

Phylogeny and taxonomy of *Cladosporium*-like hyphomycetes, including *Davidiella* gen. nov., the teleomorph of *Cladosporium s. str.*

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A phylogenetic study employing sequence data from the internal transcribed spacers (ITS1, ITS2) and 5.8S gene, as well as the 18S rRNA gene of various *Cladosporium*-like hyphomycetes revealed *Cladosporium s. lat.* to be heterogeneous. The genus *Cladosporium s. str.* was shown to represent a sister clade to *Mycosphaerella s. str.*, for which the teleomorph genus *Davidiella* is proposed. The morphology, phylogeny and taxonomy of the cladosporioid fungi are discussed on the basis of this phylogeny, which consists of several clades representing *Cladosporium*-like genera. *Cladosporium* is confined to *Davidiella* (Mycosphaerellaceae) anamorphs with coronate conidiogenous loci and conidial hila. *Pseudocladosporium* is confined to anamorphs of *Caproventuria* (Venturiaceae). *Cladosporium*-like anamorphs of the *Venturia* (conidia catenate) are referred to *Fusicladium*. Human-pathogenic *Cladosporium* species belong in *Cladophialophora* (*Capronia*, Herpotrichiellaceae) and *Cladosporium fulvum* is representative of the *Mycosphaerella/Passalora* clade (Mycosphaerellaceae). *Cladosporium malorum* proved to provide the correct epithet for *Pseudocladosporium kellermanianum* (syn. *Phaeoramularia kellermaniana*, *Cladophialophora kellermaniana*) as well as *Cladosporium porophorum*. Based on differences in conidiogenesis and the structure of the conidiogenous loci, further supported by molecular data, *C. malorum* is allocated to *Alternaria*.

Taxonomic novelties: *Alternaria malorum* (Ruehle) U. Braun, Crous & Dugan, *Alternaria malorum* var. *polymorpha* Dugan, *Davidiella* Crous & U. Braun, *Davidiella tassiana* (De Not.) Crous & U. Braun, *Davidiella allii-cepae* (M. M. Jord., Maude & Burchill) Crous & U. Braun, *Davidiella dianthi* (C. C. Burt) Crous & U. Braun, *Davidiella macrospora* (Kleb.) Crous & U. Braun, *Davidiella ornithogali* (J. E. Jacques) Crous & U. Braun

The genus *Cladosporium* was described by LINK (1816) with *Cladosporium herbarum* as type species. Surveys of the generic history of *Cladosporium* were given by DE VRIES (1952) and DAVID (1997). Early descriptions of *Cladosporium* were rather vague and the delimitations from similar genera obscure (NEES 1817, CORDA 1837, 1842, FRIES 1832, 1849, SACCARDO 1886, LINDAU 1907, etc.). Since its introduction, more than five hundred taxa have been attributed to *Cladosporium*. Due to the imprecise circumscription of *Cladosporium*, it is not surprising that numerous superficially similar but unrelated hyphomycetes have been assigned to this genus, making it very heterogeneous. DE VRIES (1952) and ELLIS (1971, 1976) maintained broad concepts of *Cladosporium* and did not contribute towards a reduction of its heterogeneity, which was later discussed in detail by VON

ARX (1983), MORGAN-JONES & JACOBSEN (1988), MCKEMY & MORGAN-JONES (1990), MORGAN-JONES & MCKEMY (1990), and DAVID (1997).

There are two ways to treat anamorphic genera, viz. the maintenance of broad, unnatural circumscriptions, based on superficial morphological similarities, implying that such genera need not be naturally classified (KENDRICK 1980), or, on the other hand, the restriction of anamorph genera to characterise natural fungal groups. The second option is desirable, but in reality often only theoretical since most anamorphic taxa are only known and examined by classical morphological methods. As far as possible, anamorphs should reflect monophyletic holomorphic taxa, but this approach is only applicable satisfactorily when the connection of anamorphs and teleomorphs has been proved experimentally or by molecular studies, so that the taxa concerned become established as holomorphs (REYNOLDS 1993).

Anamorphs are increasingly important for the classification of fungi, above all in ascomycetes (SUTTON & HENNEBERT 1994). In several groups, the diversity of anamorphs is often more important for a natural classification than that of the teleomorphs (e.g. *Erysiphales*; BRAUN & TAKAMATSU 2000). In other cases, the morphological variation in the anamorphs is much greater than in the teleomorphs, e.g. in *Mycosphaerella*.

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sphaerella (CROUS et al. 2000, CROUS, KANG & BRAUN 2001), *Venturia* (RITSCHEL 2001, SCHUBERT 2001), *Botryosphaeria* (DENMAN et al. 2000), and *Calonectria* (CROUS 2002).

The present study resulted from our trying to find a suitable genus for *Cladosporium malorum*, a widespread and relatively common, mostly saprobic hyphomycete isolated from different substrata including soil, grain, fruits, and grass litter. MARASAS & BREDELL (1974) described this fungus from South Africa as *Phaeoramularia kellermaniana*, and MATSUSHIMA (1975) treated it as *C. porophorum*. BRAUN & FEILER (1995) excluded *P. kellermaniana* from *Phaeoramularia*, and assigned it to *Cladophialophora*, which contains morphologically similar human-pathogenic hyphomycetes. Later BRAUN (1998) placed it in *Pseudocladosporium*, a genus introduced for anamorphs of *Caproventuria*. HO et al. (1999) recognized *C. malorum*, *C. porophorum* and *P. kellermaniana* as conspecific. Detailed morphological investigations of cultures of *C. malorum*, above all of the conidiogenesis and the structure of the conidiogenous loci, raised doubts concerning the correct placement of this species in either *Cladosporium* or *Pseudocladosporium*. The first aim of the present paper, therefore, was to resolve the generic affinity of *C. malorum*. Previous studies employing rDNA ITS sequence data (CROUS et al. 2000, 2001) have shown *Mycosphaerella* to be monophyletic, and *Cladosporium*-like taxa to form a sister clade to the main *Mycosphaerella* clade. A further aim was, therefore, to resolve the identity of *Cladosporium s. str.* in relation to *Mycosphaerella*.

Material and methods

DNA isolation, amplification and phylogeny

The isolation protocol of CROUS et al. (2000) was used to isolate genomic DNA from fungal mycelia grown on 2 % malt extract agar (MEA; Biolab, Midrand, Johannesburg) plates. The primers ITS1 (5'-TTT CCG TAG GTG AAC CTG C-3') and ITS4 (5'-TCC TCC GCT TAT TGA TAT GC-3') (WHITE et al. 1990) were used to amplify part of the nuclear rRNA operon spanning the 3' end of the 18S (small subunit) rRNA gene, the first internal transcribed spacer (ITS1), the 5.8S rRNA gene, the second ITS (ITS2) region and the 5' end of the 28S (large subunit) of the rRNA gene. The reaction mixture contained 5 µL of diluted sample, 1 x buffer, 8 mM MgCl₂, 500 µM of each of the dNTPs, 2.5 U (Bioline) Taq polymerase and 10 pM of each primer and made up to a total volume of 25 µl with sterile water. The cycling conditions comprised denaturing at 96 °C for 5 min, followed by 30 cycles of denaturation at 96 °C (30 s), annealing 50 °C (30 s) and elongation at 72 °C (90 s). A final elongation step at 72 °C for 7 min was included. The 5' end of the 18S rRNA gene was amplified with primers NS1 (5'-GTA GTC ATA TGC TTG TCT C-3') and NS4 (5'-CTT CCG TCA ATT CCT TTA AG-3') (WHITE et al. 1990). PCR conditions were the same for this region, except for the MgCl₂ concentration, which was lowered to 1.5

µM. PCR products were separated by electrophoresis at 75 V for 1 h in a 0.8 % (w/v) agarose gel in 0.5 x TAE buffer (0.4 M Tris, 0.05 M NaAc, and 0.01 M EDTA, pH 7.85) and visualised under UV light using a GeneGenius Gel Documentation and Analysis System (Syngene, Cambridge, UK) following ethidium bromide staining.

The amplification products were purified by using a GFX PCR DNA and Gel Band Purification Kit (Amersham Pharmacia Biotech Europe Freiburg, Germany). The cycle sequencing reaction with 20 to 40 ng of purified PCR products and 10 pmol primer in a total volume of 10 µl was carried out with an ABI PRISM BigDye Terminator v3.0 Cycle Sequencing Ready Reaction Kit (PE Biosystems, Foster City, CA) containing AmpliTaq DNA Polymerase. The reaction was set up as denaturing at 94 °C for 5 min, followed by 25 cycles of 96 °C for 10 s, 55 °C for 10 s, and 60 °C for 4 min, with a final incubation of 30 s at 60 °C. The resulting products were analysed on an ABI Prism 3100 DNA Sequencer (Perkin-Elmer, Norwalk, CN).

The nucleotide sequences generated in this study were added to the ITS outgroup, *Phomopsis vaccinii* AF317578, the 18S outgroup, *Fusarium oxysporum* f. sp. *fragariae* E17083, and other sequences obtained from GenBank (<http://www.ncbi.nlm.nih.gov>). The alignments were assembled using Sequence Alignment Editor version 2.0a11 (RAMBAUT 2002). Adjustments for improvement were made by eye where necessary. Phylogenetic analyses with neighbour joining (using the uncorrected ('p') substitution model) were done using PAUP (Phylogenetic Analysis Using Parsimony) version 4.0b10 (SWOFFORD 2000). Alignment gaps were treated as missing data and all characters were unordered and of equal weight. The robustness of the trees was evaluated by 1000 bootstrap replications (HILLIS & BULL 1993). Resulting trees were printed with TreeView Version 1.6.6 (PAGE 1996).

Morphology

Slide cultures (RIDDELL 1950) were examined at 100–1000 x to record branching patterns of conidial chains and other characters. Cultures were also transferred to half strength V8 agar to enhance sporulation (STEVENS 1981). Plates were incubated under alternating cool white fluorescent light and darkness (12 h cycles) at 25 °C. Morphological observations were made from structures mounted in lactic acid after wetting with Et-OH, and photographs were taken under an Olympus BH-2 microscope with a DP-11 digital camera.

Results

Phylogenetic analysis

For ITS, approximately 530 bases were determined for each isolate (spanning the 3' end of 18S, ITS1, the 5.8S rRNA gene, ITS2 and the 5' end of the 28S rRNA gene) and added to the alignment. The manually adjusted alignment of the ITS

nucleotide sequences contained 72 taxa and 575 characters including alignment gaps (data not shown). Approximately 1075 bases of the 5' end of the SSU gene were determined for each isolate and the manually adjusted alignment of the nucleotide sequences contained 59 taxa and 1394 characters including alignment gaps (data not shown). The SSU sequence of *Mycosphaerella juvenis* (STE-U 1004) contained an insertion spanning bases 514 to 838, which was excluded from the analysis. New sequences were deposited in GenBank (Tab. 1), and the alignments in TreeBASE (S872, M1413, M1414).

The NJ tree for the ITS sequencing data (Fig. 1) contains isolates from five main groups (Herpotrichiellaceae, Amorphythaceae, Mycosphaerellaceae, Pleosporaceae and Venturiaceae). The Herpotrichiellaceae formed a well-supported clade (100 % bootstrap support) comprising species of *Cladophialophora* and *Phialophora*. The Amorphythaceae clade was also well-supported with a bootstrap support value of 100 % and contained isolates of *Amorphytheca resiniae* (anamorph *Sorocybe resiniae*) and '*Cladosporium*' *breviramosum*. The Herpotrichiellaceae and Amorphythaceae clades were grouped together with a bootstrap support value of 75 %. The Mycosphaerellaceae consisted of isolates of *Mycosphaerella* and a strongly supported clade (100 %) of *Davidiella* containing *Cladosporium* anamorphs. *Mycosphaerella* isolates were represented in two separate groups, one of which consisted of '*Cladosporium*' *staurophorum* AF393723 and '*Phaeoramularia hachijoensis*' (STE-U 5121) (88 % bootstrap support), and the other well-supported (100 %) clade contained *Passalora arachidicola* AF297224, isolates of *P. fulva*, *P. henningsii* AF284389, *P. dissiliens* AF222835, *P. vaginiae* AF222832 and *P. bellynckii* AF222831. The clade for the Pleosporaceae was also well-supported (100 %) and contained isolates of *Alternaria malorum* and additional species of *Alternaria* and *Lewia*. An isolate of '*Mycosphaerella iridis*' (CBS 281.49) grouped with 100 % bootstrap support outside the Pleosporaceae clade. The Venturiaceae clade consisted of '*Phaeoramularia hachijoensis*' (STE-U 3679) (60 % bootstrap support) and a well-supported (100 %) clade containing *Fusicladium convolvulorum* (STE-U 3884), *Pseudocladosporium hachijoense* (STE-U 5391) and species of *Venturia* as well as isolates of *Fusicladium effusum*. *Anungitopsis amoena* (CBS 254.95) AF393682 grouped with 81 % bootstrap support outside the Venturiaceae clade.

The NJ tree for the SSU sequencing data (Fig. 2) contained isolates from the Mycosphaerellaceae, Pleosporaceae, Venturiaceae, as well as Dothioraceae, Dothideaceae, Botryosphaeriaceae, Leptosphaeriaceae and Pleosporales *inc. sed.* The Mycosphaerellaceae isolates consisted of isolates of *Mycosphaerella* and a strongly supported clade (90 %) of *Davidiella* containing *Cladosporium* spp. and a single isolate of *Sphaerulina polyspora* (STE-U 4301). *Mycosphaerella* isolates were present in a poorly supported (55 %) group, and contained, amongst others, '*Cladophialophora hachijoensis*' (STE-U 5121), *Passalora fulva* (STE-U 3688), '*Cladosporium*' *staurophorum* (STE-U 3687) and *Mycosphaerella* spp.

The Dothideaceae clade was well-supported (100 %) and was grouped inside a clade with a 98 % bootstrap support value that contained a single isolate of the 'Dothioraceae'. The Venturiaceae clade (100 % bootstrap support) consisted of *Pseudocladosporium hachijoense* (STE-U 5391), *Fusicladium convolvulorum* (STE-U 3884), as well as isolates of *Fusicladium effusum*. *Anungitopsis amoena* (CBS 254.95) grouped with 99 % bootstrap support outside the Venturiaceae clade. The Pleosporaceae clade consisted of *Pleospora betae* U43465 (100 % bootstrap support) and a well-supported (100 %) clade containing *Pleospora herbarum* (U43458), isolates of *Alternaria malorum* and species of *Alternaria* and *Lewia*. The Paraphaeosphaeriaceae clade was well supported (100 %), and was grouped inside a clade that also contained a single isolate of the Leptosphaeriaceae (100 % bootstrap support).

Morphology

Cladosporium malorum (Pleosporaceae) clade

Strains of *Cladosporium malorum*, *C. porophorum* and *Phaeoramularia kellermaniana* are morphologically identical. Conidiogenous cells of *C. malorum* possess minute, but rather conspicuous pores (Fig. 3). Conidia, therefore, can be classified as poroconidia, the product of tretic conidiogenesis. Due to the distinctly tretic nature of the conidiogenous loci, *C. malorum* has to be excluded from *Cladosporium*, *Cladophialophora* as well as *Pseudocladosporium*. Its conidiogenesis is similar to that of the genus *Alternaria*, and other species in the Pleosporaceae/Pleosporales. Furthermore, the formation of alternarioid conidia (Figs. 9–10) in the new variety of *C. malorum* described below is also reminiscent of *Alternaria* (teleomorph: *Lewia*) and allied genera with tretic conidiogenesis and catenulate conidia. Its unique mode of conidiogenesis, as well as its DNA phylogeny, support assignment of *C. malorum* to *Alternaria*:

Alternaria malorum (Ruehle) U. Braun, Crous & Dugan, **comb. nov.**

Basionym: *Cladosporium malorum* Ruehle, Phytopathology 21: 1146, 1931.

Synonyms: *Phaeoramularia kellermaniana* Marasas & Bredell, Botthalia 11: 217, 1974. *Cladophialophora kellermaniana* (Marasas & Bredell) U. Braun & Feiler, Microbiol. Res. 150: 83, 1995. *Pseudocladosporium kellermaninum* (Marasas & Bredell) U. Braun, A Monogr. *Cercosporella*, *Ramularia* and allied gen. 2: 393, 1998. *Cladosporium porophorum* Matsush., *Icones Microf. Matsushima Lect.*: 36, 1975.

Colonies effuse, floccose, velvety to woolly, olivaceous-grey to deep olivaceous-green, reverse olivaceous to blackish olive. Hyphae of two types: sterile hyphae branched, sometimes forming strands, occasionally anastomosing, smooth to faintly rough-walled, septate, occasionally constricted at the septa, subhyaline to pale olivaceous, slender, usually 1–4 μm wide; fertile hyphae with conidiophores (Fig. 3) sometimes darker, brown, to 7 μm wide, hyphal cells in old cultures sometimes swollen, becoming thick-walled, darker brown, subglobose,

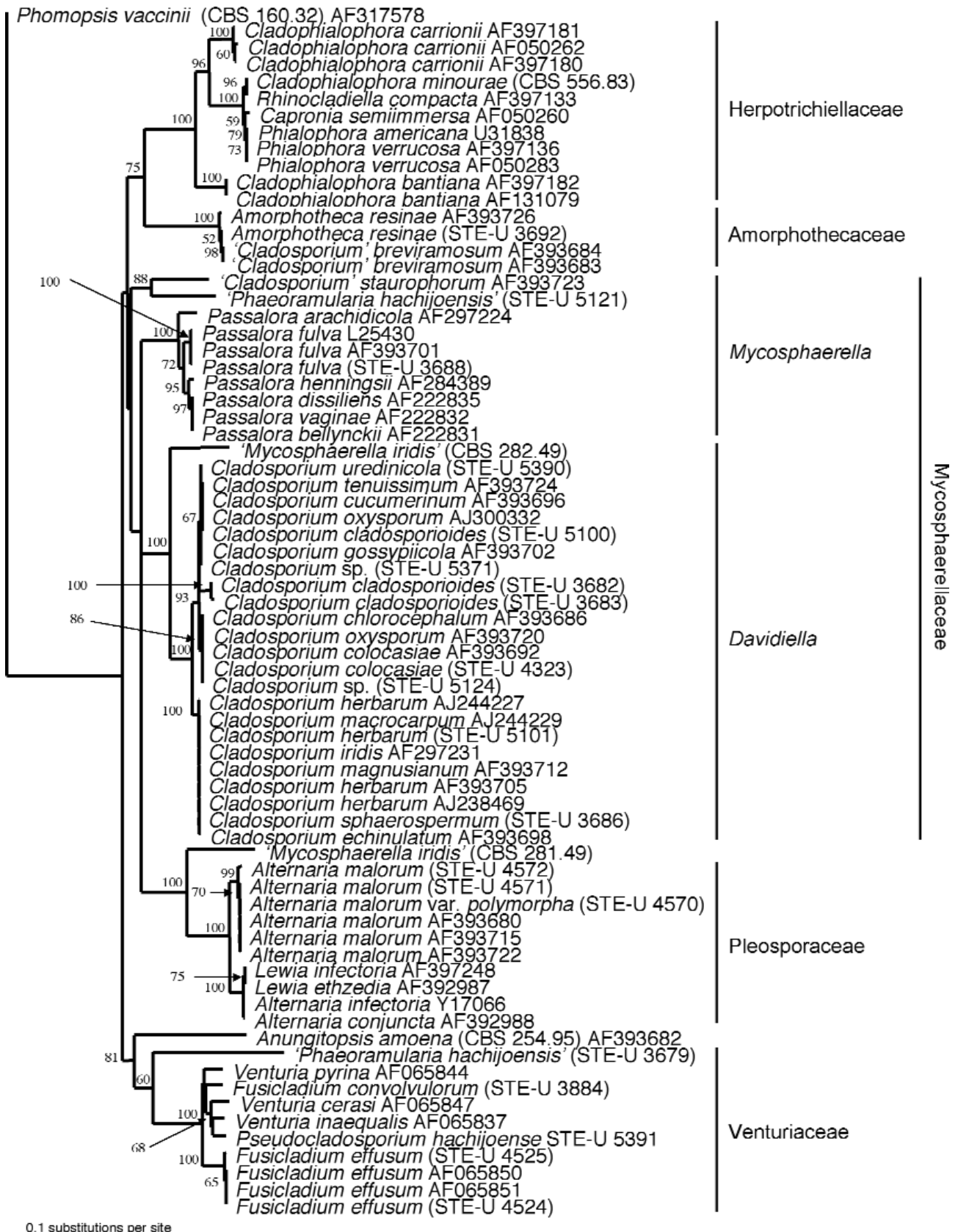


Fig. 1. Phylogram of neighbour joining tree obtained from ITS sequencing data using the uncorrected 'p' model of substitution. Bootstrap support values from 1000 replicates are shown at nodes. Due to the fact that not all nodes are clearly visible, some bootstrap values are not shown. The GenBank sequence *Phomopsis vaccinii* AF317578 was used as outgroup.

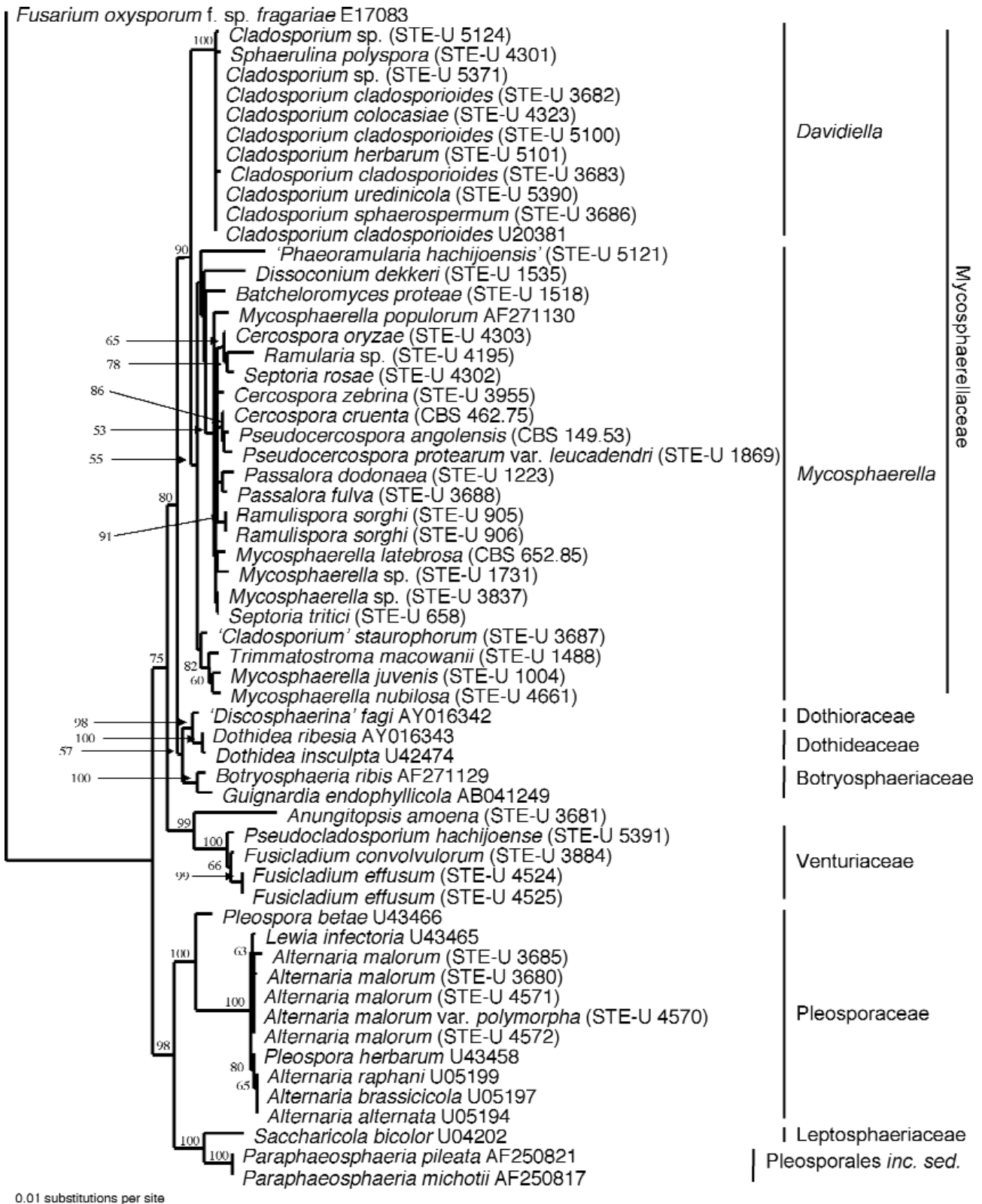


Fig. 2. Phylogram of neighbor joining tree obtained from small subunit rRNA gene sequencing data using the uncorrected 'p' model of substitution. Bootstrap support values from 1000 replicates are shown at nodes. Due to the fact that not all nodes are clearly visible, some bootstrap values are not shown. The GenBank sequence *Fusarium oxysporum* f.sp.*fragariae* E17083 was used as outgroup.

intercalary or terminal, chlamydospore-like (Fig. 4). Conidiophores pleurogenous and terminal, erect, straight, subcylindrical or somewhat attenuated towards the apex, slightly geniculate-sinuous, unbranched or rarely branched, 5–50 x 2–5(7) μm , 0–2(3)-septate, pale olivaceous to olivaceous-brown, thin-walled, smooth or almost so; conidiogenous cells integrated, terminal or conidiophores reduced to conidiogenous cells, 5–15 μm long, monotretic, determinate or polytretic, sympodial, usually with 1–2 conspicuous loci, 0.5–1.5 μm wide, unthickened, with minute central pori, 0.5–1 μm wide, usually surrounded by a narrow darker margin, dark brown. *Conidia* in long acropetal chains (Fig. 5), simple or branched, narrowly ellipsoid-ovoid, cylindrical or fusiform, aseptate, 6–14(17) x 2–4 μm , ramoconidia 0–2(3)-septate, very rarely to 6-septate, to 35 x 7 μm , subhyaline, pale olivaceous to olivaceous-brown, thin-walled, smooth, apex and base rounded to truncate, with 1–3(4) inconspicuous or conspicuous distal hila, 0.5–1 μm diam, unthickened, composed of a minute central pore, 0.3–0.5 μm wide, and a narrow darker margin or margin sometimes lacking.

Substrata and distribution: Generally saprobic, isolated from soil, grass litter (*Bromus inermis*, *Hordeum* spp., *Triticum aestivum*), stored grains, Bing cherry fruit, fruits of *Malus domestica*, *Prunus persica*, and an old polypore on *Picea* sp., Canada, Lebanon, Libya, Pakistan, South Africa, Syria, Turkey, and the USA. Pathogenic in ripe apples (RUEHLE 1931) and ripe cherries (DUGAN & ROBERTS 1994). Once recorded as the principal fungal contaminant in market wheat in Washington state, USA (SCHNELHARDT & HEALD 1936).

Material examined: CANADA, Saskatchewan, Matador, from grass litter, 27 May 1968, G. C. Bhatt 255 (IMI 144487, ATCC 38025 as *C. malorum*); from (?) soil, 18 Sept. 1973, H. A. H. Wallace (IMI 179345, as *P. kellermaniana*). Alberta, from *Bromus inermis*, 1994, R. J. Howad 397 (IMI 360655, HAL, as *P. malorum*). – PAKISTAN, Karachi, from stored grains, 5 Jan. 1967, S. S. Hussain (IMI 124270, as *P. kellermaniana*). – LEBANON, from soil, July 1987, F. Seigle-Murandi (ATCC 200938, CBS 900.87, as *C. porophorum*). – LIBYA, from *Prunus persica*, April 1975, Casay (IMI 194863, as *P. kellermaniana*). – SOUTH AFRICA, Western Cape Province, Kogvat, Calvinia, from wheat stubble, Feb. 1972, W. F. O. Marasas OP-76 (PREM 44703, holotype of *P. kellermaniana*, IMI 165252, isotype; ATCC 28332 and CBS 266.75 ex-type cultures). – SYRIA, from agricultural soil, Febr. 1980, M. I. A. Abdel-Kader (ATCC 200939, CBS 173.80, as *C. porophorum*). – TURKEY, Manisa, from *Hordeum* sp., 16 June 1971, Maksu & Selçuc (IMI 159198, as *P. kellermaniana*). – USA, New Mexico, Red River, from a polypore on *Picea* sp., 4 Sept. 1996, D. Wicklow (IMI 386094, as *P. malorum*). Washington State, from Bing cherry fruit, June 1992, F. Dugan (ATCC 96020, as *C. malorum*); from fruits of *Malus domestica*, F. D. Heald (ATCC 36953, authentic for *C. malorum*).

Alternaria malorum var. *polymorpha* Dugan, var. nov.

Figs. 3–12

Differt a var. *malorum* conidiis latioribus, ca 3.5–6 μm latis, atrioribus, leviter crassitunicatis, interdum longitudine septatis, raro alternarioidibus intermixtis.

Etymology: Referring to its variable conidial shape.

Typus: USA, Washington State, Roza Canal near Prosser, isolated from dormant buds (overwintered) of *Vitis vinifera*, Mar. 2001, F. M. Dugan. Holotype WSP 70286; STE-U 4570, FMD V5#19, CBS 112048, ex-type cultures).

Cladosporium s. str. (*Mycosphaerellaceae*) clade

The genus *Cladosporium* s. str. (incl. *Heterosporium*) is distinguished from other *Mycosphaerella* anamorphs by its unique scars and conidial hila. DAVID (1997) examined *Cladosporium* and *Heterosporium* by means of scanning electron microscopy and demonstrated both genera to have coronate conidiogenous loci (scars) and conidial hila of the ‘*Cladosporium*-type’, e.g. protuberant with a central dome surrounded by a raised rim. Based on these results, DAVID (1997) placed *Heterosporium* in *Cladosporium* as *Cladosporium* subgen. *Heterosporium*. He proposed to confine *Cladosporium* to saprobic and phytopathogenic (rarely mycoparasitic) hyphomycetes with coronate scars and hila. The peculiar and separate phylogenetic position of *Cladosporium* in relation to *Mycosphaerella* was already shown in previous studies (CROUS et al. 2000, 2001). This distant position is further supported by the ITS as well as 18S data sets derived in the present study (Figs. 1–2), where the *Cladosporium* clade clustered separately from *Mycosphaerella*. Based on the unique ‘*Cladosporium*-type’ scars and conidial hila, as well as distinct phylogeny according to ITS and 18S sequences, we therefore propose a new teleomorphic genus for those ‘*Mycosphaerella*’ species with *Cladosporium* anamorphs sensu DAVID (1997).

Davidiella Crous & U. Braun, gen. nov.

Mycosphaerella sect. *Tassiana* M. E. Barr, Contr. Univ. Michigan Herb. 9: 601, 1972.

Ascomata ut in *Mycosphaerella* sect. *Tassiana* (asci non numerosi, saccati; ascosporae obovatae, utrinque rotundatae). Differt a *Mycosphaerella* statu conidiali, i.e. *Cladosporium* sensu DAVID (1997).

Etymology: Named in honour of the British mycologist, John C. David, who has significantly contributed to our knowledge of this group of fungi.

Typus: *Davidiella tassiana* (De Not.) Crous & U. Braun 2003; status anamorphosis *Cladosporium herbarum*.

Ascomata morphologically identical to those of *Mycosphaerella* (sect. *Tassiana*), but distinct in having *Cladosporium* anamorphs sensu DAVID (1997).

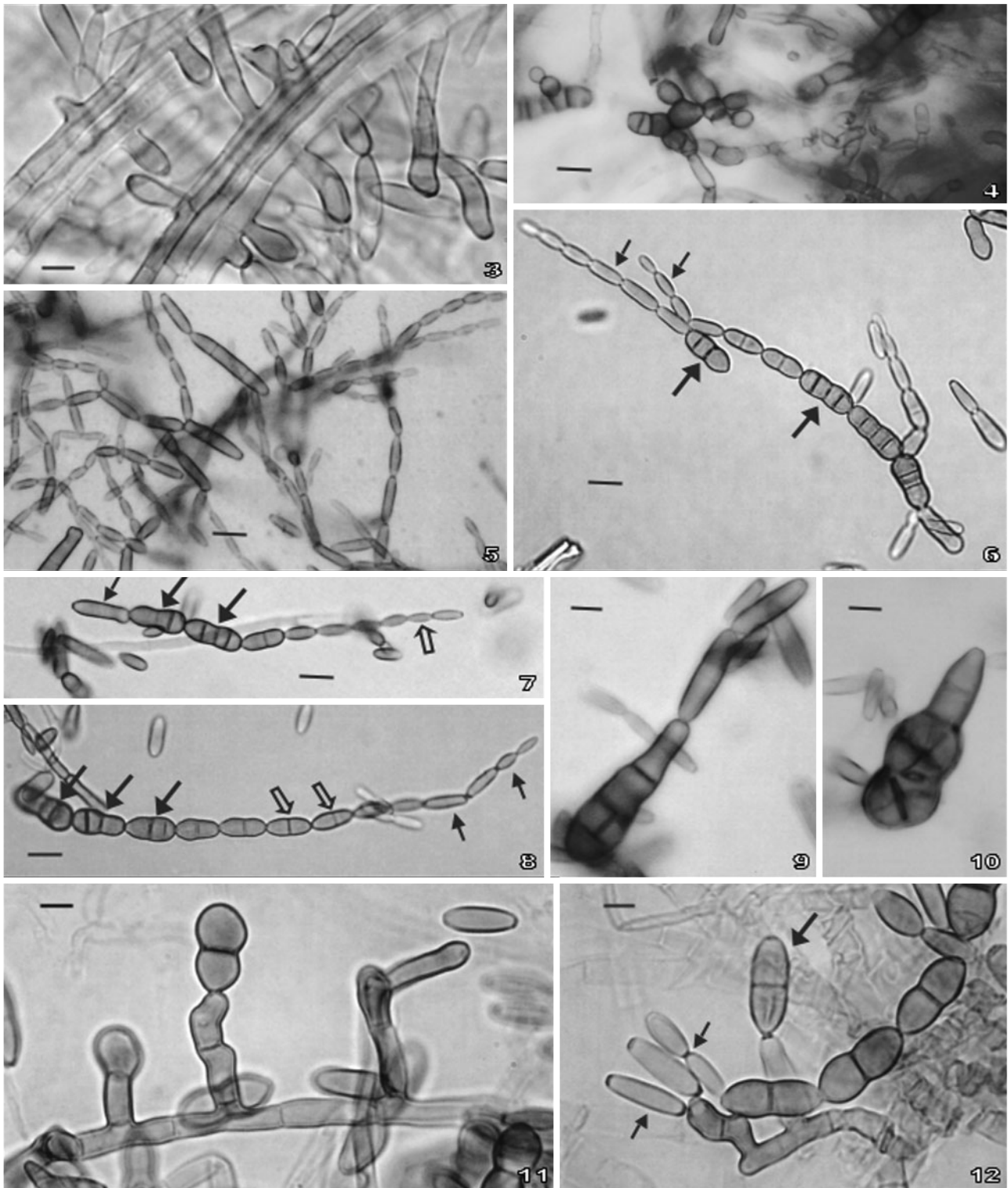
Davidiella tassiana (De Not.) Crous & U. Braun, comb. nov.

Basionym: *Sphaerella tassiana* De Not., Sferiacei Italici 1: 87, 1863.

Mycosphaerella tassiana (De Not.) Johanson, Öfvers. Förh. Kongl. Svenska Vetensk.-Akad. 9: 167, 1884.

Anamorph: *Cladosporium herbarum* (Pers.: Fr.) Link, Ges. Naturf. Freunde Berlin Mag. Neuesten Entdeck. Gesammten Naturk. 7: 37, 1816.

Basionym: *Dematium herbarum* Pers., Annl. Bot. (Usteri), 11 Stück: 32, 1794: Fr., Syst. Mycol. 3: 370, 1832.



Figs. 3–12. *Alternaria malorum* var. *polymorpha*. **Fig. 3.** Conidiophores borne on aggregated hyphae. **Fig. 4.** Chlamydo-spore-like cells. **Fig. 5.** Chains of conidia characteristic of the species. **Fig. 6.** Conidial chains containing conidia characteristic of the species (small arrows) and conidia characteristic of var. *polymorpha* (large arrows). **Fig. 7.** A chain containing conidia typical of the species (open arrow) and typical of the new variety (large arrows), subtended by a ramoconidium (small arrow) typical of the species. **Fig. 8.** A chain in which basal conidia typical of var. *polymorpha* (large arrows) are connected to distal conidia typical of the species (small arrows) by conidia intermediate in morphology (open arrows). **Fig. 9.** A typical *Alternaria* conidium, basal to two conidia typical of *A. malorum*. **Fig. 10.** An *Alternaria* conidium irregular in outline. **Fig. 11.** A 1-septate conidium typical of the var. *polymorpha*, borne on a conidiophore typical of the species. **Fig. 12.** Small aseptate conidia typical of the species (small arrows) and a larger, 1-septate conidium typical of var. *polymorpha* (large arrow) borne on a single, branched conidiophore. Bars: Figs. 3, 9–12 = 5 μ m, Figs. 4–8 = 10 μ m.

Davidiella allii-cepae (M. M. Jord., Maude & Burchill) Crous & U. Braun, **comb. nov.**

Basionym: *Mycosphaerella allii-cepae* M. M. Jord., Maude & Burchill, Trans. Br. mycol. Soc. 86: 392, 1986.

Anamorph: *Cladosporium allii-cepae* (Ranoj.) M. B. Ellis, More Dermat. Hyphom.: 337, 1976.

Basionym: *Heterosporium allii-cepae* Ranoj., Annls Mycol. 8: 399, 1910.

Davidiella dianthi (C. C. Burt) Crous & U. Braun, **comb. nov.**

Basionym: *Didymellina dianthi* C. C. Burt, Trans. Br. mycol. Soc. 20: 214, 1936.

Mycosphaerella dianthi (C. C. Burt) Jørst., Meld. Statens Plantepatol. Inst. 1: 17, 1945.

Anamorph: *Cladosporium echinulatum* (Berk.) G. A. de Vries, Contr. Gen. *Cladosporium*: 49, 1952.

Basionym: *Helminthosporium echinulatum* Berk., Gdnrs' Chron. 1870: 382, 1870.

Davidiella macrospora (Kleb.) Crous & U. Braun, **comb. nov.**

Basionym: *Didymellina macrospora* Kleb., Ber. dt. bot. Ges. 42: 60, 1924 (1925).

Mycosphaerella macrospora (Kleb.) Jørst., Meld. Statens. Plantepatol. Inst. 1: 20, 1945.

Anamorph: *Cladosporium iridis* (Fautrey & Roum.) G. A. de Vries, Contr. Gen. *Cladosporium*: 49, 1952.

Basionym: *Scolecotrichum iridis* Fautrey & Roum., Revue Mycol. 13: 82, 1891.

Davidiella ornithogali (J. E. Jacques) Crous & U. Braun, **comb. nov.**

Basionym: *Didymellina ornithogali* J.E. Jacques, Contr. Inst. Bot. Univ. Montréal 39: 35, 1941.

Anamorph: *Cladosporium ornithogali* (Klotzsch ex Cooke) G. A. de Vries, Contr. Gen. *Cladosporium*: 491, 1952.

Basionym: *Heterosporium ornithogali* Klotzsch ex Cooke, Grevillea 5: 123, 1877.

The link between the teleomorph and anamorph has not been clearly established for *Davidiella ornithogali* and *Cladosporium ornithogali*, though the discussion provided by DAVID (1997) suggests that DE VRIES (1952) was correct in stating the teleomorph to be representative of 'Mycosphaerella'. Another species that needs clarification is *Didymellina intermedia*, and its presumed anamorph *Cladosporium allii* (David 1997). Fresh collections are required to resolve this possible anamorph-teleomorph association.

When the genus *Mycosphaerella* was treated by VON ARX (1949), he divided it into three sections, including *Didymellina* (with *Cladosporium* and *Heterosporium* spp.), for which he chose *Mycosphaerella tassiana* as type. As pointed out by DAVID (1997), this was erroneous as *Didymellina* was formerly described at the generic level by VON HÖHNEL (1918), having *Dothidea iridis* (syn. *Didymellina iridis*) as type, with *Sphae-*

rella iridis (syn. *Mycosphaerella iridis*) as proposed synonyms. The literature is filled with erroneous links between *C. iridis* and a fungus initially identified as *Mycosphaerella iridis*, but later described as *M. macrospora*. This confusing situation is explained by DAVID (1997). We have examined the type specimen of *Dothidea iridis* in PC, which is a species of *Mycosphaerella* and not of *Dothidea*; it is morphologically distinct from *M. iridis* (CBS 281.49, herb. CBS 4933; CBS 282.49, herb. CBS 4907). Further, no link between *Dothidea iridis* and a *Cladosporium* has ever been established. The fungus present on the two specimens from CBS represents *M. iridis*. The cultures, however, represent two different fungi, neither of which appear to be *M. iridis*. Further studies are therefore presently underway to resolve the *Mycosphaerella* spp. occurring on *Iris*. In conclusion, we were unable to find any evidence linking a *Cladosporium* state to either *Mycosphaerella iridis* or *Dothidea iridis*, and have therefore decided not to choose the name *Didymellina* as teleomorph genus for *Cladosporium*.

Discussion

This study has provided further evidence for the separation of *Cladosporium s. str.* anamorphs from the main *Mycosphaerella* clade, and has provided the basis for the introduction of a new teleomorph genus, *Davidiella*, for this group of fungi. Furthermore, it has also shown that several *Cladosporium*-like fungi are clearly not congeneric with *Cladosporium s. str.*, and that the relatively minor differences in the scars and conidial loci, are supportive of their different phylogenetic affinities. Similarly, *C. malorum* appears to be best assigned to *Alternaria* based on its ITS and SSU phylogenetic placement, and such placement is also supported by its unique mode of conidiogenesis. As in other hyphomycetes in this complex (CROUS, KANG & BRAUN 2001), conidial septation, and the presence of oblique septa, are of less importance at the generic level. HÖLLER, GLOER & WICKLOW (2002) identified various metabolites produced by an undetermined *Cladosporium*-like hyphomycete, which was isolated from a resupinate polypore in the USA. These metabolites, which included altersolanol and macrosporin, are commonly produced by *Alternaria* spp. A culture derived from this isolate, and which was deposited at IMI, was examined by U. Braun, and identified as *C. malorum*. The taxonomic decision to place this species in *Alternaria* is thus further supported by these metabolite data from HÖLLER, GLOER & WICKLOW (2002).

The phylograms derived in the present study delineate several clades (families) in which *Cladosporium*-like taxa are presently accommodated. These are discussed below:

Herpotrichiellaceae* and *Venturiaceae

Of particular interest in the *Herpotrichiellaceae* are those species pathogenic to humans, which are presently placed in *Cladophialophora* (Fig. 1). Human-pathogenic cladosporioid

hyphomycetes have previously been placed in *Cladosporium s. lat.* and confused with true *Cladosporium* species. There is a large number of publications dealing with all aspects of these fungi, 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, GERRITS VAN DEN ENDE & DE HOOG 1999, DE HOOG et al. 2000). It has been clearly demonstrated in all phylogenetic analyses that the truly human-pathogenic *Cladosporium* species are *Capronia* anamorphs belonging to the *Herpotrichiellaceae*, and all species concerned have been placed in *Cladophialophora*. The morphological distinction between *Cladophialophora* and *Cladosporium s. str.* has also been demonstrated by several authors (BRAUN & FEILER 1995, BRAUN 1998, DE HOOG et al. 2000). *Cladophialophora* species are characterised by truncate, unthickened, barely darkened, often somewhat denticle-like conidiogenous loci, whereas *Cladosporium* loci are 'coronate' (DAVID 1997), e.g. protuberant and with raised periclinal rims that surround a central convex dome. True *Cladosporium* species also differ from *Cladophialophora* physiologically in their ability to liquefy gelatine (DE HOOG et al. 1995).

The morphological distinction between *Cladophialophora* and *Pseudocladosporium* is rather difficult, but the two genera are ecologically and phylogenetically clearly distinct, viz. species of *Pseudocladosporium* are saprobic fungi, usually isolated from leaf litter, and anamorphs of *Caproventuria* (*Venturiaceae*), whereas *Cladophialophora* spp. are true human-pathogenic fungi connected with *Capronia* (*Herpotrichiellaceae*).

Anamorphs of the *Venturiaceae* have recently been monographed by RITSCHEL (2001) and SCHUBERT (2001), including molecular examinations (rDNA ITS) of numerous taxa in which *Venturia* species and their anamorphs formed a single monophyletic clade. Some *Fusicladium* species with catenate conidia have often been confused with *Cladosporium*, e.g., *C. carpophilum* (syn. *Fusicladium carpophilum*), *C. cerasi* (syn. *F. cerasi*) and *C. caryigenum* (syn. *F. effusum*). As already discussed by MORGAN-JONES & JACOBSEN (1988), these anamorphs should rather be referred to *Fusicladium* (*Venturia* anamorphs), a conclusion supported by the present molecular data. Furthermore, the structures of the conidiogenous loci in *Fusicladium* species with solitary as well as catenate conidia are very uniform, and quite distinct from those of *Cladosporium s. str.* In *Fusicladium* the conidiogenous loci are more or less denticle-like, apically truncate to slightly convex, unthickened or almost so, and not or only slightly darkened. These loci, therefore, more closely resemble those of some saprobic genera, like *Anungitea* and *Pseudocladosporium*. The form genus *Fusicladium* is also associated with various other genera of the *Venturiaceae*, viz. *Acantharia*, *Apiosporina* and *Venturia*.

Several authors have dealt with *Phaeoramularia hachijoensis* (MATSUSHIMA 1975), but all reassessments of this species were based on non-type material, since type material and strains were not available and are possibly not extant any lon-

ger. Cultures assigned to this species are undoubtedly heterogeneous. BRAUN & FEILER (1995) considered CBS 462.82 and ATCC 96019 to be representative of *P. hachijoensis* and placed the species in *Cladophialophora*. DUGAN, ROBERTS & HANLIN (1995) found the teleomorph of ATCC 96019, and described it as *Capronia hystricoides*. A German strain was similar, but differed by having paler structures, finer conidia and a distinct habit of the colonies (BRAUN & FEILER 1995). UNTEREINER & NAVEAU (1999) provided 28S rDNA sequence data to support the fact that the BBA strain was not conspecific with *P. hachijoensis* sensu BRAUN & FEILER (1995) and DUGAN et al. (1995), but even quite unrelated. Of the three isolates of *P. hachijoensis* studied, it appears that each isolate represents a different species in distinct genera. Hence, the application of the name *P. hachijoensis* must be based on an interpretation. We propose to follow the treatment and application of this name by DUGAN, ROBERTS & HANLIN (1995) as anamorph of *Capronia hystricoides* (Syn. *Caproventuria hystricoides*). UNTEREINER (1997) reduced the latter species to synonymy with *Capronia hanliniana* (anamorph *Cladophialophora brevicatenata*), assigned it to the *Venturiaceae* and proposed the combination *Venturia hanliniana*. In the present study, the isolate of *P. hachijoensis* used by DUGAN, ROBERTS & HANLIN (1995) (ATCC 96019 = STE-U 5391) also clustered in *Venturia*, thus supporting the conclusion by UNTEREINER (1997). BRAUN (1998) recognised UNTEREINER'S (1997) exclusion of this species from *Capronia*. He discussed some distinctive features supporting *C. hanliniana* and *C. hystricoides*, which are well-distinguished by their anamorphs, and also from true *Venturia* species. BRAUN (1998) therefore introduced the new genus *Caproventuria* for the teleomorphs, and *Pseudocladosporium* for the anamorphs. In the present phylogram, it can be seen that *Caproventuria/Pseudocladosporium* is unrelated to the *Herpotrichiellaceae* (*Capronia/Cladophialophora*), but rather clusters within *Venturiaceae* (Figs. 1–2). The genus *Pseudocladosporium* is tentatively maintained and confined to anamorphs of *Caproventuria*, awaiting the treatment of more taxa.

Amorphothecaceae

Sorocybe resinae (syn.: *Hormoconis resinae*; teleomorph *Amorphotheca resinae*) belongs to a group of hyphomycetes characterised by having more or less distinctly denticulate, pigmented conidiogenous cells and 0–2-septate, pigmented conidia formed in long, often branched chains. This assemblage of anamorphs can be considered as a counterpart to the *Dactylaria* (DE HOOG 1985) complex distinguished by catenate conidia. The delimitations of these genera and some allied ones, e.g., *Anungitea*, *Pleurotheciopsis* and *Polyscytalum*, is difficult and partly vague, since morphology and conidiogenesis are very similar to each other. It is still unclear in this complex which characteristics are appropriate for a generic delimitation. PARTRIDGE & MORGAN-JONES (2002) reduced *Hormoconis* (VON ARX 1973) to synonymy with *Sorocybe*.

They considered *H. resinae* to be the mononematous form of *S. resinae*, and noted that the connection between *Amorphotheca* (PARBERY 1969) as teleomorph and *S. resinae* as anamorph, remains to be resolved. *Sorocybe resinae*, the type species of this genus, differs from species of allied genera in having rather inconspicuous, not distinctly denticle-like conidiogenous loci (DE VRIES 1952; PARTRIDGE & MORGAN-JONES 2002). The clustering of two isolates of '*Cladosporium*' *breviramosum* (AF393683, 393684) in the *Amorphothecaceae* is unusual, and the original strains will have to be re-examined to resolve their identity and position.

Incertae sedis

The status of *Anungitopsis amoena* (syn. *Cladosporium amoenum*) (HO et al. 1999) is unclear, and the correct placement of this species in *Anungitopsis* is not certain. The type species of the latter genus and the other species assigned to it have long rachis-like conidiogenous cells with numerous, dense, rather inconspicuous conidiogenous loci. The loci in *A. amoena* are less numerous, scattered and more distinct, partly almost denticle-like.

Pleosporaceae

This study has shown that *Cladosporium malorum* belongs to *Alternaria* (Figs. 1–2). Conidiogenesis and the structure of the conidiogenous loci of this fungus were undoubtedly misinterpreted by all previous mycologists, who placed this fungus in *Cladosporium*, *Cladophialophora*, *Phaeoramularia* or *Pseudocladosporium*, suggesting that the conidiogenesis was holoblastic. These treatments were undoubtedly influenced by the cladosporioid habit of this fungus, e.g., pigmented, 0–2-septate conidia formed in long acropetal chains (Fig. 5). However, the conidiogenous cells possess minute, but conspicuous pores, and should rather be regarded as poroconidia. Within the genus *Alternaria*, however, *A. malorum* is not totally unique in having largely aseptate, cylindrical conidia, as this is also found in other species of *Alternaria*, e.g. *A. cetera* (SIMMONS 1996).

Alternaria malorum var. *polymorpha* is distinguished from var. *malorum* by the production of an additional class of 1(–3)-septate conidia which differ from normal *A. malorum* conidia largely by the degree of septation, greater width, deeper colour and somewhat thicker walls (Figs. 6–8). In addition, these alternative conidia could become longitudinally septate and, in rare instances, distinctly alternarioid (Figs. 9–10). The alternative conidia are borne on the same kinds of conidiophores as those bearing regular conidia (Fig. 11), and sometimes from a single, branched conidiophore (Fig. 12). The alternative forms of conidia could occur together with the regular conidia in the same chain (Figs. 6–8) and could be subtended by normal ramo-conidia within the chain (Fig. 7). That the division between the regular conidia and those with alternative morphologies is not absolute can be seen by occasional production of intermediate types (Fig. 8). A small minority of the

dictyoconidia were regularly (Fig. 9) or irregularly (Fig. 10) alternarioid in shape. Conidiogenesis is the same for normal conidia and those characterising var. *polymorpha*, and the alternative conidia occur mixed together with normal *P. malorum* conidia, so that classification as a variety seems to be appropriate. The two varieties appeared similar, however, based on the molecular data presented here.

Mycosphaerella (*Mycosphaerellaceae*)

This clade contains *Mycosphaerella* species and cercosporoid anamorphs that are now placed in *Passalora s.lat.* (incl. *Fulvia*, *Mycovellosiella* and *Phaeoramularia*). Comprehensive morphological and molecular analyses of this fungal group were recently conducted (CROUS et al. 2000, 2001), in which it was shown that *Mycosphaerella* isolates form a single large monophyletic clade, with species of *Mycosphaerella* with *Cladosporium s. str.* anamorphs in a distinct subclade. These molecular data further showed that *Passalora fulva* [= *Fulvia fulva*, *Cladosporium fulvum*, *Mycovellosiella fulva*] is also a part of the *Mycosphaerella* clade, clustering together with other taxa with *Passalora s.lat.* anamorphs. Furthermore, the conidiogenous loci of *P. fulva* are quite distinct from *Cladosporium s. str.* scars, and agree better with cercosporoid scar types (BRAUN 1995).

Various authors confused *Cladosporium* with *Biharia*, *Fulvia*, *Mycovellosiella* and *Stenella*. For instance, VON ARX (1981) reduced these names to synonymy with *Cladosporium*. ELLIS (1971) listed *Biharia* as a synonym of *Mycovellosiella*, but since the superficial hyphae of the type species, *B. vanguardiae*, are verruculose, DEIGHTON (1979) reduced *Biharia* to synonymy with *Stenella*. VON ARX (1983) recognised *Mycovellosiella*, including *Fulvia*, but maintained *Biharia* and *Stenella* as synonyms of *Cladosporium*. However, *Passalora s.lat.* and *Stenella* are easily distinguishable from *Cladosporium s. str.* by their distinct conidiogenous loci (scars) and conidial hila, which are truncate to pileate, barely protuberant, somewhat thickened and darkened, but always without a raised periclinal rim. Furthermore, the separation of *Cladosporium*, *Passalora s.lat.* and *Stenella* is also supported by molecular data (CROUS et al. 2000, 2001, Crous unpubl.).

Davidiella (*Mycosphaerellaceae*)

Cladosporium herbarum, the lectotype species of *Cladosporium* (CLEMENS & SHEAR 1931), is the anamorph of *Davidiella tassiana* (VON ARX 1950, BARR 1958), which has also been confirmed by molecular examinations (MASCLAUX et al. 1995, DE HOOG et al. 1999). All species of *Cladosporium s. str.* examined represent a monophyletic clade (DE HOOG et al. 1999, UNTEREINER & NAVEAU 1999, CROUS et al. 2000, 2001) (Figs. 1–2).

True *Cladosporium* species are easily separable from all other *Cladosporium*-like hyphomycetes by their distinctive conidiogenous loci, which were described in detail by DAVID (1997), who pointed out that this scar type is a significant ge-

neric character. The first detailed examinations of *Cladosporium* scars were published by ROQUEBERT (1981). The conidiogenous loci (scars) and conidial hila are usually distinctly protuberant, thickened, darkened and composed of a raised periclinal rim that surrounds a central convex part (dome or mound, DAVID 1997). This type of scar has been called 'coronate' (DAVID 1997) or it may simply be described as 'Cladosporium-type', since it is so characteristic and unique. *Cladosporium s. str.* should be confined to *Davidiella* anamorphs with coronate conidiogenous loci. The first clear circumscription in this sense, including a clear description of the peculiar scars has been published by DAVID (1997).

The genus *Heterosporium* was reduced to synonymy with *Cladosporium* by DE VRIES (1952), a view endorsed by HUGHES (1958) and ELLIS (1971, 1976). VON ARX (1981, 1983) reinstated *Heterosporium* and various authors followed his decision. DAVID (1997) examined the conidiogenous loci (scars) and conidial hila of *Cladosporium* and *Heterosporium* species, showed that these structures are generally uniform in all species of the two 'genera', and so reduced *Heterosporium* to synonymy with *Cladosporium*. DAVID'S (1997) taxonomic decisions are fully supported by our study, in which several *Heterosporium* species that have *Davidiella* teleomorphs, cluster within the *Cladosporium* clade.

Acknowledgements

Uwe Braun and Pedro W. Crous acknowledge the 'Volkswagenstiftung' (Hannover, Germany) for financial support.

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Accepted: 10.3.2003

Tab. 1: Isolates of *Cladosporium* and allied genera studied

Sequence data	Species	Accession no. ^a	GenBank accession no.	Substrate	Origin
SSU	<i>Alternaria alternata</i>	–	U05194	<i>Brassica rapa</i> ssp. <i>oleifera</i>	Alberta, Canada
SSU	<i>Alternaria brassicicola</i> (syn. <i>Helminthosporium brassicicola</i>)	–	U05197	<i>Brassica oleracea</i> ssp. <i>capitata</i>	British Columbia, Canada
ITS	<i>Alternaria conjuncta</i>	'EGS' 37-139	AF392988	<i>Pastinaca sativa</i>	Switzerland
ITS	<i>Alternaria ethzedia</i> / <i>Lewia ethzedia</i>	'EGS' 37-143	AF392987	<i>Brassica</i> sp.	Switzerland
ITS	<i>Alternaria infectoria</i> / <i>Lewia infectoria</i>		Y17066	Linseed	–
SSU	<i>Alternaria infectoria</i> / <i>Lewia infectoria</i>	IMI 303186	U43465	<i>Triticum</i> sp.	UK
ITS	<i>Alternaria infectoria</i> / <i>Lewia infectoria</i>	STE-U 4271	AF397248	<i>Triticum</i> sp.	UK
ITS	<i>Alternaria malorum</i> (syn. <i>Cladosporium porophorum</i>)	ATCC 36953 CBS 135.31	AF393715	Fruit of <i>Malus</i> <i>sylvestris</i>	USA
ITS; SSU	<i>Alternaria malorum</i> (syn. <i>Cladosporium porophorum</i>)	ATCC 200939 CBS 173.80 STE-U 3685	AF393722; AY251128	Agricultural soil	Syria
ITS; SSU	<i>Alternaria malorum</i> (syn. <i>Phaeoramularia kellermaniana</i>)	ATCC 28332 CBS 266.75 STE-U 3680	AF393680; AY251127	Straw of <i>Triticum aestivum</i>	Western Cape, South Africa
ITS; SSU	<i>Alternaria malorum</i>	STE-U 4572	AY251079; AY251131	<i>Festuca idahoensis</i>	Washington, USA
ITS; SSU	<i>Alternaria malorum</i>	STE-U 4571	AY251081; AY251130	<i>Bromus tectorum</i>	Washington, USA
ITS; SSU	<i>Alternaria malorum</i> var. <i>polymorpha</i>	STE-U 4570 CBS 112048 ^b	AY251080; AY251129	<i>Vitis vinifera</i>	Washington, USA
SSU	<i>Alternaria raphani</i>	–	U05199	<i>Brassica rapa</i> ssp. <i>oleifera</i>	Saskatchewan, Canada
ITS; SSU	<i>Anungitopsis amoena</i> (syn. <i>Cladosporium amoenum</i>)	ATCC 200947 CBS 254.95 STE-U 3681	AF393682; AY251122	<i>Eucalyptus grandis</i>	Cuba
SSU	<i>Batcheloromyces proteae</i>	STE-U 1518	AY251102	<i>Protea cynaroides</i>	Western Cape, Stellenbosch, South Africa
ITS	<i>Capronia semiimmersa</i>	MUCL 39979	AF050260	Rotten wood, <i>Acer</i> sp.	USA
SSU	<i>Cercospora zebrina</i>	STE-U 3955	AY251104	<i>Trifolium pratense</i>	Canada
ITS	<i>Cladophialophora bantiana</i> (syn. <i>Xylohypha bantiana</i>)	WC 2907	AF397182	–	USA
ITS	<i>Cladophialophora bantiana</i> (syn. <i>Xylohypha bantiana</i>)	UTHSC 94-986	AF131079	–	–
ITS	<i>Cladophialophora carrionii</i> (syn. <i>Cladosporium carrionii</i>)	ATCC 16264 CBS 160.54	AF050262	Man, chromoblasto- mycosis	Australia
ITS	<i>Cladophialophora carrionii</i> (syn. <i>Cladosporium carrionii</i>)	FMC 248	AF397181	–	Venezuela
ITS	<i>Cladophialophora carrionii</i> (syn. <i>Cladosporium carrionii</i>)	IMTSP 690	AF397180	–	USA
ITS	<i>Cladophialophora minourae</i> (syn. <i>Cladosporium minourae</i>)	ATCC 52853 CBS 556.83 ^b	AY251087	Decaying wood	Japan
ITS	' <i>Cladosporium</i> ' <i>breviramosum</i>	ATCC 64696	AF393684	Vinyl wallpaper	Georgia, USA
ITS	' <i>Cladosporium</i> ' <i>breviramosum</i>	ATCC 76215	AF393683	Discolored wallpaper	Georgia, USA
ITS	<i>Cladosporium chlorocephalum</i> (syn. <i>Periconia chlorocephala</i>)	ATCC 38011	AF393686	<i>Paeonia suffruticosa</i> leaf	Japan
SSU	<i>Cladosporium cladosporioides</i>	–	U20381	–	–
ITS; SSU	<i>Cladosporium cladosporioides</i>	CBS 109.21 ATCC 11277 STE-U 3682	AY251073; AY251093	<i>Hedera helix</i>	UK
ITS; SSU	<i>Cladosporium cladosporioides</i>	CBS 401.80 ATCC 200941 STE-U 3683	AY251074; AY251091	<i>Triticum aestivum</i>	Netherlands
ITS; SSU	<i>Cladosporium cladosporioides</i>	ATCC 66669 STE-U 5100	AY251070; AY251094	Creosote-treated southern pine pole	Binghamton, New York, USA
ITS	<i>Cladosporium colocasiae</i>	ATCC 38014	AF393692	<i>Colocasia esculenta</i> leaf	Japan

Tab. 1: Isolates of *Cladosporium* and allied genera studied (continued)

Sequence data	Species	Accession no. ^a	GenBank accession no.	Substrate	Origin
ITS; SSU	<i>Cladosporium colocasiae</i>	STE-U 4323	AY251075; AY251092	<i>Colocasia esculenta</i>	Fiji islands
ITS	<i>Cladosporium cucumerinum</i>	ATCC 26211	AF393696	<i>Cucumis sativa</i>	–
ITS	<i>Cladosporium echinulatum</i> / <i>Davidiella dianthi</i> (syn. <i>Mycosphaerella dianthi</i>)	ATCC 56129	AF393698	<i>Dianthus caryophyllus</i> leaves	Portugal
ITS	<i>Cladosporium gossypicola</i>	ATCC 38026 CBS 674.82	AF393702	Seed of <i>Gossypium</i> sp.	Jaffa, Israel
ITS	<i>Cladosporium herbarum</i> / <i>Davidiella tassiana</i> (syn. <i>Mycosphaerella tassiana</i>)	ATCC 201090	AF393705	Asymptomatic cherry fruits, <i>Prunus avium</i> cv. 'Bing'	Wenatchee, Washington, USA
ITS	<i>Cladosporium herbarum</i> / <i>Davidiella tassiana</i> (syn. <i>Mycosphaerella tassiana</i>)	CBS 399.80	AJ244227	Skin of man, foot	Geleen, Netherlands
ITS	<i>Cladosporium herbarum</i> / <i>Davidiella tassiana</i> (syn. <i>Mycosphaerella tassiana</i>)	CBS 111.82	AJ238469	<i>Arctostaphylos uva-ursi</i>	Alvaneu, Graubünden, Switzerland
ITS; SSU	<i>Cladosporium herbarum</i> / <i>Davidiella tassiana</i> (syn. <i>Mycosphaerella tassiana</i>)	ATCC 66670 STE-U 5101	AY251078; AY251096	CCA-treated Douglas-fir pole	Geneva, New York, USA
ITS	<i>Cladosporium iridis</i> / <i>Davidiella macrospora</i> (syn. <i>Mycosphaerella macrospora</i>)	–	AF297231	<i>Iris germanica</i>	Indiana, USA
ITS	<i>Cladosporium macrocarpum</i>	CBS 175.62	AJ244229	Grain of <i>Hordeum vulgare</i>	Netherlands
ITS	<i>Cladosporium magnusianum</i> (syn. <i>Heterosporium magnusianum</i>)	ATCC 200946 CBS 842.91	AF393712	Green leaf of <i>Nartheicum ossifragum</i>	Bjerkreim County, Norway
ITS	<i>Cladosporium oxysporum</i>	CBS 125.80	AJ300332	Seedcoat of <i>Cirsium vulgare</i>	Netherlands
ITS	<i>Cladosporium oxysporum</i>	ATCC 76499	AF393720	Decayed leaf, <i>Lespedeza bicolor</i>	Lee Co., Alabama, USA
ITS; SSU	<i>Cladosporium</i> sp.	STE-U 5371	AY251072; AY251099	<i>Spinacia</i> sp.	Gaborone, Botswana
ITS; SSU	<i>Cladosporium</i> sp.	STE-U 5124	AY251076; AY251090	<i>Apium graveolens</i>	New Zealand
ITS; SSU	<i>Cladosporium sphaerospermum</i>	ATCC 11290 CBS 188.54 STE-U 3686	AY251077; AY251098	–	–
ITS; SSU	<i>Cladosporium staurophorum</i> (syn. <i>Hormodendrum staurophorum</i>)	ATCC 200934 CBS 375.81 STE-U 3687	AF393723; AY251121	Soil	Cruz Verde, Cundinamarca, Colombia
ITS	<i>Cladosporium tenuissimum</i>	ATCC 38027	AF393724	Soil	New Caledonia
ITS; SSU	<i>Cladosporium uredinicola</i>	ATCC 46649 STE-U 5390	AY251071; AY251097	Hyperparasite on <i>Cronartium fusiforme</i> f. sp. <i>quercum</i> on <i>Quercus nigra</i> leaves	Alabama, USA
SSU	' <i>Discosphaerina</i> ' <i>fagi</i> (syn. <i>Guignardia fagi</i>)	CBS 171.93 IMI 189460A	AY016342	Leaf of <i>Populus</i> sp.	UK
SSU	<i>Dissoconium dekkeri</i> / <i>Mycosphaerella lateralis</i>	CBS 567.89 STE-U 1535	AY251101	<i>Juniperus chinensis</i> , 'Old Gold'	Maarssen, Netherlands
SSU	<i>Dothidea insculpta</i>	–	U42474	–	–
SSU	<i>Dothidea ribesia</i>	CBS 195.58	AY016343	<i>Ribes</i> sp.	Gunzgen, Kt. Solothurn, Switzerland
ITS	<i>Fusicladium effusum</i> (syn. <i>Cladosporium caryigenum</i>)	–	AF065850	Pecan nuts	Georgia, USA
ITS; SSU	<i>Fusicladium effusum</i> (syn. <i>Cladosporium caryigenum</i>)	STE-U 4524	AY251084; AY251125	Pecan nuts	Georgia, USA
ITS; SSU	<i>Fusicladium effusum</i> (syn. <i>Cladosporium caryigenum</i>)	STE-U 4525	AY251085; AY251126	Pecan nuts	Georgia, USA

Tab. 1: Isolates of *Cladosporium* and allied genera studied (continued)

Sequence data	Species	Accession no. ^a	GenBank accession no.	Substrate	Origin
ITS	<i>Fusicladium effusum</i> (syn. <i>Cladosporium caryigenum</i>)		AF065851	Pecan nuts	Louisiana, USA
ITS; SSU	<i>Fusicladium convolvulorum</i>	IMI 383037 STE-U 3884	AY251082; AY251124	–	New Zealand
ITS	<i>Fusicladium pomi</i> (syn. <i>Spilocaea pomi</i>) / <i>Venturia inaequalis</i>	–	AF065837	<i>Malus</i> sp.	–
ITS	<i>Fusicladium pyrorum</i> / <i>Venturia pyrina</i>	–	AF065844	Pear	Israel
SSU	<i>Fusicoccum</i> sp. / <i>Botryosphaeria ribis</i>	–	AF271129	–	–
SSU	<i>Guignardia endophyllicola</i>	CBS 398.80 IFO 33062	AB041249	–	New Zealand
SSU	<i>Saccharicola bicolor</i> (syn. <i>Leptosphaeria bicolor</i>)	ATCC 42652	U04202	<i>Saccharum officinarum</i>	Kenya
ITS	<i>Mycosphaerella iridis</i> (syn. <i>Sphaerella iridis</i>)	CBS 282.49	AY251088	Leaf spot in <i>Iris pseudacorus</i>	Baarn, Netherlands
ITS	<i>Mycosphaerella iridis</i> (syn. <i>Sphaerella iridis</i>)	CBS 281.49	AY251089	Leaf spot in <i>Iris pseudacorus</i>	Glattfelden, Zürich, Switzerland
SSU	<i>Mycosphaerella latebrosa</i> (syn. <i>Sphaerella latebrosa</i>)	CBS 652.85	AY251114	Leaf spot in <i>Acer pseudoplatanus</i>	Baarn, Netherlands
SSU	<i>Mycosphaerella nubilosa</i> (syn. <i>Sphaerella nubilosa</i>)	STE-U 4661	AY251120	<i>Eucalyptus globulus</i>	Ponte Areas, Spain
SSU	<i>Mycosphaerella populorum</i>	–	AF271130	–	–
SSU	<i>Mycosphaerella</i> sp.	STE-U 1731	AY251115	<i>Protea</i> sp.	Drakensberg, Kwazulu-Natal, South Africa
SSU	<i>Mycosphaerella</i> sp.	STE-U 3837	AY251116	<i>Acacia</i> sp.	Venezuela
SSU	<i>Paraphaeosphaeria michotii</i> (syn. <i>Sphaeria michotii</i>)	CBS 591.73	AF250817	<i>Juncus squarrosus</i>	France
SSU	<i>Paraphaeosphaeria pilleata</i>	CBS 102207	AF250821	<i>Juncus roemerianus</i>	North Carolina, USA
ITS	<i>Passalora arachidicola</i> (syn. <i>Cercospora arachidis</i>) / <i>Mycosphaerella arachidis</i>	–	AF 297224	<i>Arachis hypogaea</i>	USA
ITS	<i>Passalora bellynckii</i> (syn. <i>Mycovellosiella bellynckii</i>)	CBS 150.49 STE-U 3635	AF222831	<i>Cynanchum vincetoxicum</i>	Switzerland
ITS	<i>Passalora dissiliens</i> (syn. <i>Phaeoramularia dissiliens</i>)	CBS 219.77	AF222835	Living leaf of <i>Vitis vinifera</i>	Basrah Province, Iraq
SSU	<i>Passalora dodonaeae</i>	STE-U 1223 ^b	AY251108	<i>Dodonaea</i> sp.	Western Cape, South Africa
ITS	<i>Passalora fulva</i> (syn. <i>Cladosporium fulvum</i>)	ATCC 44960	AF393701	Tomato	Netherlands
ITS	<i>Passalora fulva</i> (syn. <i>Cladosporium fulvum</i>)	IMI 050487	L25430	<i>Lycopersicon esculentum</i>	Zimbabwe
ITS; SSU	<i>Passalora fulva</i> (syn. <i>Cladosporium fulvum</i>)	CBS 119.46 STE-U 3688	AY251069; AY251109	<i>Lycopersicon esculentum</i>	Netherlands
ITS	<i>Passalora henningsii</i> (syn. <i>Cercospora henningsii</i>)	–	AF284389	<i>Manihot esculenta</i>	Pernambuco, Brazil
SSU	<i>Passalora janseana</i> (syn. <i>Napicladium janseanum</i>)	CBS 145.37 IMI 303642 STE-U 4303	AY251103	<i>Oryza sativa</i>	Arkansas, USA
ITS	<i>Passalora vaginae</i> (syn. <i>Mycovellosiella vaginae</i>)	CBS 140.34	AF222832	<i>Saccharum officinarum</i>	Taiwan
ITS; SSU	' <i>Phaeoramularia hachijoensis</i> '	ATCC 96545 STE-U 5121	AY251068; AY251100	Air	Long Island, New York, USA
ITS	' <i>Phaeoramularia hachijoensis</i> '	CBS 462.82 STE-U 3679	AY251086	<i>Pinus</i> sp.	De Vuursche, Baarn, Netherlands
ITS	<i>Phialophora americana</i>	CDC 10	U31838	Paper pulp	Wisconsin, USA

Tab. 1: Isolates of *Cladosporium* and allied genera studied (continued)

Sequence data	Species	Accession no. ^a	GenBank accession no.	Substrate	Origin
ITS	<i>Phialophora americana</i>	FMC 2214	AF397136	–	Colombia
ITS	<i>Phialophora americana</i>	CBS 840.69 MUCL 15537	AF050283	Decaying timber	Helsinki, Finland
SSU	<i>Pleospora betae</i>	IMI 156653	U43466	Seed of <i>Beta</i> sp.	UK
SSU	<i>Pseudocercospora cruenta</i> (syn. <i>Cercospora cruenta</i>)	CBS 462.75	AY251105	<i>Phaseolus</i> sp.	Labasa, Fiji
SSU	<i>Pseudocercospora protearum</i> var. <i>leucadendri</i> (syn. <i>Cercospora</i> <i>protearum</i> var. <i>leucadendri</i>)	STE-U 1869	AY251107	<i>Leucadendron</i> sp.	Western Cape, Stellenbosch, South Africa
ITS; SSU	<i>Pseudocladosporium hachijoense</i>	ATCC 96019 STE-U 5391	AY251083; AY251123	<i>Prunus avium</i>	Wenatchee, Washington, USA
SSU	<i>Pseudocercospora angolensis</i> (syn. <i>Cercospora angolensis</i>)	ATCC 11669 CBS 149.53	AY251106	Leaf of <i>Citrus sinensis</i>	Bié, Angola
SSU	<i>Ramularia</i> sp.	STE-U 4195	AY251112	–	–
SSU	<i>Ramulispora sorghi</i>	STE-U 905	AY251110	<i>Sorghum</i> sp.	KwaZulu-Natal, South Africa
SSU	<i>Ramulispora sorghi</i>	STE-U 906	AY251111	<i>Sorghum</i> sp.	KwaZulu-Natal, South Africa
ITS	<i>Rhinocladiella compacta</i> (syn. <i>Hormodendrum compactum</i>)	IMTSP 373	AF397133	–	–
SSU	<i>Septoria rosae</i>	ATCC 24311 CBS 355.58 STE-U 4302	AY251113	Leaf of <i>Rosa</i> sp.	–
SSU	<i>Septoria tritici</i>	STE-U 658	AY251117	<i>Triticum</i> sp.	Western Cape, South Africa
SSU	<i>Sphaerulina polyspora</i>	CBS 354.29 STE-U 4301	AY251095	–	–
SSU	<i>Stemphyllium herbarum</i> / <i>Pleospora herbarum</i>	ATCC 11681	U43458	Onion leaf	Colorado
ITS	<i>Sorocybe resinae</i> (syn. <i>Hormodendrum resinae</i>) / <i>Amorphotheca resinae</i>	ATCC 200942 CBS 406.68	AF393726	Soil	UK
ITS	<i>Sorocybe resinae</i> (syn. <i>Hormodendrum resinae</i>) / <i>Amorphotheca resinae</i>	ATCC 11841 CBS 184.54 STE-U 3692	AY251067	Creosote-treated wooden pole	St Louis, Missouri, USA
SSU	<i>Trimmatostroma macowanii</i>	STE-U 1488	AY251118	<i>Protea</i> sp.	Hermanus, Western Cape, South Africa
SSU	<i>Uwebraunia juvenis</i> / <i>Mycosphaerella juvenis</i>	STE-U 1004 ^b	AY251119	Leaves of <i>Eucalyptus grandis</i>	Hazyview, Gauteng, South Africa
ITS	<i>Venturia cerasi</i>	ATCC 12119 CBS 444.54	AF065847	<i>Prunus cerasus</i>	East Germany

^a ATCC: American Type Culture Collection, Virginia, U.S.A.;

IMI: International Mycological Institute, CABI-Bioscience, Egham, Basingstoke, U.K.;

E.G.S.: E. Simmons, 717 Thornwood Road, Crawfordsville, Indiana U.S.A.;

STE-U: Department of Plant Pathology, University of Stellenbosch, South Africa;

CBS: Centraalbureau voor Schimmelcultures, Utrecht, The Netherlands;

MUCL: Université Catholique de Louvain, Louvain-la-Neuve, Belgium;

WC: Wadsworth Center for Laboratories and Research Collection (New York State Department of Health);

UTHSC: University of Texas Health Science Centre, U.S.A.;

FMC: Venezuelan School of Medicine;

IMTSP: Institute of Tropical Medicine of São Paulo;

CDC: Centre for Disease Control and Prevention, U.S. Department of Health and Human Services.

IFO: Institute for Fermentation, Osaka, Japan.

^b Ex-type isolates.