New species of *Cladosporium* associated with human and animal infections

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**Key words**
Capnodiales  
Cladosporiaceae  
Dothideomycetes  
phylogeny  
taxonomy

**Abstract** *Cladosporium* is mainly known as a ubiquitous environmental saprobic fungus or plant endophyte, and to date, just a few species have been documented as etiologic agents in vertebrate hosts, including humans. In the present study, 10 new species of the genus were isolated from human and animal clinical specimens from the USA. They are proposed and characterized on the basis of their morphology and a molecular phylogenetic analysis using DNA sequences from three loci (the ITS region of the rDNA, and partial fragments of the translation elongation factor 1-alpha and actin genes). Six of those species belong to the *C. cladosporioides* species complex, i.e., *C. albo-flavescens*, *C. angulosum*, *C. anthropophilum*, *C. crousii*, *C. flavivirens* and *C. xantochromaticum*, three new species belong to the *C. herbarum* species complex, i.e., *C. rocosum*, *C. subcinereum* and *C. tuberosum*; and one to the *C. sphaerospermum* species complex, namely, *C. succulentum*. Differential morphological features of the new taxa are provided together with molecular barcodes to distinguish them from the currently accepted species of the genus.

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**INTRODUCTION**

The genus *Cladosporium* (*Cladosporiaceae, Capnodiales*) is a large genus of the Ascomycota. It comprises 189 species, mostly saprobes with a worldwide distribution and isolated from a wide range of substrates (David 1997, Bensch et al. 2012, 2015, Crous et al. 2014). The genus also includes common endophytes, plant pathogens often causing leaf spots or other lesions, as well as hyperparasites of other fungi (Bensch et al. 2012). Certain species are relevant as potential biocontrol agents for plant diseases (Köhler et al. 2015) or, in the food industry, as fruit contaminants causing spoilage in low temperature storage or on cereals such as barley, oat, rye and wheat (Samson et al. 2010, Kulik et al. 2014, Frasz & Miller 2015). The role of *cladosporia* is not well understood in human pathology. Their small conidia are easily dispersed, making them one of the most common air-borne microorganisms (David 1997, De Hoog et al. 2011). They are among the most important allergenic fungi linked to allergic rhinitis and respiratory arrest in asthmatic patients (Black et al. 2000, Sellart-Altisent et al. 2007). Some species are described as a cause of opportunistic phaeohyphomycosis, including subcutaneous and deep infections in humans and animals (De Hoog et al. 2011, Sandoval-Denis et al. 2015), although, their ubiquitous nature suggests that in some reports they may be mere colonizers.

Species identification in *Cladosporium* has always relied on the morphology of the conidiogenous apparatus together with data on host ranges (Crous et al. 2007b, Bensch et al. 2012). Traditionally, those dematiaceous fungi showing branched acropetal chains of aspitate conidia were included in *Cladosporium*, which has made it a large and complex group of fungi difficult to differentiate (Bensch et al. 2012). However, recent phylogenetic studies have helped to clarify the taxonomy of these fungi and demonstrated that most of the well-known morphologically-defined species comprises several phylogenetically cryptic species practically impossible to identify using morphological criteria alone (Braun et al. 2003, 2008; Crous et al. 2007b, Zalar et al. 2007, Schubert et al. 2007, 2009, Bensch et al. 2010, 2012, 2015). In its current circumscription, the genus *Cladosporium* includes dematiaceous fungi with solitary to fasciculate conidiophores, proliferating mostly sympodially and forming unbranched or branched acropetal conidial chains. However, the most characteristic feature is the presence of a thick refractive to darkened cladosporioid or coronate scar, defined as a raised pericilinal rim with a central convex dome (Schubert et al. 2007, Bensch et al. 2012). The sexual morph (previously assigned to the genus *Davidelia*) is characterised by pseudohyphal ascocoma, 8-spored obovate to subcylinodral asci, and hyaline, obovate to ellipsoid ascospores showing irregular lumenal inclusions (Schubert et al. 2007).

In recent years, the survey of unexplored habitats and sources by using molecular techniques has expanded our knowledge of fungal diversity. Similarly, clinical specimens have become an important source of undescribed fungi, including both true pathogens and/or also contaminants/colonizers (Gilgado et al. 2005, Perdomo et al. 2013, Giraldo et al. 2014, Guinea et al. 2015, Sandoval-Denis et al. 2015) that had not been recognizable previously because of their poor morphological differentiation (De Hoog et al. 2015).

In order to assess the real prevalence of *Cladosporium* in the clinical setting and the spectrum of species associated with clinical samples, we studied a large set of *Cladosporium* isolates from human and animal clinical origin using both molecular characterisation and phenotypic features (Sandoval-Denis et al. 2015). Surprisingly, we found that nearly 40 % of the isolates could not be assigned to any known species and probably represented new species for the genus. The objective of the present study is therefore to determine the phylogenetic relationships of those previously unidentified isolates by using the criteria currently accepted in the taxonomy of this genus.

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### Table 1

| Species                                      | Strain numbera | Substrater | ITS     | tef1     | ActA             |
|----------------------------------------------|----------------|------------|---------|----------|------------------|
| *Cladosporium aphidis*                      | CBS 116456     | Human, BAL | FMR 13338 |         |                  |
| *Cladosporium acalyphae*                    | CBS 125982b    | Acalypha australis | HM147994 | HM148235 | HM148481         |
| *Cladosporium aciculare*                    | CBS 140488b    | Syzygium corynanthum | KT600411 | KT600509 | KT600607         |
| *Cladosporium aggregatocorticaticum*         | CBS 140493c    | Culture contaminant | KT600448 | KT600547 | KT600645         |
| *Cladosporium alboaffinevens*                | CBS 140490c = UTHSC DI-13-225 = FMR 13338 | Animal, BAL | LN834420 | LN834516 | LN834604         |
| *Cladosporium allicium*                      | CBS 121.47     | Food, frozen Phaseolus vulgaris | KT600364 | KT600461 | KT600560         |
| *Cladosporium angustisporum*                 | CBS 11526      | Hardeum vulgar | EF679350 | EF679425 | EF679502         |
| *Cladosporium angulosum*                     | CBS 101.81     | Allium porum | JN906977 | JN906983 | JN906996         |
| *Cladosporium angulosum*                     | CBS 140492c = UTHSC DI-13-235 = FMR 13348 | Human, BAL | LN834425 | LN834521 | LN834609         |
| *Cladosporium cycadicola*                    | CPC 11122      | Phytolacca americana | HM148127 | HM148371 | HM148616         |
| *Cladosporium cycadicola*                    | CPC 14566      | Corymbia foelschneana | HM148147 | HM148391 | HM148636         |
| *Cladosporium flavovirens*                   | CPC 18494      | Ananas comosus | KT600413 | KT600511 | KT600609         |
| *Cladosporium flavovirens*                   | CPC 18496      | Ananas comosus | KT600414 | KT600512 | KT600610         |
| *Cladosporium angustusporus*                 | CBS 125983t    | Alloxyon wickhami | HM147995 | HM148236 | HM148482         |
| *Cladosporium angustusporus*                 | CBS 140479t    | Pinus ponderosa | KT600378 | KT600475 | KT600574         |
| *Cladosporium asperulatum*                   | CPC 11122      | Phytolacca americana | HM148127 | HM148371 | HM148616         |
| *Cladosporium angulosum*                     | CBS 117435     | Unknown       | HM148007 | HM148248 | HM148494         |
| *Cladosporium angulosum*                     | CBS 140485t = UTHSC DI-13-269 = FMR 13382 | Human, BAL | LN834437 | LN834533 | LN834621         |
| *Cladosporium echinulatum*                   | CPC 11122      | Phytolacca americana | HM148019 | HM148260 | HM148506         |
| *Cladosporium echinulatum*                   | CPC 14566      | Corymbia foelschneana | HM148147 | HM148391 | HM148636         |
| *Cladosporium alboflavescens*                | CPC 18494      | Ananas comosus | KT600413 | KT600511 | KT600609         |
| *Cladosporium alboflavescens*                | CPC 18496      | Ananas comosus | KT600414 | KT600512 | KT600610         |
| *Cladosporium angustusporus*                 | CBS 125983t    | Alloxyon wickhami | HM147995 | HM148236 | HM148482         |
| *Cladosporium angustusporus*                 | CBS 140479t    | Pinus ponderosa | KT600378 | KT600475 | KT600574         |
| *Cladosporium angustusporus*                 | CBS 117435     | Unknown       | HM148007 | HM148248 | HM148494         |
| *Cladosporium angustusporus*                 | CBS 140485t = UTHSC DI-13-269 = FMR 13382 | Human, BAL | LN834437 | LN834533 | LN834621         |
| *Cladosporium echinulatum*                   | CPC 11122      | Phytolacca americana | HM148019 | HM148260 | HM148506         |
| *Cladosporium echinulatum*                   | CPC 14566      | Corymbia foelschneana | HM148147 | HM148391 | HM148636         |
| *Cladosporium alboflavescens*                | CPC 18494      | Ananas comosus | KT600413 | KT600511 | KT600609         |
| *Cladosporium alboflavescens*                | CPC 18496      | Ananas comosus | KT600414 | KT600512 | KT600610         |
| *Cladosporium angustusporus*                 | CBS 125983t    | Alloxyon wickhami | HM147995 | HM148236 | HM148482         |
| *Cladosporium angustusporus*                 | CBS 140479t    | Pinus ponderosa | KT600378 | KT600475 | KT600574         |
| *Cladosporium angustusporus*                 | CBS 117435     | Unknown       | HM148007 | HM148248 | HM148494         |
| *Cladosporium angustusporus*                 | CBS 140485t = UTHSC DI-13-269 = FMR 13382 | Human, BAL | LN834437 | LN834533 | LN834621         |
| *Cladosporium echinulatum*                   | CPC 11122      | Phytolacca americana | HM148019 | HM148260 | HM148506         |
| *Cladosporium echinulatum*                   | CPC 14566      | Corymbia foelschneana | HM148147 | HM148391 | HM148636         |
| *Cladosporium alboflavescens*                | CPC 18494      | Ananas comosus | KT600413 | KT600511 | KT600609         |
| *Cladosporium alboflavescens*                | CPC 18496      | Ananas comosus | KT600414 | KT600512 | KT600610         |
| *Cladosporium angustusporus*                 | CBS 125983t    | Alloxyon wickhami | HM147995 | HM148236 | HM148482         |
| *Cladosporium angustusporus*                 | CBS 140479t    | Pinus ponderosa | KT600378 | KT600475 | KT600574         |
| *Cladosporium angustusporus*                 | CBS 117435     | Unknown       | HM148007 | HM148248 | HM148494         |
| *Cladosporium angustusporus*                 | CBS 140485t = UTHSC DI-13-269 = FMR 13382 | Human, BAL | LN834437 | LN834533 | LN834621         |

*Note:* ITS, tef1, and ActA are the GenBank accession numbers for the respective markers.

- aSpecies
- bStrain number
- cSubstrate
| Species                  | Strain number | Substrate | GenBank accession numbers |
|-------------------------|---------------|-----------|--------------------------|
| Cladosporium fusicolusum| CBS 121212     | Ficus carica | HM14809 HM148337 HM148582 |
| Cladosporium fusiforme  | CBS 121219†   | Leaf of Vigna umbellata | HM148094 HM148338 HM148583 |
| Cladosporium gamsianum  | CBS 122194†   | Hypersaline water | DQ780368 JN906988 EF101372 |
| Cladosporium globisporum| CBS 812.96†   | Stem rust sp. | HM148095 HM148339 HM148584 |
| Cladosporium limoniforme| CBS 114271†   | Leaves of Grevillea sp. | JF770450 JF770472 JF770473 |
| Cladosporium halotolerans| CBS 114916† | Hypersaline water | DQ780364 JN906989 EF101397 |
| Cladosporium herbaroides| CBS 112626     | Human, scalp | LN834374 LN834470 LN834585 |
| Cladosporium herbarum   | CBS 121621†   | Hypersaline water | EF679357 EF679432 EF679509 |
| Cladosporium hillianum  | CBS 129588†   | Leaf of Tilia sp. | HM148097 HM148341 HM148586 |
| Cladosporium inveriscolor| CBS 143.65     | Leaf of Tilia | HM148100 HM148344 HM148589 |
| Cladosporium iridis      | CBS 138.40†   | Leaf of Trichium aestivum | HM148101 HM148345 HM148590 |
| Cladosporium iridis      | CBS 138.40†   | Leaf of Iris | EF679370 EF679447 EF679523 |
| Cladosporium lagoosporicoides| CBS 185.54† | From P. orbicularis and Physcia sp. on Acer platanoides | HM148111 HM148355 HM148600 |
| Cladosporium licheninum  | CBS 125990†   | Leaf of Tilia sp. | HM148097 HM148341 HM148586 |
| Cladosporium limoniforme| CBS 113737     | Grape berry | KT600396 KT600493 KT600591 |
| Cladosporium longicatenatum| CBS 140484†  | Musa acuminate | KT600397 KT600494 KT600592 |
| Cladosporium longissimum | CBS 130.97†   | Soil along coral reef coast | DQ780352 EU570295 EF101385 |
| Cladosporium macrocarpum | CBS 121623†   | Leaf of Tilia | EF679375 EF679453 EF679529 |
| Cladosporium macrocarpum | CBS 121623†   | Spinae oloracea | EF679453 EF679495 EF679529 |
| Cladosporium monticellum | CBS 140486†  | Pine needles | KT600406 KT600504 KT600602 |
| Cladosporium myrtacearum | CBS 13650†    | Taraxacum sp. | KT600407 KT600505 KT600603 |
| Cladosporium oxyssporum  | CBS 123630†   | Corymbia foetidaea | HM148117 HM148361 HM148606 |
| Cladosporium parasclidiasporoides | CBS 171.54† | Soil | HM148121 HM148364 HM148609 |
| Cladosporium perangustum  | CBS 126365     | From gall of Apiospora morbus on Prunus sp. | HM148121 HM148356 HM148601 |
| Cladosporium perangetum  | CBS 126365     | Cuassia sp. | HM148121 HM148365 HM148610 |
| Cladosporium phlei       | CBS 13118†    | Onoclea sinensis | HM148121 HM148372 HM148617 |
| Cladosporium phyllactiniicola | CBS 126353     | Chasmothecia of Phyllactinia guttata on leaves of Corylus avellana | HM148121 HM148373 HM148622 |
| Cladosporium phyllactiniicola | CBS 13118†    | Chasmothecia of Phyllactinia guttata on leaves of Corylus avellana | HM148121 HM148373 HM148621 |
| Cladosporium phyllactiniicola | CBS 13183†    | Chasmothecia of Phyllactinia guttata on leaves of Corylus avellana | HM148121 HM148373 HM148621 |
| Cladosporium phyllactiniicola | CBS 126353     | Chasmothecia of Phyllactinia guttata on leaves of Corylus avellana | HM148121 HM148373 HM148621 |
| Cladosporium phyllactiniicola | CBS 13183†    | Chasmothecia of Phyllactinia guttata on leaves of Corylus avellana | HM148121 HM148373 HM148621 |
| Cladosporium phyllactiniicola | CBS 126353     | Chasmothecia of Phyllactinia guttata on leaves of Corylus avellana | HM148121 HM148373 HM148621 |
| Cladosporium phyllactiniicola | CBS 13183†    | Chasmothecia of Phyllactinia guttata on leaves of Corylus avellana | HM148121 HM148373 HM148621 |
| Cladosporium phyllactiniicola | CBS 126353     | Chasmothecia of Phyllactinia guttata on leaves of Corylus avellana | HM148121 HM148373 HM148621 |
| Cladosporium phyllactiniicola | CBS 125992†    | Chasmothecia of P. guttata on leaves of Corylus avellana | HM148121 HM148373 HM148621 |
| Cladosporium pini-ponderosa | CBS 124446†   | Pinus ponderosa | FJ936160 FJ936164 FJ936167 |
| Cladosporium pseud Kirids  | CBS 116483†   | Iris sp. | EF679383 EF679461 EF679537 |
| Cladosporium pseudocladosporoides | CBS 140490†  | Pine needles | KT600415 KT600513 KT600611 |
| Cladosporium pseudod cladiosporoides | CBS 586.90† | Malus sylvestris | HM148165 HM148409 HM148584 |
| Cladosporium pseudod cladiosporoides | CBS 125993†   | Outside air | HM148165 HM148402 HM148474 |
| Cladosporium pseudocladiosporoides | CBS 13683†   | Eucalyptus platycalyx | HM148173 HM148417 HM148662 |
| Cladosporium pseudocladiosporoides | CBS 14020†   | Wheat | HM148165 HM148429 HM148674 |
| Cladosporium pseudocladiosporoides | CBS 14295†    | Soil | HM148168 HM148432 HM148677 |
| Cladosporium pseudophragmioides | CBS 121626†  | Human, arm drainage | LN834406 LN834502 LN834590 |
| Cladosporium pseudophragmioides | CBS 121626†  | Human, skin | LN834414 LN834508 LN834598 |
| Speciesa | Strain numberb | Substrate | GenBank accession numbers |
|----------|---------------|-----------|-------------------------|
| Cladosporium pseudodasycospora (cont.) | UTHSC DI-13-218 = FMR 13331 | Human, BAL | LN834418 LN834514 LN834602 |
| | UTHSC DI-13-227 = FMR 13340 | Human, sputum | LN834422 LN834518 LN834606 |
| | UTHSC DI-13-234 = FMR 13347 | Human, sputum | LN834424 LN834520 LN834608 |
| | UTHSC DI-13-238 = FMR 13351 | Human, leg | LN834426 LN834522 LN834610 |
| | UTHSC DI-13-241 = FMR 13354 | Human, foot | LN834427 LN834523 LN834611 |
| | UTHSC DI-13-245 = FMR 13358 | Human, toe | LN834428 LN834525 LN834613 |
| | UTHSC DI-13-251 = FMR 13364 | Human, BAL | LN834432 LN834528 LN834616 |
| | UTHSC DI-13-251 = FMR 13364 | Human, BAL | LN834432 LN834528 LN834616 |
| | UTHSC DI-13-261 = FMR 13371 | Human, BAL | LN834418 LN834514 LN834602 |
| | UTHSC DI-13-263 = FMR 13381 | Human, toenail | LN834436 LN834532 LN834620 |
| | UTHSC DI-13-269 = FMR 13381 | Human, toenail | LN834436 LN834532 LN834620 |
| | UTHSC DI-13-270 = FMR 13383 | Human, nail | LN834436 LN834534 LN834622 |
| Cladosporium psychrotolerans | CBS 1194T | Hyposaline water | DQ79386 EF793515 |
| Cladosporium puyae | CBS 274.80AT | Hypersaline water | DQ780374 JN906993 EF101390 |
| Cladosporium ramototellum | CBS 126358T | Hypersaline water | EF679386 EF793462 EF795938 |
| Cladosporium subinflatum | CBS 12166AT | Human, nasal tissue | LN834385 LN834481 LN834568 |
| Cladosporium subuliforme | CBS 126500T | Human, sputum | LN834422 LN834518 LN834606 |
| Cladosporium subtilissimum | CBS 126355T | Human, sputum | LN834422 LN834518 LN834606 |

**a** New species described in this study are in **bold italic**.

**b** ATCC, American Type Culture Collection, Manassas, VA, USA; CBS, CBS-KNAW Fungal Biodiversity Centre, Utrecht, the Netherlands; CPC, collection of Pedro Crous at CBS; FMR, Facultad de Medicina, Universitat Rovira i Virgili, Reus, Spain; UTHSC, Fungus Testing Laboratory at the University of Texas Health Science Center, San Antonio, Texas, USA.

**c** BAL fluid, bronchoalveolar lavage fluid specimen; CSF, cerebrospinal fluid.

**d** NT Ex-neotype strain.

**e** ET Ex-epitype strain.

**f** T Ex-type strain.
MATERIALS AND METHODS

Fungal isolates
A total of 48 isolates from clinical origin and belonging to the genus Cladosporium were included in this study, 35 of which corresponded to putatively undescribed species (Table 1). All the isolates were obtained from human and animal clinical specimens from the United States, submitted to the Fungus Testing Laboratory at the University of Texas Health Science Center at San Antonio (UTHSCSA) from different geographic regions of the country for either identification purposes and/or antifungal susceptibility studies.

Phenotypic studies
Macroscopic cultural characteristics of the isolates were recorded after incubation for 14 d at 25 °C, using oatmeal agar (OA) (30 g of filtered oat flakes, 20 g of agar, water 1 L), potato dextrose agar (PDA: Pronadisa, Spain) and synthetic nutrient-poor agar (SNA: KH₂PO₄ 1 g, KNO₃ 1 g, MgSO₄ · 7H₂O 0.5 g, KCl 0.5 g, glucose 0.2 g, sucrose 0.2 g, agar 14 g, water 1 L) with and without pieces of sterilised paper as carbon source. In descriptions, colour notations of the colonies were from Kommerup & Wanscher (1978). Observations and measurements of the microscopic structures were carried out from colonies on SNA after incubation for 7 d at 25 °C, mounted on Shear’s solution (Schubert et al. 2007, Zalar et al. 2007, Crous et al. 2009, Bensch et al. 2012). Photographs were made using a Zeiss Axios Imager M1 light microscope (Zeiss, Oberkothen, Germany) with a mounted DeltaPlex Infinity X digital camera using Nomarski differential interference contrast and phase contrast optics. Scanning electron microscope (SEM) micrographs were obtained with a Jeol JSM-6400 apparatus, following the protocols described by Figuerras & Guarro (1988). Cardinal temperatures of growth were determined culturing the isolates on PDA for 14 d at temperatures ranging from 15 °C to 35 °C at intervals of 5 °C.

DNA extraction, PCR amplification and sequencing
Total genomic DNA was extracted, amplified and sequenced in a previous work, using protocols described elsewhere (Bensch et al. 2012, Sandoval-Denis et al. 2015). Briefly, the primer pair ITS5/ITS4 (White et al. 1990) was used to amplify a region spanning the internal transcribed spacers 1 and 2 and the 5.8S gene of the rRNA (ITS), and the primer pairs EF-728F/EF-986R and ACT-512F/ACT-783R (Carbone & Kohn 1999) were used to amplify a partial fragment of the translation elongation factor 1-α gene (tef1) and the actin gene (actA), respectively. Sequences were generated using the same PCR primers at Macrogen Europe (Macrogen Inc. Amsterdam, The Netherlands). Consensus sequences were assembled using SeqMan v. 7.0.0 (DNASTar Lasergene, Madison, WI, USA).

Sequence alignment and phylogenetic analyses
Multiple sequence alignments of each locus were performed with MEGA v. 6.06 (Tamura et al. 2013), using the ClustalW algorithm (Thompson et al. 1994) and refined with MUSCLE (Edgar 2004) or manually if necessary. The alignment included sequences from the clinical isolates complemented with sequences representing all the available ex-types and numerous reference strains of Cladosporium spp. retrieved from GenBank and mainly published by Bensch et al. (2012, 2015). These latter sequences were selected on the basis of sequence similarity with the putative new taxa as determined by BLAST searches on the NCBI database using ITS, tef1 and actA loci (Table 1). Phylogenetic reconstructions were performed using the maximum-likelihood (ML) and Bayesian Inference (BI) approaches under MEGA v. 6.06 and MrBayes v. 3.2 (Huelsenbeck & Ronquist 2001), respectively. MrModelTest v. 2.3 (Nylander 2004) was used to determine the best nucleotide substitution model for each dataset (SYM+G for ITS and GTR+G+I for tef1 and actA). Sequence alignments generated in this study were deposited in TreeBASE (http://treebase.org).

For the ML analyses, support for the internal branches was assessed by a search of 1 000 bootstrapped sets of data. A bootstrap support (bs) of ≥ 70 % was considered significant. For BI analyses, four Markov chains were performed in two simultaneous runs for 10 000 000 generations with a sampling rate of 1 000 generations. Once checked for the convergence of the runs (average standard deviation of split frequencies parameter below 0.01), the 50 % majority-rule consensus tree and posterior probability values (pp) were calculated after discarding 2 500 trees for burn-in. A pp value ≥ 0.95 was considered significant. Phylogenetic concordance of the ITS, tef1 and actA gene datasets was evaluated with the partition-homogeneity test implemented with PAUP v. 4.0b10 (Swoford 2003) and also by visual comparison of the individual phylogenies in order to assess for any incongruent results between nodes with high statistical support. Taxonomic novelties were deposited in MycoBank (Crous et al. 2004).

RESULTS

Phylogeny
The different partitions were congruent as determined by visual comparison of the individual phylogenies (data not shown) and by the partition homogeneity test (p = 0.16). Phylogenies obtained by ML and BI also showed topological congruence. The final combined analysis of the three mentioned loci datasets encompassed 197 sequences representing 101 taxa, including Cercospora beticola (CBS 116456) as the outgroup, and comprised 1 026 bp (ITS 448 bp, tef1 357 bp and actA 221 bp) from which 546 bp were variable (ITS 108 bp, tef1 291 bp and actA 147 bp) and 399 bp phylogenetically informative (ITS 42 bp, tef1 234 bp and actA 123 bp). Unique site pattern values for the Bayesian analyses were 92, 322 and 167 for ITS, tef1 and actA datasets, respectively (Fig. 1). Of the 35 unidentifed isolates, 21 clustered into ten groups that received strong statistical support with the exception of two monotypic lineages (CBS 140465 and CBS 140466), which, however, were genetically and morphologically differentiated from their closest phylogenetic relatives. The remaining 14 isolates were identified here as C. pseudocladosporoides (13 isolates) and C. allicinum (one isolate). The isolates representing putative new taxa grouped mainly in the C. cladosporioides species complex in which 16 isolates were distributed in three terminal clades and three monotypic lineages. Five isolates belonged to the C. herbarum species complex, two of them (CBS 140693 and UTHSC DI-13-219) grouped in a terminal clade, located in a basal position to the remaining species of the complex, while three isolates formed monotypic lineages. The C. sphaerosperrnum species complex included a single unidentified isolate (CBS 140466) forming a genetically and morphologically distinct lineage. The 10 phylogenetic groups are thus considered new species of Cladosporium and are described in the taxonomy section below.

TAXONOMY

Cladosporium alboflavescens Sandoval-Denis, Gené & Cano, sp. nov. — MycoBank MB815332; Fig. 2

Etymology. From Latin albus ‘white’ flavus ‘yellow’, referring to the colony colour of the species.

Colonies on OA attaining 20–23 mm diam after 14 d at 25 °C, white to grey-yellow (4A1/C4), flat, velvety, margin regular and with abundant submerged mycelium; reverse olive brown (4D5/F8),
Fig. 1 Maximum likelihood (ML) tree obtained from the combined ITS, tef1 and actA sequences of 196 strains from Cladosporium species. The tree is rooted with Cercospora beticola CBS 116456. Numbers on the branches represent ML bootstrap support values of 70 % and higher, followed by Bayesian posterior probabilities (pp) above 0.94. Fully supported branches are thickened and names of species newly described here are indicated in **bold**. Coloured blocks represent the species complex affinity of the novelties described here. Branch lengths are proportional to distance.

- Ex-type strain
- ET Ex-epitype strain
- NT Ex-neotype strain
without diffusible pigments. On PDA attaining 34–36 mm diam after 14 d at 25 °C, yellow-grey to olive brown (4B2/D4), with prominent light yellow (3A4) exudate, flat or umbonate, folded, margin regular; reverse grey-yellow to olive brown (4B4/F4) to black. On SNA reaching 22–25 mm after 14 d at 25 °C, obverse and reverse olive (3D5/E8), flat, velvety with granular centre, margin undulate and with abundant submerged mycelium. 

Mycelium superficial and immersed, composed of septate, branched, 2.5–5 μm wide, subhyaline to pale brown, smooth to slightly roughened, thin-walled hyphae. Conidiophores erect, straight, cylindrical, non-nodulose, septate, simple or branched, up to 130 μm long, 2.5–4 μm wide, pale brown, smooth or sparingly verrucose with darkened and refractive scars. Conidiogenous cells terminal or intercalary, cylindrical, geniculate, 7–36 × 2–4 μm, with up to five apical loci of 1.5–2 μm diam, thickened and refractive. Ramoconidia aseptate, subcylindrical...
Conidiophores to cylindrical, 11–36 × 2–3 μm, pale brown, smooth-walled. Conidia forming branched chains with up to three conidia in the terminal unbranched part, pale brown, sparingly verrucose, with protuberant, somewhat darkened and refractive conidial hilum; small terminal conidia aseptate, oval, 5–6.5 × 2–3 μm (av. (± SD) 5.9 (± 0.4) × 2.8 (± 0.4)); intercalary conidia aseptate, ellipsoidal to almost cylindrical with attenuated ends, 7–13 × 2.5–3 μm (av. (± SD) 10.6 (± 2.5) × 2.6 (± 0.2)); secondary ramoconidia 0–1-septate, ellipsoidal, 8.5–18 × 2–3 μm (av. (± SD) 14.3 (± 3.3) × 2.6 (± 0.5)).

Cardinal temperature for growth — Optimum 20–25 °C, maximum 30 °C, minimum 15 °C.

Specimen examined. USA, California, from animal bronchoalveolar lavage fluid, Mar. 2009, D.A. Sutton (holotype CBS H-22379, culture ex-type CBS 140690 = UTHSC DI-13-225 = FMR 13338).

Notes — *Cladosporium alboflavescens* is morphologically similar to *C. pini-ponderosae* and *C. verrucocladosporioides* (Schubert et al. 2009, Bensch et al. 2010). However, the new species differs mainly by its pale coloured vegetative struc-
and its yellow to pale olive colonies on OA and PDA vs olivaceous grey in the two latter species. The phylogenetically closely related species C. iranicum (Bensch et al. 2010) also shows similar micro-morphological characteristics to C. alboflavescens, but it differs in forming longer conidial chains with up to 10 conidia in the terminal unbranched part and often showing subrostrate intercalary conidia, while conidial chains of the novel species are much shorter and intercalary conidia ellipsoidal to cylindrical being also genetically well differentiated (99.8 %, 87.9 % and 90.1 % sequence similarity for ITS, tef1 and actA, respectively).

**Cladosporium angulosum** Sandoval-Denis, Deanna A. Sutton & Guarro, sp. nov. — MycoBank MB815333; Fig. 3

*Etymology.* From Latin *angulosus* ‘full of corners’, referring to the shape of the conidiophore.

Colonies on OA reaching 52–55 mm after 14 d at 25 °C, olive brown (4E3/F8), flat, velvety to granular, with regular margin; reverse olive brown (4D4/F6) to black. On PDA attaining 50–56 mm diam after 14 d at 25 °C, olive brown (4F4/F8), with a raised or umbonate centre and radially folded towards the periphery, velvety to dusty or granular, with regular margin; reverse dark green (30F8) to black. On SNA reaching 37–40 mm after 14 d at 25 °C, olive brown (4D4/F6), flat, velvety, with lobulated margin; reverse olive brown (4D4/F6) to black. *Mycelium* superficial and immersed, composed of septate, branched, 1.5–3 μm wide, pale olivaceous brown, with smooth and thin-walled hyphae. *Conidiophores* erect, cylindrical, non-nodulose, septate, septa darkened, branched, frequently branching near the base in a 90° angle, up to 150 μm long, 3–4 μm wide, pale brown, smooth and thin-walled. *Conidiogenous cells* terminal or intercalary, cylindrical, 8–46 × 2–3.5 μm, bearing up to four conidiogenous loci of 1–1.5 μm diam, darkened and refringent. *Ramoconidia* aseptate, subcylindrical, straight, 24.5–46 × 2–3.5 μm, pale brown, finely roughened, with scars protuberant, thickened and darkened. *Conidia* forming long branched chains with up to 14 conidia in the terminal unbranched part, pale olivaceous brown, smooth and thin-walled, with protuberant conidial hila, not darkened; small terminal conidia aseptate, obovate to nearly...
cylindrical, 3.5–4.5 × 2–2.5 μm (av. ± SD) 4.1 (± 0.3) × 2.3 (± 0.3)); intercalary conidia aseptate, ellipsoidal, 4–6 × 2–3 μm (av. ± SD) 5.3 (± 0.6) × 2.4 (± 0.4)); secondary ramoconidia 0–1-septate, usually constricted at septum, subcylindrical, 8–17 × 2.5–3 μm (av. ± SD) 12.2 (± 2.6) × 2.8 (± 0.3)).

Cardinal temperature for growth — Optimum 25 °C, maximum 35 °C, minimum 15 °C.

Specimen examined. USA, Texas, from human bronchoalveolar lavage fluid, Sept. 2008, D.A. Sutton (holotype CBS H-22380, culture ex-type CBS 140692 = UTHSC DI-13-235 = FMR 13348).

Notes — The clade representative of *C. angulosum* includes several strains previously identified as *C. per­angustum*, a species accepted with a considerable morphological and genetic diversity by Bensch et al. (2010, 2012, 2015). However, it shows a sufficient genetic distance (ITS, 100 %; tef1, 77 %; actA, 85.4 % similarity) with respect to the ex-type strain of *C. per­angustum* to be considered a distinct species. Morphologically, *C. angulosum* can be mainly differentiated from *C. per­angustum* by its conidiophores, which are usually branched forming a 90° angle, while those of the latter are only occasionally branched. In addition, the new species produces smaller secondary ramoconidia and intercalary conidia (up to 17 μm and 6 μm long, respectively, in *C. per­angustum* (Bensch et al. 2012). Another closely related species is *C. xantochromaticum*, but it is genet­ically well differentiated from *C. angulosum* (99.1 %, 81.1 % and 90.8 % similarity for ITS, tef1 and actA, respectively), and morphologically it has longer conidiogenous cells (up to 32 μm long vs 27 μm in *C. angulosum*), smaller ramoconidia (up to 39 μm long vs 46 μm long in *C. angulosum*) and does not grow at 35 °C.

*Cladosporium anthropophilum* Sandoval-Denis, Gené & Wiederhold, sp. nov. — MycoBank MB815334, Fig. 4

Etymology. From the Greek ἄνθρωπος (áνθρωπος) ‘human’ and φίλος (φίλος) ‘fondness’, referring to the source of the ex-type, human clinical samples.

Colonies on OA attaining 27–32 mm diam after 14 d at 25 °C, olive to olive brown (3F2/4F8), flat, dusty or granular, aerial mycelium scarce, with fimbriate margin; reverse olive brown (4F8) to black, without diffusible pigment. On PDA attaining 17–39 mm diam after 14 d at 25 °C, grey-green to deep green (28D7/D8), flat or folded, velvety to dusty or granular, aerial mycelium scarce, sometimes showing cottony to floccose white to grey cushions, with a regular margin; reverse dark green (28F8) to black. On SNA reaching 23–26 mm after 14 d at 25 °C, olive to olive brown (3F2/4F8), flat, dusty to cottony, aerial mycelium abundant, often with irregular to arachnoid margins; reverse olive to olive brown (3F2/4F8). Mycelium superficial and immersed, composed of septate, branched, 2–3 μm wide, subhyaline to pale green, smooth and thick-walled, anastomosing hyphae. Conidiophores erect, cylindrical, non-nodulose, geniculate, septate, usually branched, up to 550 μm long, 2–5 μm wide, pale green-brown, slightly roughened to verruculose toward the base, with a thickened and refractive wall. Conidiogenous cells terminal and intercalary, cylindrical or subcylindrical, 15–54 × 3–5 μm, often with a swollen apex, bearing 3–8(–10), protuberant, subdenticulate, 1–2.5 μm diam, thickened and somewhat darkened conidiogenous loci. Ramoconidia aseptate, cylindrical, 20–42 × 2–5 μm, pale green, smooth, with conidial scars protuberant, thickened and darkened. Conidia forming short branched chains with up to four conidia in the terminal unbranched part of the chain, aseptate, smooth or finely roughened, reticulate under SEM; small terminal conidia oval to ellipsoidal, 3.5–9 × 2–3 μm (av. ± SD) 5.6 (± 1.2) × 2.5 (± 0.4)), subhyaline; intercalary conidia limoniform to ellipsoidal, 4.5–11 × 2–3 μm (av. ± SD) 6.9 (± 1.8) × 2.7 (± 0.3)), light green-brown; secondary ramoconidia 0–1-septate, ellipsoidal to subcylindrical, usually attenuated at the centre, 7–28 × 2–5 μm (av. ± SD) 13.7 (± 4.8) × 3.4 (± 0.6)).

Cardinal temperature for growth — Optimum 25 °C, maximum 35 °C, minimum 5 °C.

Specimens examined. USA, Minnesota, from human bronchoalveolar lavage fluid, Sept. 2012, D.A. Sutton (holotype CBS H-22381, culture ex-type CBS 140685 = UTHSC DI-13-269 = FMR 13382); from human bronchoalveolar lavage fluid, Sept. 2012, D.A. Sutton, UTHSC DI-13-168 = FMR 13293; California, from a hand, Oct. 2010, D.A. Sutton, UTHSC DI-13-179 = FMR 13304; Florida, from human bronchoalveolar lavage fluid, Jan. 2007, D.A. Sutton, UTHSC DI-13-271 = FMR 13384; from human bronchoalveolar lavage fluid, Mar. 2007, D.A. Sutton, UTHSC DI-13-246 = FMR 13399; from an animal abscess, Jan. 2012, D.A. Sutton, UTHSC DI-13-178 = FMR 13303; Massachusetts, from human bronchoalveolar lavage fluid, Mar. 2012, D.A. Sutton, UTHSC DI-13-169 = FMR 13294; Texas, from human cerebrospinal fluid, Mar. 2009, D.A. Sutton, UTHSC DI-13-207 = FMR 13320; Florida, from human bronchoalveolar lavage fluid, Jan. 2007, D.A. Sutton, UTHSC DI-13-226 = FMR 13339; from human foot skin, May 2008, D.A. Sutton, UTHSC DI-13-228 = FMR 13341; from human pleural fluid, Apr. 2008, D.A. Sutton, UTHSC DI-13-244 = FMR 13357.

Fig. 4 Cladosporium anthropophilum CBS 140685. a–c. Colonies on (a) PDA, (b) SNA and (c) OA after 14 d at 25 °C; d–e. conidiophores and chains of conidia; f–g. detail of conidial ornamentation. — Scale bars: a–c = 10 mm; d–e = 5 μm; f–g = 1 μm.
Notes — *Cladosporium anthropophillum* is probably a common saprobic fungus, as determined by the number of isolates evaluated, and can also represent a clinically relevant fungus, being the second most prevalent species identified in a set of clinical isolates from the USA after *C. halotolerans* (Sandoval-Denis et al. 2015). The new taxon is morphologically similar to *C. cladosporioides* and *C. pseudocladosporioides*, but phylogenetically distinct. Although the three species are difficult to separate morphologically, *C. anthropophillum* mainly differs by its longer (up to 550 μm) conidiophores and oval to ellipsoidal terminal conidia (3.5–9 μm long) showing a fine reticulation under SEM. The conidiophores of *C. cladosporioides* and *C. pseudocladosporioides* are 10–250 μm and 15–155 μm long, respectively, and their terminal conidia are subglobose to limoniform ((3–)4–8–(11) μm long) and with a irregularly reticulate or striped wall in the former, and obovoid to ellipsoidal (3–5.5 μm long) and smooth-walled or almost so in the latter species (De Vries 1952, Bensch et al. 2012). *Cladosporium anthropophillum* also resembles *C. tenuissimum*, a species previously described as human opportunistic pathogen (De Hoog et al. 2011). However both are genetically well differentiated (99.3 %, 87.7 % and 89.9 % similarity for ITS, *tef1* and *actA*, respectively) and, morphologically, *C. anthropophillum* shows longer terminal conidia (3.5–9 μm long (av. (± SD) 5.6 (± 1.2)) vs (2–)2.5–5–(6) μm long (av. (± SD) 3.7 ± 1.0) in *C. tenuissimum*) and shorter intercalary conidia (4.5–11 μm long (av. (± SD) 6.9 (± 1.8)) vs (2–)2.5–4 μm long (av. (± SD) 2.3 (± 0.3))) in *C. tenuissimum* (Bensch et al. 2012).

**Cladosporium crousii** Sandoval-Denis, Cano & Guarro, sp. nov. — MycoBank MB815341; Fig. 5

*Etymology.* In honour of Pedro W. Crous for his extensive work on *Cladosporium.*

Colonies on OA attaining 47–50 mm diam after 14 d at 25 °C, olive to dark green (3F8/30F8), flat, velvety to granular, aerial mycelium scarce, margin fimbriate and with abundant submerged mycelia; reverse olive to dark green (3F8/30F8), to black, without diffusible pigment. On PDA attaining 73–77 mm diam after 14 d at 25 °C, olive brown (4E3/E6), radially folded, velvety or granular with floccose centre and regular margin; reverse at first dark brown (7F8) turning black. On SNA reaching 39–41 mm after 14 d at 25 °C, olive brown (4D5/F8), flat, velvety with floccose centre, margin fimbriate and with abundant submerged mycelium; reverse black. *Mycelium* superficial and immersed, composed of septate, branched, 2.5–3.5 μm wide, subhyaline hyphae, with slightly roughened walls. *Conidiophores* erect, cylindrical, septate, usually unbranched or sparingly branched, up to 230 μm long, 2–3.5 μm wide, pale green-brown, smooth-walled. *Conidiogenous cells* terminal and intercalary, cylindrical, sometimes geniculate toward the apex, 11–23 × 2.5–4 μm, bearing 1–4 conidiogenous loci of 1.5–2 μm diam, protuberant, black and refringent. *Ramoconidia* 0–1-septate, subcylindrical to cylindrical, 19–39 × 2–3 μm, pale brown, smooth. *Conidia* forming long branched chains with up to seven conidia in the terminal unbranched part of the chain, subhyaline, smooth, with protuberant, thickened and darkened conidial hila; small terminal conidia aseptate, ellipsoidal to subcylindrical, with a central constriction, 7–9 × 2–2.5 μm (av. (± SD) 7.8 (± 0.7) × 2.2 (± 0.2)); intercalary conidia aseptate, ellipsoidal to cylindrical, slightly curved, aseptate, 9–10 × 2–3 μm (av. (± SD) 9.5 (± 0.5) × 2.3 (± 0.4)); secondary ramoconidia 0–1-septate, cylindrical, 9.5–24 × 2.5–3.5 μm (av. (± SD) 15.7 (± 4.4) × 2.8 (± 0.3)).

*Cardinal temperature for growth — Optimum 25 °C, maximum 30 °C, minimum 15 °C.*

*Specimen examined.* USA, South Carolina, from human bronchoalveolar lavage fluid, May 2008, D.A. Sutton (holotype CBS H-22385, culture ex-type CBS 140686 = UTSHC DI-13-247 = FMR 13360).

Notes — *Cladosporium crousii* is closely related to *C. gamsianum*, but morphologically they are clearly differentiated. The first species is characterised by longer (up to 230 μm long) and pale coloured conidiophores with unthickened walls, and longer ellipsoidal terminal conidia (7–9 μm long). In contrast, *C. gamsianum* exhibits dark brown and thick-walled conidiophores of 10–146 μm long, and obovoid terminal conidia of 3–6 μm long (Bensch et al. 2010).

**Cladosporium flavovirens** Sandoval-Denis, Gené & Guarro, sp. nov. — MycoBank MB814508; Fig. 6

*Etymology.* From Latin *flavus* ‘yellow’ and *virens* ‘green’, referring to the colony colour on OA.

Colonies on OA attaining 53–55 mm diam after 14 d at 25 °C, olive yellow to olive (2D8/3F8) with olive grey to olive (2F2/E2) patches, flat, velvety to floccose, margin fimbriate and with abundant submerged mycelium; reverse olive yellow to olive...
(2D8/3F8) to black, without diffusible pigment. On PDA attaining 63–65 mm diam after 14 d at 25 °C, obverse and reverse green-grey to dark green (30F2/F8), flat or umbonate and radially folded, velvety, with regular margin. On SNA reaching from 30–32 mm after 14 d at 25 °C, olive to olive brown (2E8/3E8), flat, velvety to granular, margin slightly irregular and with abundant submerged mycelium; reverse olive yellow (2D8) to black. Mycelium superficial and immersed composed of septate, branched, 2–3 μm wide, subhyaline to pale green-brown, rough- and thick-walled hyphae, with abundant anastomoses. Conidiophores erect, cylindrical, sometimes geniculate, non-nodulose, septate, simple or branched, up to 170 μm long, 4–5 μm wide, medium green-brown, slightly roughened to verruculose, with thick and refractive walls. Conidiogenous cells terminal or intercalary, subcylindrical or cylindrical, 15–54 × 3–5 μm, bearing up to four conidiogenous loci of 1–2 μm diam, darkened and refringent. Ramoconidia 0–1-septate, subcylindrical to cylindrical, often geniculate, 27–75 × 3–4 μm, smooth or finely verruculose. Conidia forming branched chains with up to five conidia in the terminal unbranched part, pale green-brown, smooth- and thick-walled, with protuberant and darkened conidial hila; small terminal conidia aseptate, obovoidal to short ellipsoidal, 5–7 × 2.5–3 μm (av. (± SD) 5.9 (± 0.6) × 2.9 (± 0.2)); intercalary conidia aseptate, ellipsoidal, 7–10 × 3–3.5 μm (av. (± SD) 8.3 (± 0.9) × 3.2 (± 0.2)); secondary ramoconidia 0–2-septate, ellipsoidal to cylindrical, 9–30 × 3.5–4 μm (av. (± SD) 16.2 (± 6.7) × 3.8 (± 0.3)).

Cardinal temperature for growth — Optimum 25 °C, maximum 35 °C, minimum 15 °C.

Specimen examined. USA, Florida, from human toenail, Nov. 2006, D.A. Sutton (holotype CBS H-22326, culture ex-type CBS 140462 = UTHSC DI-13-273 = FMR 13386).

Notes — Cladosporium flavovirens is morphologically and phylogenetically related to C. flabelliforme. However, the new species is genetically well differentiated (99.8 %, 80.9 % and 81.8 % sequence similarity for ITS, tef1 and actA, respectively) and produces somewhat longer secondary ramoconidia (up to 30 μm) which are often septate, in contrast to the aseptate secondary ramoconidia of C. flabelliforme which are up to 27 μm long (Bensch et al. 2012).

Fig. 6 Cladosporium flavovirens CBS 140462. a–c. Colonies on (a) PDA, (b) SNA and (c) OA after 14 d at 25 °C; d, e. conidiophores and chains of conidia; f. conidia. — Scale bars: a–c = 10 mm, d–f = 5 μm.

Fig. 7 Cladosporium floccosum CBS 140463. a–c. Colonies on (a) PDA, (b) SNA and (c) OA after 14 d at 25 °C; d–e. conidiophores and conidia; f. chain of conidia. — Scale bars: a–c = 10 mm, d–f = 5 μm.
**Cladosporium floccosum** Sandoval-Denis, Cano & Guarro, *sp. nov.* — MycoBank MB814509; Fig. 7

*Etymology.* From Latin *floccosus* — MycoBank MB814511; Fig. 8

Colonies on OA reaching 24–27 mm after 14 d at 25 °C, grey-beige to olive brown (4C1/F4), slightly umbonate and radially folded, velvety to dusty with regular margins; reverse olive brown (4D4/F4), without diffusible pigments. On PDA attaining 47–50 mm diam after 14 d at 25 °C, grey-green to dark green (30E5/F7), flat to umbonate and slightly folded, velvety with white cottony centre and regular margin; reverse olive brown (4D8/E8) with black patches. On SNA reaching 15–20 mm after 14 d at 25 °C, olive brown (4D2/F4), flat, velvety to floccose with abundant grey aerial mycelium, margin lobate and fimbriate with abundant submerged mycelium; reverse olive brown to dull green (4E4/30E4).

**Mycelium** — Mycelium superficial and immersed composed of septate, branched, 1.5–4.5 μm wide, subhyaline to pale brown, verruculose and thin-walled hyphae. **Conidiophores** erect, flexuous, subcylindrical, distinctly geniculate, septate, mostly unbranched, up to 100 μm long, 4–5 μm wide, pale to medium olivaceous brown, smooth to slightly roughened, with thickened, darkened and refractive walls. **Conidiogenous cells** terminal, cylindrical, nodulose, 16–24 × 3–5 μm, smooth and thick-walled, bearing up to three conspicuous, refractive, slightly darkened conidiogenous loci of 1.5–2.5 μm diam. **Ramoconidia** not observed. **Conidia** forming unbranched chains with up to three conidia, pale brown, echinulate, with protuberant and darkened conidial hila; small terminal conidia 0–1-septate, sometimes slightly constricted at septa, obvoidal to ovoidal, 8–12.5 × 6–8.5 μm (av. (± SD) 10.7 ± 1.8) × 6.8 ± 0.9); intercalary conidia 0–1-septate, ellipsoidal, 12–15 × 6–8.5 μm (av. (± SD) 13.7 ± 1.0) × 7.5 ± 0.8); secondary ramoconidia not observed.

Cardinal temperature for growth — Optimum 25 °C, maximum 30 °C, minimum 15 °C.

**Specimen examined.** USA, Minnesota, from human ethmoid sinus, Sept. 2010, D.A. Sutton (holotype CBS H-23237, culture ex-type CBS 140463 = UTHSC DI-13-212 = FMR 13325).

Notes — *Cladosporium floccosum* is morphologically similar to *C. sinuosum*, which is also its closest phylogenetic relative; both species have distinctly geniculate conidiophores and do not form ramoconidia. However, *C. floccosum* has considerably smaller (up to 100 μm long) and rarely branched conidiophores and slightly shorter terminal conidia (up to 12.5 μm long) respect to those of *C. sinuosum*, which has conidiophores up to 380 μm long and terminal conidia up to 15 μm long (Schubert et al. 2007, Bensch et al. 2015).

**Cladosporium subcinereum** Sandoval-Denis, Deanna A. Sutton & Gené, *sp. nov.* — MycoBank MB814511; Fig. 8

*Etymology.* From Latin *subcinereum* ‘somewhat grey’, referring to the colony colour.

Colonies on OA reaching 29–32 mm after 14 d at 25 °C, yellow-grey to olive grey (3B2/E2), flat, velvety to cottony, with regular margin, abundant crystalline exudates occasionally present; reverse yellow-grey to olive grey (3B2/E2) to black. On PDA attaining 34–37 mm diam after 14 d at 25 °C, yellow-grey to olive (3B2/F8), flat to radially folded, velvety to floccose, with regular margin; reverse dark green (3F8) to black. On SNA reaching 14–16 mm after 14 d at 25 °C, obverse and reverse white to olive (3A1/E3), flat, velvety to cottony, with regular margin. **Mycelium** superficial and immersed, composed of branched, septate, 2–5 μm wide, subhyaline hyphae with smooth or minutely verruculose and unthickened walls. **Conidiophores** erect, flexuous, geniculate and nodulose, septate, simple or branched, up to 140 μm long, 4–6 μm wide, pale to medium-brown, smooth to verruculose and thick-walled. **Conidiogenous cells** terminal, subcylindrical, nodulose, geniculate, 16–38 × 4–6 μm, thick-walled, bearing up to three conidiogenous loci of 2–3 μm diam, protuberant, darkened and refractive. **Ramoconidia** rarely formed, 0–2-septate, cylindrical, nodulose, 19–59 × 3–6 μm, pale brown, finely roughened. **Conidia** forming unbranched chains with up to three conidia, pale brown, echinulate, with protuberant and darkened conidial hila; small terminal conidia 0–1-septate, globose to subglobose, 5–7 × 4.5–6.5 μm (av. (± SD) 5.6 ± 0.7) × 5.3 ± 0.6); intercalary conidia 0–1-septate, subglobose, obvoidal to ellipsoidal, 6–10 × 5–6.5 μm (av. (± SD) 8.9 ± 1.4) × 5.9 ± 0.6); secondary ramoconidia 0–2-septate, sometimes constricted at septum, ellipsoidal to subcylindrical, often inflated at the apex, 8–27 × 4–7 μm (av. (± SD) 16.3 ± 5.6) × 5.0 ± 0.8).

Cardinal temperature for growth — Optimum 25 °C, maximum 30 °C, minimum 15 °C.

**Specimen examined.** USA, Montana, from human sputum, Sept. 2007, D.A. Sutton (holotype CBS H-23239, culture ex-type CBS 140465 = UTHSC DI-13-257 = FMR 13370).

![Fig 8 Cladosporium subcinereum CBS 140465. a–c. Colonies on (a) PDA, (b) SNA and (c) OA after 14 d at 25 °C; d–e. conidiophores and chains of conidia; f–g. detail of conidial ornamentation. — Scale bars: a–c = 10 mm; d–e = 5 μm; f–g = 1 μm.](image-url)
Notes — This species is phylogenetically related to *C. angusttherbarum* and *C. variabile*. However, *C. angusttherbarum* produces shorter and narrower conidiophores (up to 60 μm long and 4 μm wide) and does not form ramoconidia, while *C. variabile* produces multisepitate ramoconidia and long chains of broadly ellipsoidal conidia with a fine granulate ornamentation under SEM (De Vries 1952, Bensch et al. 2012). In *C. subcinereum* and *C. ornamento* they are 0–2-septate, and its conidia are subglobose, obovoidal to ellipsoidal, exhibiting a much prominent muricate to pustulate ornamentation under SEM (De Vries 1952, Bensch et al. 2012). In *C. variabile* the conidia are subglobose, obovoidal, with abundant production of ramoconidia and by its oval to short clavate terminal conidium. However, the new species can be differentiated by the length and number of septa of their ramoconidia. In *C. variabile* there are 15–37 μm and (11.5–)20.5–40(–48) μm long, respectively, and they have up to five septa (Zalar et al. 2007, Bensch et al. 2012), while in *C. succulentum* the ramoconidia are 20–36 μm long with 0–1 septa. The phylogenetically closest species to *C. succulentum* are *C. fusiforme* and *C. velox* (sequence similarities less than 99.8 %, 80.7 % and 86.6 % for ITS, *tef1* and *actA*, respectively), but the new species can be differentiated by the abundant production of ramoconidia and by its oval to short clavate terminal conidium. Ramoconidia in *C. fusiforme* and *C. velox* are rarely formed and their terminal conidia are obovoid to fusiform in the first species and globose to ovoid in the latter one (Zalar et al. 2007).

*Cladosporium succulentum* Sandoval-Denis, Deanna A. Sutton & Cano, *sp. nov.* — MycoBank MB814512; Fig. 9

**Etymology.** From Latin *succo* 'juice' and *ulentum* 'full of', referring to the abundant production of exudates on PDA.

Colonies on OA reaching 23–25 mm after 14 d at 25 °C, dark green (30F3/F8), flat, granular to floccose, with fimbriate margin; reverse olive to dark green (3F8/30F4) turning black. On PDA attaining 28–35 mm diam after 14 d at 25 °C, olive brown (4F4/F8), flat, velvety to granular, white, with regular margin; producing abundant dark green exudates after 20–25 d; reverse black-blue (20F8) to black. On SNA reaching 27–32 mm after 14 d at 25 °C, obverse and reverse olive to olive brown (3EB/4EB), flat, downy to granular, with regular margin. Mycelium superficial and immersed, composed of septate, branched, 1.5–3.5 μm wide, subhyaline, smooth- and thin-walled hyphae. *Conidiophores* erect, straight or flexuous, septate, highly branched, up to 190 μm long, 2.5–4 μm wide, subhyaline, pale green-brown, smooth to finely roughened and thin-walled. *Conidigenous cells* terminal and intercalary, cylindrical, 13–30 × 2–4 μm, thin-walled, bearing 2–6 conidiogenous loci of 1–2.5 μm diam, darkened and refractive. *Ramoconidia* 0–1-septate, cylindrical to subcyindrical, flexuous, 20–36 × 2–4 μm, pale green-brown, smooth to finely roughened. *Conidia* in branched chains, with up to six conidia in the terminal unbranched part, asperate, pale green-brown, smooth- and thin-walled, with protuberant and darkened conidial hila; small terminal conidia oval to short clavate, 3–4 × 2–3 μm (av. (± SD) 3.6 (± 0.4) × 2.2 (± 0.4)), aseptate, with conspicuous and darkened conidial scars; intercalary conidia ovoid to limoniform, 4–6 × 2–3 μm (av. (± SD) 5.1 (± 0.6) × 2.3 (± 0.4)), with protuberant and not darkened conidial scars; secondary ramoconidia ellipsoidal to subcylindrical, 5–10 × 2–4.5 μm (av. (± SD) 8.2 (± 1.5) × 2.5 (± 0.4)).

Cardinal temperature for growth — Optimum 25 °C, maximum 35 °C, minimum 15 °C.

**Specimen examined.** USA, Florida, from a dolphin bronchus, July 2007, D.A. Sutton (holotype CBS H-22330, culture ex-type CBS 140466 = UTHSC DI-13-262 = FMR 13373).

Notes — *Cladosporium succulentum* is morphologically similar but genetically distant to *C. halotolerans* (98.4 %, 66.5 % and 79.8 % sequence similarity for ITS, *tef1* and *actA*, respectively) and *C. sphaerospermum* (97.5 %, 72.7 % and 83.8 % sequence similarity for ITS, *tef1* and *actA*, respectively). The latter two species can be differentiated from *C. succulentum* by having a maximum growth temperature at 30 °C (Zalar et al. 2007, Bensch et al. 2012) (35 °C in *C. succulentum*), and in the length and number of septa of their ramoconidia. In *C. halotolerans* and *C. sphaerospermum* these are 15–37 μm and (11.5–)20.5–40(–48) μm long, respectively, and they have up to five septa (Zalar et al. 2007, Bensch et al. 2012), while in *C. succulentum* the ramoconidia are 20–36 μm long with 0–1 septa. The phylogenetically closest species to *C. succulentum* are *C. fusiforme* and *C. velox* (sequence similarities less than 99.8 %, 80.7 % and 86.6 % for ITS, *tef1* and *actA*, respectively), but the new species can be differentiated by the abundant production of ramoconidia and by its oval to short clavate terminal conidium. Ramoconidia in *C. fusiforme* and *C. velox* are rarely formed and their terminal conidia are obovoid to fusiform in the first species and globose to ovoid in the latter one (Zalar et al. 2007).

*Cladosporium tuberosum* Sandoval-Denis, Cano & Wiederhold, *sp. nov.* — MycoBank MB815339; Fig. 10

**Etymology.** From Latin *tuberōsus* 'lumpy' (full of protuberances), because of the nodulose shape of its conidiophores.

Colonies on OA reaching 23–26 mm after 14 d at 25 °C, olive brown (4D5/F7), flat, velvety to floccose, margin regular and with abundant submerged mycelium; reverse olive brown (4D5/
F7) to black. On PDA attaining 44–50 mm diam after 14 d at 25 °C, dull green to dark green (30E4/F7), flat and radially folded, velvety to dusty, margin regular and white; reverse olive brown (4E8) to black. On SNA reaching 13–20 mm after 14 d at 25 °C, olive brown (4E4/F4), flat, velvety with cottony patches, margin irregular and with abundant submerged mycelium; reverse olive brown (4E4/F4) to black. Mycelium superficial and immersed, composed of septate, branched, 3–4.5 μm wide, subhyaline, smooth and thin-walled hyphae. Conidiophores erect, flexuous, cylindrical-oblong, nodulose, or bent once or several times being geniculate, laterally swollen, septate, unbranched or rarely laterally branched, up to 390 μm long, 5–6 μm wide, pale brown to olivaceous brown, smooth- and thick-walled. Conidiogenous cells terminal or intercalary, cylindrical or subnodulose, 15–38 × 4–6.5 μm, proliferating sympodially, forming lateral shoulders, bearing 1–2 conidiogenous loci at each shoulder, loci protuberant, 2–2.5 μm diam, darkened and refringent. Ramoconidia not observed. Conidia in branched chains, with up to three conidia in the terminal part, 0–1-septate, green-brown to yellow-brown, verrucose to echinulate and thick-walled with protuberant and darkened conidial hila; small terminal conidia oval, obovate or short elliptical, 4–5 × 2.5–3.5 μm (av. (± SD) 13.7 (± 0.7) × 8.5 (± 0.9)); secondary ramoconidia elliptoidal to subcylindrical, 14–18 × 6–10 μm (av. (± SD) 16.1 (± 1.2) × 7.1 (± 1.3)).

Cardinal temperature for growth — Optimum 25 °C, maximum 30 °C, minimum 5 °C.

Specimens examined. USA, Florida, from human nasal biopsy, Dec. 2009, D.A. Sutton (holotype CBS H-22387, culture ex-type CBS 140693 = UTHSC DI-13-217 = FMR 13330); Washington, from human foot, Oct. 2009, D.A. Sutton, UTHSC DI-13-219 = FMR 13332.

Notes — This species is represented by two isolates of human clinical origin which cluster in a lineage clearly differentiating and together with C. basiinflatum group in a position basal to the remaining species of the C. herbarum complex (Fig. 1). Despite this basal position, it shows the typical morphological features of the species of the complex. Cladosporium tuberosum morphologically resembles C. sinuosum in the production of short conidial chains and the absence of ramoconidia (Schubert et al. 2007). However, in C. tuberosum the conidiophores are not as geniculate as in C. sinuosum and the conidia are always grouped forming short chains, while the conidia in C. sinuosum are often solitary although short chains can be also present (Bensch et al. 2015). In addition, C. tuberosum exhibits a faster growth rate on PDA, forming colonies almost black at the obverse rather than the olivaceous grey to pale olivaceous grey colonies of C. sinuosum (Bensch et al. 2015).

Cladosporium xantochromaticum Sandoval-Denis, Gené & Cano, sp. nov. — MycoBank MB815340; Fig. 11

Etymology. From Greek xanthós (ξανθός) ‘yellow’ and khrôma (χρῶμα) ‘colour’, referring to the production of a yellow diffusible pigment on PDA.

Colonies on OA reaching 40–50 mm after 14 d at 25 °C, obverse and reverse olive brown to grey-green (4F8/30E7), flat, granular, radiate, margin regular and with abundant submerged mycelium; diffusible pigment absent. On PDA attaining 60–67 mm diam after 14 d at 25 °C, olive brown (4E8/F8), flat or folded at centre, dusty or granular, velvety toward the periphery, margin regular, white to yellow, and with abundant submerged mycelium; reverse black, with a light yellow to grey-yellow (2A5/B5) diffusible pigment. On SNA reaching 35–37 mm after 14 d at 25 °C, olive brown (4E5/E8), flat, velvety to granular, radiate, margin regular and with abundant submerged mycelium; reverse olive brown (4E5/E8) to black, without diffusible pigment. Mycelium superficial and immersed, composed of septate, branched, 1.5–3 μm wide, pale brown, smooth and thin-walled hyphae. Conidiophores erect, flexuous, cylindrical, non-nodulose, septate, simple or branched typically immediately before a septum, up to 210 μm long, 2–4 μm wide, pale brown, smooth and thin-walled. Conidiogenous cells terminal, cylindrical, sometimes geniculate, 12–32 × 3–4 μm, bearing up to three conidiogenous loci of 1–1.5 μm diam, darkened and refringent. Ramoconidia aseptate, subcylindrical to cylindrical, 18–36 × 2–3.5 μm, pale brown, smooth or finely roughened. Conidia forming branched chains, with up to four conidia in the terminal unbranched part, pale green-brown, smooth- and thin-walled, with protuberant, not darkened conidial hila; small terminal conidia aseptate, obovate to short elliptoidal 4–5 × 2–2.5 μm (av. (± SD) 4.3 (± 0.3) × 2.2 (± 0.2)); intercalary conidia aseptate, elliptoidal to limoniform, 5–7 × 2.5–3.5 μm (av. (± SD) 5.8 (± 0.6) × 2.6 (± 0.3)); secondary ramoconidia 0–1-septate, subcylindrical, sometimes slightly constricted at the centre, 10–28 × 3–4 μm (av. (± SD) 15.7 (± 5.2) × 3.3 (± 0.4)).
Cardinal temperature for growth — Optimum 20 °C, maximum 30 °C, minimum 5 °C.

Specimen examined. USA, Texas, from human bronchoalveolar lavage fluid, Sept. 2010, D.A. Sutton (holotype CBS H-22388, culture ex-type CBS 140691 = UTHSC DI-13-211 = FMR 13324).

Notes — This species belongs to the C. cladosporioides species complex and clusters with C. angulosum and C. perangustum, forming a basal lineage characterised by narrow conidia and slightly roughened conidiophores and conidia. Bensch et al. (2012) considered C. perangustum a species with considerable genetic variability but morphologically uniform. The new species, however, is genetically (99.1 %, 75 % and 89.1 % sequence similarity for ITS, tef1 and actA, respectively) and phenotypically well differentiated from C. perangustum. Cladosporium xantochromaticum has smaller ramoconidia (18–36 × 2–3.5 μm) and smooth-walled conidiophores, while in C. perangustum the ramoconidia are 25–45 × 2.5–3(–4.5) μm and the conidiophores are more or less rough-walled especially towards the base, asperulate-verruculose, and smooth to almost so at the apex (Bensch et al. 2010).

**DISCUSSION**

The genus Cladosporium has been extensively reviewed in recent years in efforts to clarify the phylogeny and taxonomic structure of its species and allied fungi, and has resulted in a modern redefinition of the genus (Crous et al. 2007a, b, Schubert et al. 2007, Zalar et al. 2007, Bensch et al. 2010, 2012, 2015). However, until recently, no attempt had been made to study the impact of these new approaches in the diversity of Cladosporium species of clinical interest.

In a previous study, we demonstrated that the species diversity of Cladosporium associated to clinical samples was underestimated (Sandoval-Denis et al. 2015). Furthermore, we found that species traditionally considered clinically relevant, identified by phenotypic criteria alone, were among the least represented. In fact, several morphologically similar sibling species were found to be more prevalent, including putative new taxa (De Hoog et al. 2011, Sandoval-Denis et al. 2015). Those previously undescribed lineages are characterised here using both molecular and phenotypic criteria and resulting in the proposal of 10 new Cladosporium species. Sampling for this study was limited to isolates from the USA, and a wider sampling area is expected to provide a more precise reflection of the real distribution of these new species around the world. The new species proposed here have been mostly isolated from human respiratory samples, which might be explained by the fact that Cladosporium conidia are easily dispersed by air (David 1997). However, the clinical relevance of the species of this genus, at least to produce invasive disease, has been questioned by their inability to grow at 37 °C (De Hoog et al. 2011, Sandoval-Denis et al. 2015), which was also confirmed with the new species. Nevertheless, despite the large number of species involved in this study, some of them were represented by numerous isolates, such as C. anthropophilum, which could be linked to a certain degree of specialisation towards colonisation of the human respiratory tract.

Within a given species complex, the different species of Cladosporium are often difficult to identify from morphological characters alone. However, some key differential features have been identified and have been detailed in a series of monographic papers (Schubert et al. 2007, Zalar et al. 2007, Bensch et al. 2012). We have followed the criteria from those papers in order to distinguish potentially new species from their closest phylogenetic and morphological relatives. As is usual in this genus, no sexual morphs were observed in any of them. In fact, sexual structures have been observed in vitro in only eight accepted species of Cladosporium (Bensch et al. 2012). Among the species described here, the most relevant differential morphological traits were the presence of ramoconidia, the length, complexity and ornamentation of the conidiophores, intercalary and terminal conidia. However, given the overlapping of these features, and the need for standardisation using special culture media and scanning electron microscopy procedures, the use of a molecular approach should be mandatory for correct identification of the species in this complex fungal group. With these studies, we have considerably expanded the list of Cladosporium species as potential human opportunistic fungi, which makes their identification difficult given their high morphological similarity (De Hoog et al. 2015). That said, distinguishing morphologically similar species of Cladosporium seems not to be as relevant from a clinical perspective because the in vitro antifungal response does not differ considerably between species of the same species complex (Sandoval-Denis et al. 2015). In contrast, in vitro antifungal susceptibilities do differ between

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**Fig. 11** Cladosporium xantochromaticum CBS 140691. a–c. Colonies on (a) PDA, (b) SNA and (c) OA after 14 d at 25 °C; d–f. conidiophores and chains of conidia. — Scale bars: a–c = 10 mm, d–f = 5 μm.
species complexes, with the C. sphaerospermum complex showing higher inhibitory concentrations against amphotericin B, azoles and caspofungin (Sandoval-Denis et al. 2015).

Our phylogenetic studies agree with previous revisions of the genus (Schubert et al. 2007, Zalar et al. 2007, Bensch et al. 2012). The most phylogenetic informative markers were actA and tef1, while ITS sequences were usually identical for species of the same complex as previously reported by Bensch et al. (2010). Although most of the taxa in the present study are consistently separated in terms of their genetic and morphological differences, a high genetic variability was observed in the clades representing the new species C. anthropophilum and C. tuberosum, as well in clades representing well-known species, i.e. C. allicinum, C. perangustum, C. pseudocladosporioides, C. sinusum and C. tenuissimum. This might indicate an ongoing process of active divergence and speciation as it has been described for other fungi, which demands further study (Gao et al. 2015).

Several studies have shown a higher number of species in the C. cladosporioides complex (Bensch et al. 2010, 2012, 2015) and our results agree with them. Of the taxa that were newly described here, six species belonged to the C. cladosporioides complex, whereas only three and one, belonged to the C. herbarum and C. sphaerospermum species complexes, respectively. The C. cladosporioides complex is phylogenetically well-defined and includes a large group of species characterised by unbranched or branched, almost cylindrical conidiophores, bearing aroid to ellipsoidal intercalary and terminal conidia, smooth or rarely showing a fine ornamentation (Bensch et al. 2012). Although most of the known species of this complex do not tolerate high temperatures, our results showed that in the C. cladosporioides complex at least three of the new species (C. angulosum, C. anthrophilum and C. flavovirens), as well as several isolates identified as C. pseudocladosporioides are able to grow at 35 °C, which might explain their relatively high rate of isolation from homoeothermic hosts.

The C. herbarum species complex is also phylogenetically and morphologically very well-defined and contains a less diverse group of species characterized by nodulose conidiophores, bearing distinctly ornamented, globose to subglobose terminal conidia (Schubert et al. 2007). It is interesting that none of the new species of this complex were able to grow at temperatures higher than 30 °C. In contrast, the only new species described in the C. sphaerospermum complex was able to growth and sporulate, although poorly, at 35 °C. The members of the C. sphaerospermum species complex are morphologically homogeneous, characterised by conidiophores that are usually branched and lacking nodose inflations, producing both smooth-walled and ornamented conidia (Zalar et al. 2007). Most species currently included in this group exhibit a high degree of osmotic tolerance, but are unable to grow at temperatures exceeding 30 °C (Zalar et al. 2007, Bensch et al. 2012). However, it has been suggested previously that this complex does not represent a monophyletic group, but most likely represents various species complexes instead (Bensch et al. 2012). This was also suggested by our phylogenetic results which revealed that the species currently included in the C. sphaerospermum complex consistently grouped together as a polyphyletic arrangement in both combined and individual analyses, forming at least five different lineages with high statistical support and important genetic differences. The new species C. succulentum grouped in a lineage with C. aciculare, C. fusiforme, C. longissimum, C. sphaerospermum and C. velox. However, as previously described, there are no phenotypic differences to discriminate among these closely related taxa that would warrant the establishment of additional species complexes to accommodate these lineages (Zalar et al. 2007, Bensch et al. 2015).

In this study, the analysis of isolates from human and animal clinical specimens has allowed us to considerably increase the known diversity of species for the genus, expanding substantially the spectrum of species of potential clinical interest. Further studies are needed to fully understand the ecology and importance of these new species in the aetiology of infections in warm-blooded hosts.

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