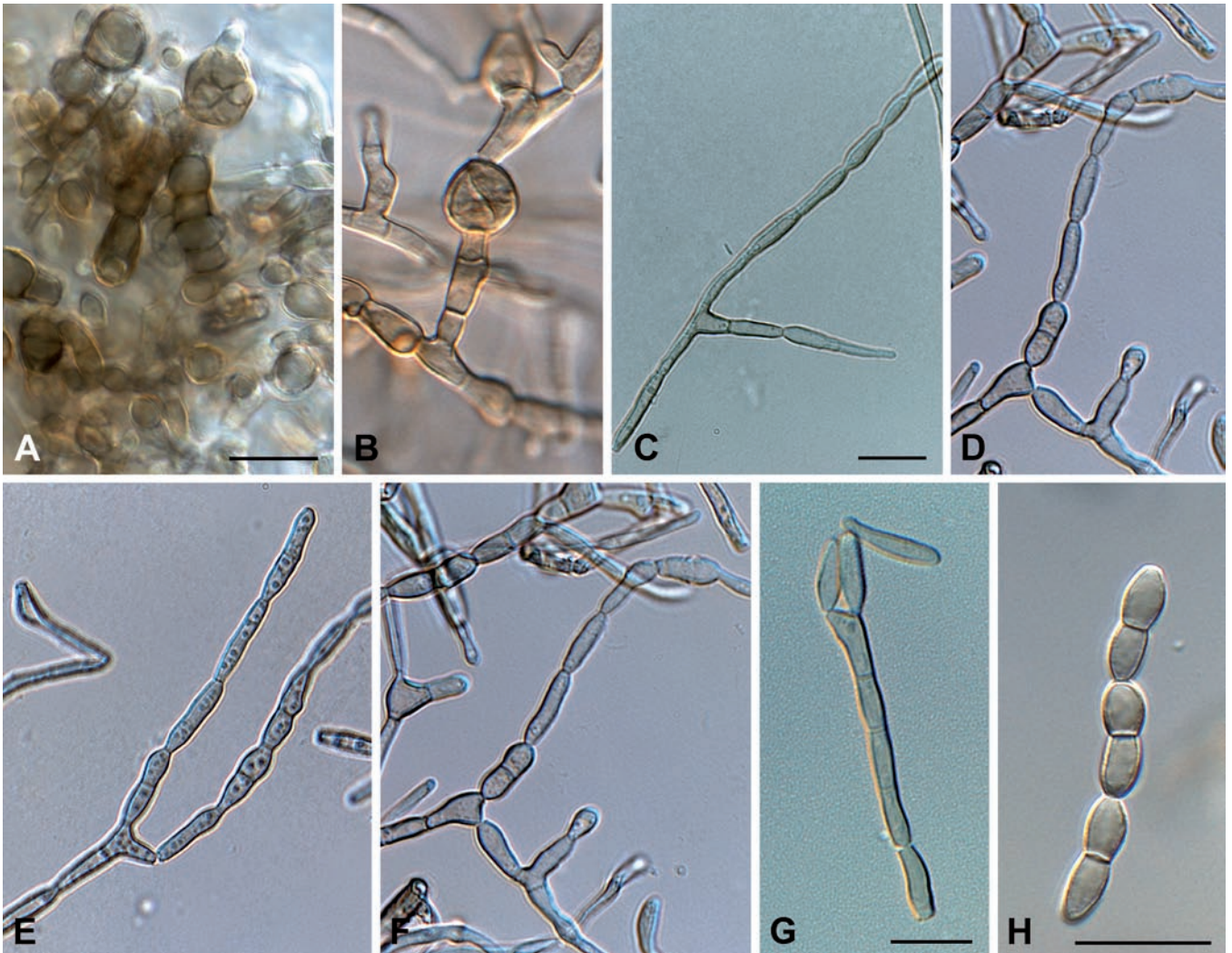


Fig. 6. *Devriesia americana* (type material). A–B. Chlamydospore-like structures formed in culture. C–F. Conidiophores giving rise to conidial chains. G–H. Conidia. Scale bars = 10 μm

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 8–15 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 \times 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 chlamydospores 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 chlamydospores, beside *D. shelburniensis* N.L. Nick. & Seifert, but the latter species is easily distinguishable by its long and narrow conidiophores (ca 100–200 \times 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 & Marciano, *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, septate, 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

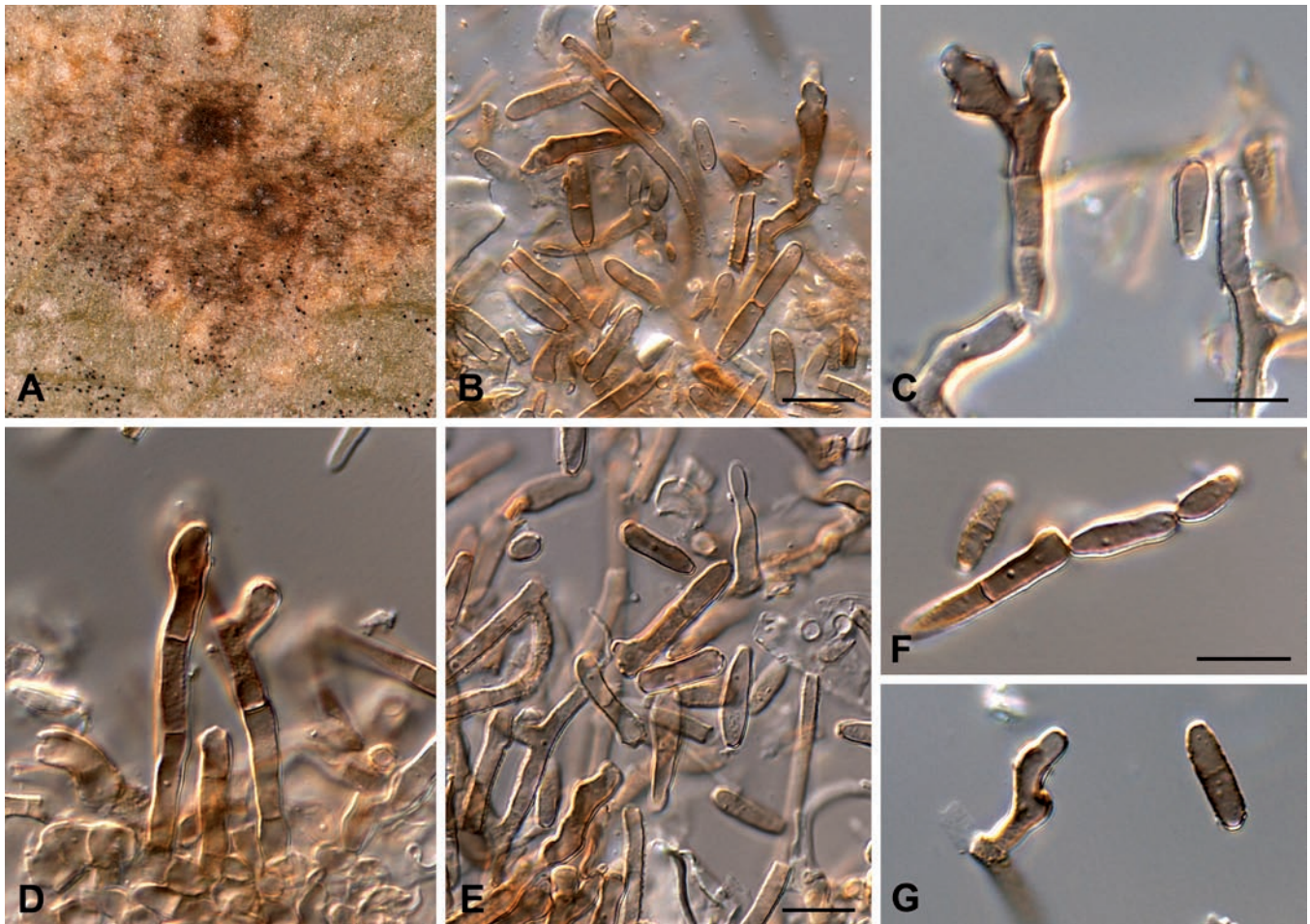


Fig. 7. *Stenella araguata* (syntype material, IMI 34905). A. Leaf spot. B. Conidiophore, conidia and verruculose hypha on leaf surface. C–D. Conidiophore with terminal conidiogenous cells. E–G. Ramoconidia and conidia. Scale bars = 10 µm.

or branched, $20\text{--}40 \times 3\text{--}4$ µm. *Conidiogenous cells* terminal or lateral, unbranched, medium brown, finely verruculose, tapering to slightly or flat-tipped loci, proliferating sympodially, $5\text{--}20 \times 3\text{--}4$ 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, $(7\text{--})13\text{--}20(\text{--}25) \times 3(\text{--}3.5)$ 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, $10\text{--}70 \times 3\text{--}4$ µm; frequently swollen and constricted at septa, thick-walled, medium brown, verruculose. *Conidiogenous cells* terminal and intercalary, subcylindrical, straight, but frequently branched laterally, $6\text{--}20 \times 3\text{--}4$ µm, with 1–3 flat-tipped loci that can be subdentate, 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, $12\text{--}25 \times 3.5\text{--}4(\text{--}5)$ µm, 1(–4)-septate. *Conidia* occurring in short chains (–8), subcylindrical to narrowly ellipsoid, 0–1(–3)-septate, $(7\text{--})10\text{--}15(\text{--}20) \times (2\text{--})3\text{--}3.5(\text{--}4)$ 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, $(7\text{--})10\text{--}15(\text{--}20) \times (2\text{--})3\text{--}3.5(\text{--}4)$ µm, while those of the type specimen of *S. araguata* were similar, namely 0–3-septate, $(7\text{--})13\text{--}20(\text{--}25) \times 3(\text{--}3.5)$ µm. Furthermore, both collections have verruculose hyphae, which is the primary feature distinguishing *Stenella* from *Passalora* Fr. (Crous & Braun 2003).



Fig. 8. *Stenella araguata* (CBS 105.75). A–B. Conidiophore fascicles on a pine needle and tap-water agar, respectively. C–D, G. Conidiophores giving rise to conidial chains. E–F, H–J. Conidial chains with ramoconidia and conidia. Scale bars = 10 µm.

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.Differt a *Hyalodendro* et *Retroconi* conidiophoris dimorphis, cicatricibus incrassatis et conidiis ultimo brunneis.

Morphologically similar to *Hyalodendron* and *Retroconis*, but distinct in that it has dimorphic 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 conidiogenous 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 betulae* Crous, sp. nov.***Hyalodendriella betulae*** Crous **sp. nov.** MycoBank MB504436. Fig. 9.

Mycelium ex hyphis ramosis, septatis, 1.5–2 µm latis, levibus, hyalinis vel pallide brunnei compositum. Conidiophora dimorphosa: (A) Conidiophora ex hyphis lateraliter oriunda, subcylindrical, 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, loco conidiogeno singulare et terminale, cellula ellipsoidea (conidio?), persistente, interdum cellulis catenulatis (ad 6), pallide brunneo, apice subacutate rotundato, basi truncata, 5–7 × 3–4 µm. (B) Conidiophoris 10–20 × 2–3 µm, 1–2-septatis, subcylindraceutis, rectis vel curvatis, subhyalinis vel pallide brunneis, levibus. Cellulae conidiogenae pallide brunneae, leviae, subcylindraceutae, locis numerosis, aggregatis, inconspicuis vel subdenticulatis, leviter protuberantes, 0.5 µm diam, incrassatis et fuscatis. Conidia catenulata (2–3), (4–)5–6(–7) × 2.5–3 µm, limoniformes vel ellipsoidea, non septata, levia, pallide brunnea, utrinque attenuata, apiculata, 0.5–1 × 0.5 µm, incrassata et fuscata, 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.

Specimen examined: **Netherlands**, Oostelijk Flevoland, Jagersveld, isolated from *Alnus glutinosa* (*Betulaceae*), May 1982, W. Gams, **holotype** CBS-H 19895, culture ex-type CBS 261.82.

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.Differt a *Cladosporio* et generis cladosporioidibus diversis conidiophoris cum cellulis basalibus 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 conidiogenous cells and ramoconidia, continuous to septate, wall thin or slightly thickened, pale brown. *Conidiogenous cells* integrated, terminal or intercalary, subcylindrical to doliiform, pale brown, thin-walled, smooth; unilocal or multilocal, 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 conidiogenous 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.≡ *Cladosporium elatum* (Harz) Nannf., in Melin & Nannfeldt, Svenska Skogsvardsfoereren Tidskr. 32: 397. 1934.≡ *Cadophora elatum* (Harz) Nannf., in Melin & Nannfeldt, Svenska Skogsvardsfoereren Tidskr. 32: 422. 1934.

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 conidiogenous 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). *Conidiogenous 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*

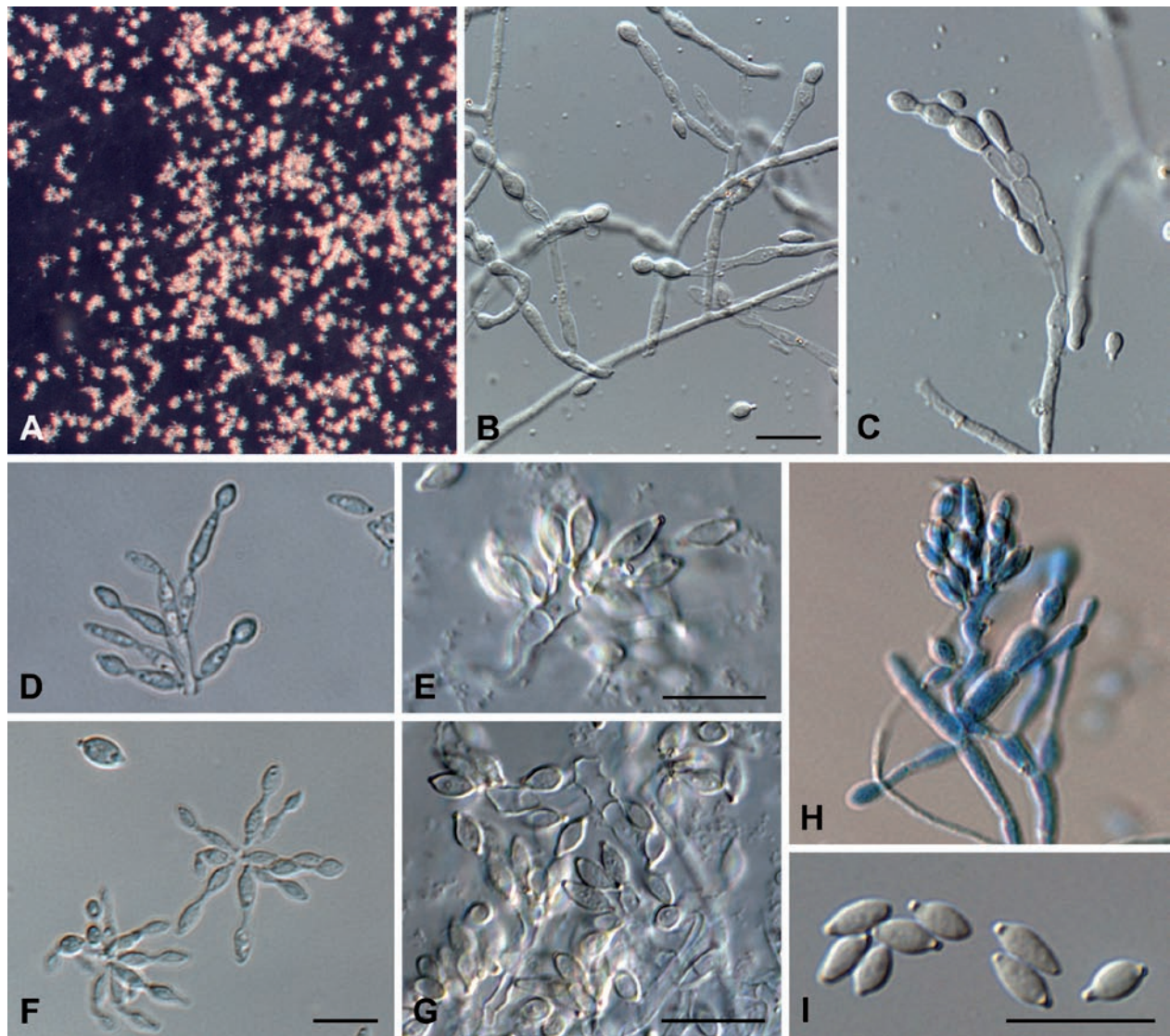


Fig. 9. *Hyalodendriella betulae* (type material). A. Conidiophores on PDA. B–C. Microconidiophores. D–H. Macroconidiophores with fascicles of conidiogenous cells. I. Conidia with darkened, thickened hila. Scale bars = 10 µm.

subcylindrical to ellipsoid, hyaline to pale brown, smooth to finely verruculose, $10\text{--}40 \times 3\text{--}5$ µm, 0(–1)-septate, giving rise to branched chains of conidia (up to 20 per chain) that are subcylindrical to ellipsoid, aseptate, $(7\text{--}8\text{--}10\text{--}14) \times (3\text{--}4\text{--}4.5)$ 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 its collection site, within a cooled incubation room.

Differs from *O. elato* conidiophores distinctly dimorphic, macroconidiophores majoribus, ad $600 \times 5\text{--}7$ µm, septis incrassates, cellulis basalibus T-formibus et conidiis leniter brevioribus et latioribus, $(6\text{--}7\text{--}8\text{--}10) \times (4\text{--}4.5\text{--}5\text{--}6)$ 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, $10\text{--}20 \times 4\text{--}6$ µm, giving rise to (1)–2–4 secondary branches, 0–1-septate, subcylindrical, $8\text{--}13\text{--}20 \times 4\text{--}5$ µm, or giving rise directly to conidiogenous cells. **Conidiogenous cells** subcylindrical to doliform, pale brown, smooth, $8\text{--}15 \times 3\text{--}4$ µm, loci somewhat protruding 1–2 µm wide, neither

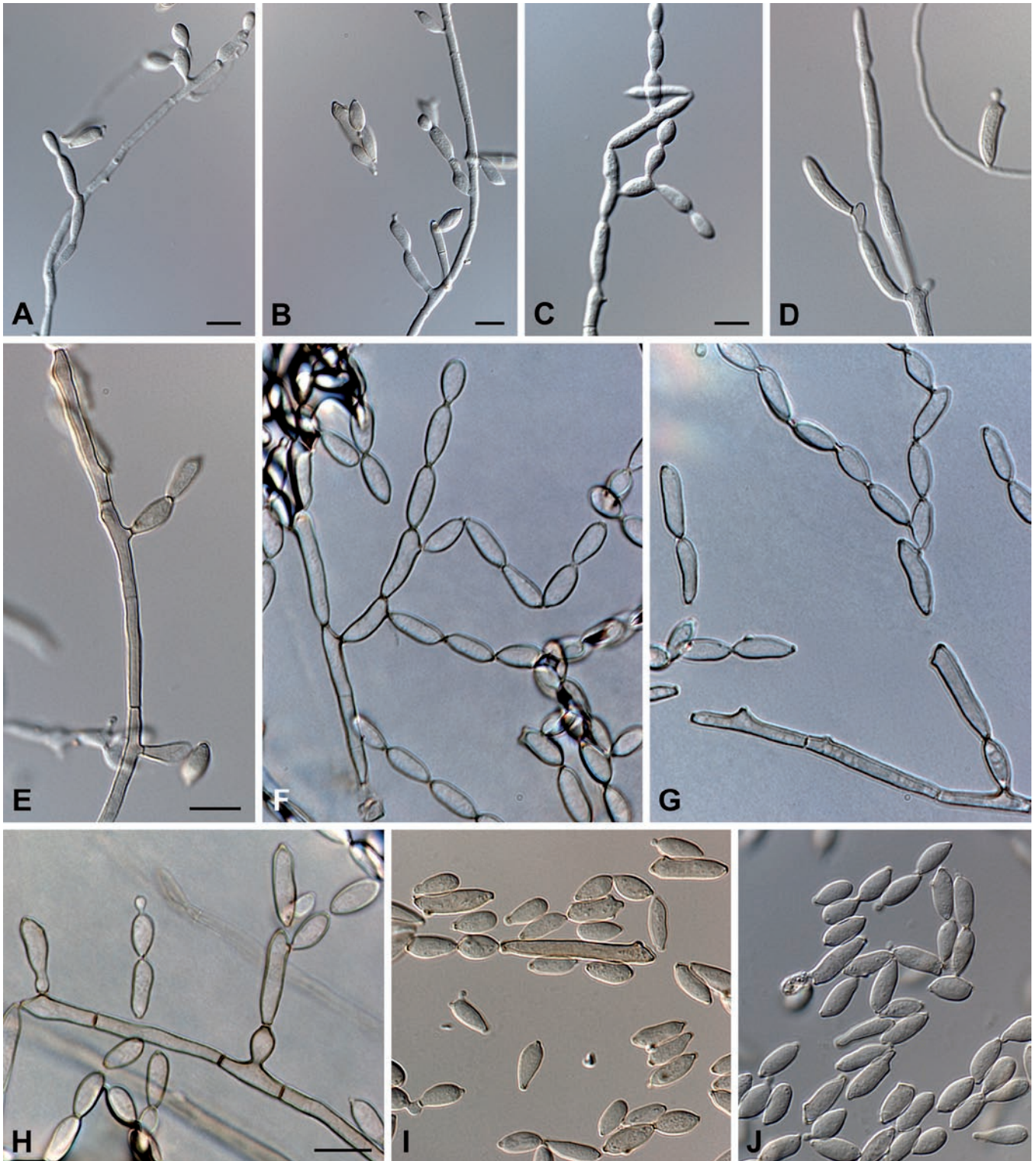


Fig. 10. *Ochrocladosporium elatum* (CBS 146.33). A–C, E. Microconidiophores. D. Macro- and microconidiophore. F–H. Macroconidiophores. I–J. Ramoconidia and conidia. Scale bars = 10 µm.

thickened, darkened, nor refractive. *Micronematous conidiophores* erect, pale brown, smooth, subcylindrical, reduced to conidiogenous cells, or up to 4-septate, $15\text{--}90 \times 2\text{--}3.5$ 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, $1\text{--}1.5$ 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 $(6\text{--})7\text{--}8\text{--}(10) \times (4\text{--})4.5\text{--}5\text{--}(6)$ µm; hila $0.5\text{--}1$ 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

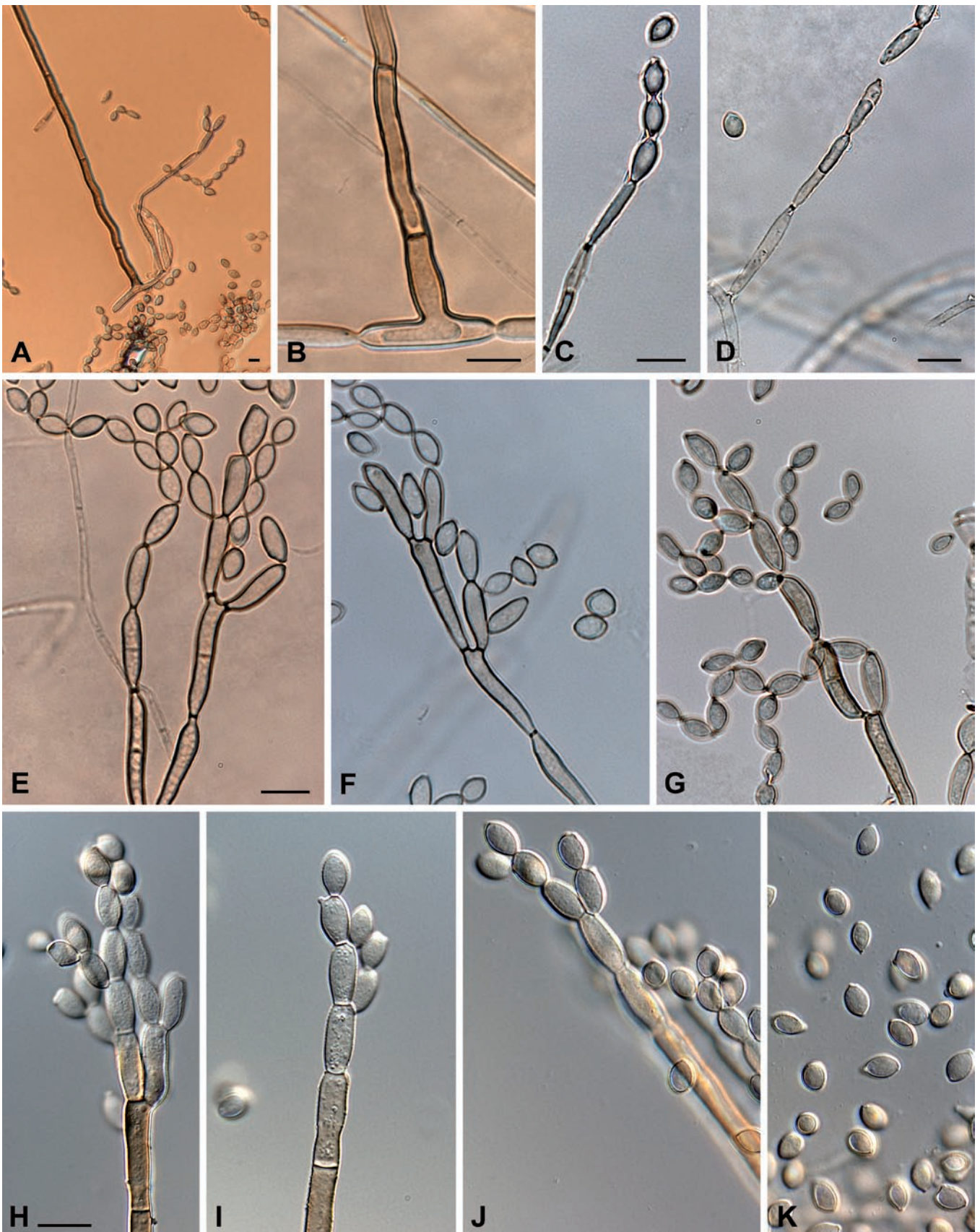


Fig. 11. *Ochrocladosporium frigidarii* (type material). A. Macro- and microconidiophores. B. Foot cell of macroconidiophore. C–D. Microconidiophore. E–J. Macroconidiophores. K. Conidia. Scale bars = 10 μm .

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) \times (4–)4.5–5(–6) μm , than those of *O. elatum* which are (7–)8–10(–14) \times (3–)4(–4.5) μm .



Fig. 12. *Rhizocladosporium argillaceum* (type material). A–E. Conidiophores with pigmented ramoconidia and hyaline conidia. F. Rhizoids forming at the foot cells of macroconidiophores. Scale bar = 10 μ m.

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 basalibus lobatis vel rhizoidibus, cellulis conidiogenis monoblasticis, determinatis, locis margine leviter incrassatis et fuscatis, non refractivis, non coronatis, ramoconidiis brunneis sed conidiis hyalinis, hiliis non incrassatis, non fuscatis-refractivis.

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 μ m wide hyphae. *Conidiophores* solitary, macronematous, erect, arising from superficial mycelium; base somewhat inflated, lobed or with rhizoids, up to 10 μ m wide; conidiophore stipe subcylindrical, straight to curved, rarely geniculate-sinuous, wall up to 1 μ m 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 \times 4–6 μm ; locus flattened, undifferentiated or very slightly darkened and thickened along the rim, not refractive, 1.5–2 μm wide. *Conidia* occurring in branched chains. *Ramoconidia* subcylindrical to narrowly ellipsoidal, straight to geniculate-sinuuous, 17–35 \times 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) \times (3.5–)4(–4.5) μm , in branched chains (–6), hyaline or subhyaline, guttulate, ellipsoidal-fusiform, with obtuse ends, or tapering to obconically subtruncate ends with hila that are inconspicuous (neither darkened nor 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 *Rhizocladosporium*. 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 acropetal chains, but the conidiophores proliferate percurrently, the conidiogenous cells are polyblastic and ramoconidia are lacking, i.e., the conidia are formed in unbranched chains. *Parapleurotheciopsis* P.M. Kirk (Kirk 1982) is very similar to *Rhizocladosporium*. The conidiophores possess a single terminal unilocal conidiogenous cell giving rise to a single ramoconidium which forms several chains of acropetal, 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* (MUCL 41089), belongs to the *Xylariales* (Fig. 2). The occasionally occurring conidiogenous cells with two loci and the aseptate conidia connect *Rhizocladosporium* with *Subramaniomyces* Varghese & V.G. Rao (Varghese & Rao 1979, Kirk 1982) in which, however, terminal ramoconidia are lacking. Furthermore, the type species, *S. fusisaprophyticus* (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).

Key to *Cladosporium* and morphologically similar genera

(bearing simple or branched acropetal chains of amero- to phragmosporous blastoconidia)

1. Conidiophores and conidia hyaline 2
1. At least conidiophores pigmented 4
2. Conidia in simple chains **Hormiactis**
2. Conidia in branched chains 3
3. Conidiogenous cells sympodial, with distinct conidiogenous loci (scars), thickened and darkened; conidia amero- to phragmosporous; plant pathogenic, leaf-spotting fungi (*Mycosphaerella* anamorphs; *Mycosphaerellaceae*) **Ramularia**
3. Terminal conidiogenous cells with denticle-like loci, giving rise to ramoconidia which form simple or branched conidial chains; lignicolous **Hyalodendron**
[Conidiophores dimorphic; mycelium, conidiophores and conidia at first hyaline, later turning pale brown; conidia in short chains, see *Hyalodendriella*]
- 4(1). Conidia distoseptate, in simple chains **Lylea**
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
5. Conidiophores well-differentiated, semimacronematous (but multilocal and/or conidiogenous loci well-differentiated) to macronematous 12
6. Conidiophores and conidia delicate, thin-walled, in long, easily disarticulating chains 7
6. Conidiophores and conidia robust, wall thickened, dark, conidial chains often seceding with difficulty 9
7. Conidiophores semimacronematous, simple to often irregularly branched; conidia delicate, narrow, 1–3 μm wide, hyaline to pale olivaceous **Polyscytalum**

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 (*Venturia*, *Venturiaceae*) **Fusicladium s. lat.** (incl. *Pseudocladosporium*)
- 9(6). Conidia aseptate, rarely 1-septate; lignicolous, 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 **Taeniolina**
11. Conidia unbranched **Taeniolella**
- 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 conidiogenous locus, 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) **Castanedaea**
15. Conidiophores little differentiated, semimacronematous, unbranched or with short lateral branchlets, base undifferentiated, without percurrent proliferations; conidiogenous cells terminal and occasionally intercalary-pleurogenous; conidia terminally and subterminally formed, 0–2-septate (lignicolous, on decorticated wood) **Websteromyces**
- 16(14). Conidiophores unbranched, with a simple terminal conidiogenous cell, non-geniculate-sinuose, subcylindrical 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; hyperparasitic on rusts **Digitopodium**
17. Conidiophores without rhizoid-digitate base; tips of the conidiogenous cells subcylindrical 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 synnematos 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, doliiform or clavate, non-denticulate; conidia at least partly globose, dark brown when mature; colonies effuse, dark; wood-inhabiting **Phaeoblastophora**

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 ramoconidia which form secondary ramoconidia and conidia	Penidiella p.p. [<i>P. strumelloidea</i>]
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, periconioid branched conidiophores formed on overwintered stem of <i>Paeonia</i> spp., unbranched cladosporioid conidiophores on leaf spots, biotrophic] (belonging to the <i>Capnodiales</i>)	Dichocladosporium
23. Penicillate apex looser, neither compact nor subglobose	24
24. Branched head 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-protuberant, flat, conspicuous, thickened and darkened, at least around the rim; conidia solitary or in short chains	Periconiella
24. Ramoconidia often present; conidiogenous cells distinct, sympodial, somewhat geniculate or subdentate; 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 <i>Asterina</i> spp.	Parapericoniella
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 (<i>Teratosphaeriaceae</i> , <i>Capnodiales</i>)	Penidiella
26. Penicillate apex always dense, metula-like, base of the conidiophores swollen or lobed, often with rhizoid hyphae; plant pathogenic [on banana] (<i>Chaetothyriales</i>)	Metulocladosporiella
27(21). Conidiophores simple or branched; septa of the conidiophores and conidia becoming thick-walled and dark; conidiogenous loci subdentate, 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)	Toxicocladosporium
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 (<i>Capnodiales</i>)	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	31
29. Mycelium smooth; conidiophores and conidia smooth or almost so, at most faintly rough-walled; conidiophores solitary, fasciculate, sporodochial to synnematus; biotrophic, usually leaf-spotting (<i>Mycosphaerella</i> anamorphs, <i>Mycosphaerellaceae</i>)	Passalora emend. (incl. <i>Mycovellosiella</i> , <i>Phaeoramularia</i> , etc.)
29. At least mycelium distinctly verruculose	30
30. Mycelium, conidiophores and conidia coarsely verruculose-verrucose; conidial shape variable, often irregular; isolated from a lichen (<i>Dirina</i>)	Verrucocladosporium
30. Mycelium verruculose; conidiophores mostly smooth, sometimes somewhat rough-walled, conidia smooth to distinctly verruculose; biotrophic, often leaf-spotting	Stenella
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	Parapleurotheciopsis

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 **Parapleurotheciopsis 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 **Heteroconium**
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*) **Cladophialophora p.p.** (e.g. *C. chaetospora*) [similar anamorphs of the *Venturiaceae*, see *Fusicladium* (incl. *Pseudocladosporium*)]
- 38(35). Conidiophores often branched; conidiogenous loci distinctly denticle-like or subdentate; conidia aseptate; 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 subdentate; 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 resiniae*)
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.) 41
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.) **Hormoconis**
- 42(38). Conidiophores simple or branched; conidiogenous cells monoblastic or occasionally polyblastic; conidiogenous loci subdentate, 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, subdentate, unthickened or slightly so, not to somewhat darkened-refractive 43
43. Conidiophores simple or branched; in culture forming abundant chlamydospores; mostly soil-borne and heat-resistant (*Teratosphaeriaceae*, *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*) **Cladophialophora**
45. Without phialidic synanamorphs; saprobic or plant pathogenic; phylogenetically distinct 46
46. Conidiophores usually unbranched (*Venturia*, *Venturiaceae*) **Fusicladium s. lat.** (incl. *Pseudocladosporium*) [similar, barely distinguishable taxa, also clustering in the *Venturiaceae*, but apart from the *Venturia* clade are tentatively referred to as *Anungitea* until this genus will be resolved by sequences of its type species]

46. Conidiophores simple to often irregularly branched; conidia delicate, narrow, 1–3 µm wide, hyaline to pale olivaceous (not belonging to the *Venturiaceae*) **Polyscytalum**

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./*Cladophialophora* Borelli). *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 *Fusicladium* 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 saprobic 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, *Metulocladosporiella* with *C. musae* as type species. *Digitopodium* U. Braun, Heuchert & K. Schub. (type species: *Cladosporium hemileiae* 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 *Paeonia* spp. The present study introduced yet several additional cladosporium-like genera, which could be distinguished based on their morphology and distinct DNA phylogeny, namely *Ochrocladosporium* (*Pleosporales*), *Rhizocladosporium* (*incertae sedis*), *Rachicladosporium*, *Toxicocladosporium* and *Verrucocladosporium* (*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 cladosporioid 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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