

New and interesting chaetothyrialean fungi from Spain

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Abstract

In the course of taxonomic studies on saprobic microfungi from Spain, several slow-growing, dematiaceous hyphomycetes were isolated from soil, submerged plant material and river sediments. Sixteen of these strains were identified as members of the ascomycete order Chaetothyriales on the basis of morphology and DNA sequence analyses of the internal transcribed spacer region and partial large subunit ribosomal RNA gene. These included three novel species (*Cladophialophora pseudocarrionii*, *Cyphellophora chlamydospora*, and *Rhinocladiella amoena*) and five interesting, little-known or clinically-relevant species (*Cyphellophora suttonii*, *Exophiala aquamarina*, *E. lacus*, *E. radialis*, and *Rhinocladiella similis*). In addition, *Exophiala oligosperma*, an emerging opportunistic fungus, was found for the first time in an aquatic freshwater environment (river sediments). *Cladophialophora pseudocarrionii* resembles *C. carrionii* in the branching pattern of its conidial chains, but differs from the latter species in its inability to grow at 30 °C. *Cyphellophora chlamydospora* differs from other species of the genus in the absence of conidiation, producing only chlamydospores in vitro. *Rhinocladiella amoena* shows branched conidiophores similar to those of *R. anceps*, *R. atrovirens*, *R. basitona* and *R. similis*, but differs from them in conidial shape and size. The ex-type strain of *Phialophora livistonae*, included in the phylogenetic study, clustered with high statistical support with members of the genus *Cyphellophora* and is transferred to this genus.

Keywords

Black yeasts, Chaetothyriales, *Cladophialophora*, *Cyphellophora*, *Exophiala*, *Rhinocladiella*

Introduction

Chaetothyriales is a species-rich, ecologically diverse order of Ascomycota (Geiser et al. 2006; Gueidan et al. 2014). It includes saprophytes associated with soil and decaying plant material (Iwatsu 1984; Decock et al. 2003; Badali et al. 2011), numerous clinically-relevant species (de Hoog et al. 2000; Badali et al. 2008; Feng et al. 2012), and fungi causing disease in aquatic, cold-blooded animals (de Hoog et al. 2011; Vicente et al. 2012). In addition, a number of species in this order are associated with living plants, occurring either as apparently harmless epi- or endophytes (Narisawa et al. 2007; Chomnunti et al. 2012) or as pathogens (Crous et al. 2006, 2007b; Gueidan et al. 2014). Some Chaetothyriales are abundant in humid indoor habitats (Matos et al. 2002; Döğen et al. 2013), but other species, by contrast, colonize harsh environments where they have to cope with drought, scarce nutrient availability, extreme temperatures and high UV-light exposure (Gueidan et al. 2008; Tsuneda et al. 2011). This order has also received special attention due to the recent discovery of mutualistic interactions with ant species (Voglmayr et al. 2011; Nepel et al. 2014), and to the ability of certain species to degrade aromatic hydrocarbon contaminants (Prenafeta-Boldú et al. 2001; Badali et al. 2011).

Chaetothyrialean fungi may be difficult to isolate from environmental samples due to their slow growth rates. On common mycological media, they are usually overgrown by fast-growing molds such as *Aspergillus*, *Penicillium* or members of the Mucorales. Therefore, special isolation techniques may be necessary. Previous authors have successfully implemented methods using experimental inoculations in laboratory animals (Gezuele et al. 1972; Dixon et al. 1980), high incubation temperatures (Sudhadham et al. 2008), extraction with mineral oil (Satow et al. 2008; Vicente et al. 2008), enrichment on atmospheres with aromatic hydrocarbons (Prenafeta-Boldú et al. 2001; Zhao et al. 2010) and media containing cycloheximide (Salgado et al. 2004). In our experience, media with cycloheximide proved to be very useful to isolate members of the Chaetothyriales. Using such media, we isolated the recently described taxa *Cladophialophora multiseptata*, *Cyphellophora catalaunica*, and *Knufia tsuneda* (Crous et al. 2013). In this study, we report the results of a morphological and molecular characterization of 16 strains of chaetothyrialean fungi obtained with the aid of cycloheximide-containing media, from diverse Spanish environmental samples.

Materials and methods

Sampling areas, fungal isolation and strains studied

Samples of soil, submerged plant material and river sediments were collected in forest areas and urban sites of five Spanish autonomous communities, i.e. Aragon, Asturias, Castile-La Mancha, Castile-Leon, and Catalonia. Samples were placed into polyethylene bags and kept in a refrigerator at 4–7 °C until processed. Approximately 1 g of each sample was diluted in 9 ml of sterile water and a Digiralsky spreader was used to spread a 500- μ L aliquot of the mix on the surface of plates with potato-dextrose agar (PDA; Difco Laboratories, USA) or dichloran rose-bengal chloramphenicol agar (DRBC; Oxoid, UK), both supplemented with cycloheximide at a final concentration of 0.1 mg/mL. The plates were incubated at 25 °C in the dark and observed weekly. Pure cultures were obtained by transferring conidia from slow-growing, darkly pigmented colonies growing on the primary cultures to PDA plates,

with the aid of a sterile dissection needle. These PDA plates were incubated at 25 °C for 14 days in the dark and then DNA extraction and subculturing onto other media for morphological studies were performed. Strains were preserved in the fungal culture collections of the Medicine Faculty, Rovira i Virgili University, Reus, Spain (FMR collection), and at the CBS-KNAW Fungal Biodiversity Centre, Utrecht, The Netherlands (CBS).

Phenotypic characterization

Colony morphology was studied on malt extract agar (MEA; Oxoid) and oatmeal agar (OA; 30 g filtered oat flakes, 20 g agar, 1 L distilled water) after 14 days at 24 °C in the dark. Cardinal growth temperatures were determined from cultures on MEA at temperatures ranging from 6 to 36 °C at intervals of 6 °C. Microscopic morphology was studied from slide cultures on OA at 24 °C after 21 days. For one strain, i.e. CBS 127581, which did not sporulate on OA, slide cultures were also prepared on MEA and potato-carrot agar (PCA; 20 g of potatoes, 20 g of carrots, 20 g of agar, 1 L of distilled water). Photomicrographs were obtained using a Zeiss Axioskop 2 Plus light microscope.

DNA sequence analyses

DNA extraction and purification was performed directly from colonies on PDA by following the Fast DNA kit protocol (Bio 101, Vista, CA, USA), with the homogenization step repeated five times with a FastPrep FP120 instrument (Thermo Savant, Holbrook, NY, USA). The internal transcribed spacer region (ITS) and the D1/D2 domains of the large subunit rRNA gene (LSU) were sequenced with the primer pairs ITS5/ITS4 and NL1/NL4 as described by White et al. (1990) and O'Donnell (1993), respectively. Purification of PCR products was carried out with the GFXTM PCR DNA kit (Pharmacia Biotech, Cerdanyola, Spain) and these were stored at –20 °C until sequencing. PCR products were sequenced with the same primers used for amplification and following the *Taq* Dydeoxy Terminator cycle sequencing kit protocol (Applied Biosystems, Gouda, The Netherlands). DNA sequencing reaction mixtures were analyzed on a 310 DNA sequencer (Applied Biosystems). Consensus sequences were obtained from the complementary sequences of each strain using the SeqMan software (Lasergene, Madison, WI, USA). BLAST searches (Altschul et al. 1990) were performed with the ITS and LSU sequences of the strains studied in order to compare them with those of species deposited in GenBank. For molecular species identification, percent identities of just the ITS locus were considered, because it offers a higher resolution than the relatively conserved LSU gene (Iwen et al. 2002). If the identity of the ITS sequence of a studied strain to its closest match was $\geq 99\%$, they were considered conspecific (Zeng et al. 2007). In rare cases where more than one species yielded 99 % identity, but none of them reached 100 %, the studied strain was identified only to genus level.

The level of variation among ITS sequences of all taxa included in this study was too high to obtain a reliable, non-ambiguous alignment. Therefore, the phylogenetic studies included a general LSU-based tree with all new species and records, and related members of Chaetothyriales (Fig. 1), and four ITS-based phylogenetic trees for specific genera, including: (1) *Cladophialophora* (Fig. 2), (2) *Cyphellophora* (Fig. 3), (3) *Exophiala* (Fig. 4), and (4) *Rhinocladiella* and morphologically similar chaetothyrialean genera, such as *Fonsecaea*, *Thysanorea*, and *Veronaea* (Fig. 5), all of which produce sympodial, denticulate

conidiogenous cells (de Hoog et al. 2000; Arzanlou et al. 2007). The *Cyphellophora* and *Rhinocladiella* ITS trees included all members of those genera for which ITS sequences are currently available at GenBank. However, in the *Cladophialophora* and *Exophiala* ITS trees, the ingroup only included species belonging in Herpotrichiellaceae, the family which includes the type species of these genera, i.e. *C. carrionii* and *E. salmonis*, respectively (de Hoog et al. 2000). BLAST searches and previous literature (Réblová et al. 2013; Gueidan et al. 2014) revealed that several species in these genera are related to other families in Chaetothyriales. Excluded members of *Cladophialophora* include three species in Epibryaceae (*C. humicola*, *C. minutissima*, and *C. sylvestris*), three species in Trichomeriaceae (*C. modesta*, *C. proteae* and *C. pucciniophila*), and two species related to Cyphellophoraceae (*C. hostae* and *C. scillae*, the latter used as outgroup). Excluded *Exophiala* spp. include *E. eucalyptorum* (Chaetothyriaceae), and *E. encephalarti* and *E. placitae* (both members of Trichomeriaceae, of which the latter was used as outgroup). ITS and LSU sequences were aligned with the MUSCLE webserver (<http://www.ebi.ac.uk/Tools/msa/muscle/>, Edgar 2004) and then adjusted manually with a text editor to correct misalignments and exclude ambiguous regions. Phylogeny reconstructions were performed with the maximum likelihood method with MEGA 6 (Tamura et al. 2013), using the best DNA substitution models chosen by that software. The statistical support for the groupings was assessed by bootstrap analysis of 1000 replicates. The DNA sequences and alignments generated during this study were deposited in GenBank (Table 1) and TreeBASE (study accession URL: <http://purl.org/phylo/treebase/phyloids/study/TB2:S18979>), respectively.

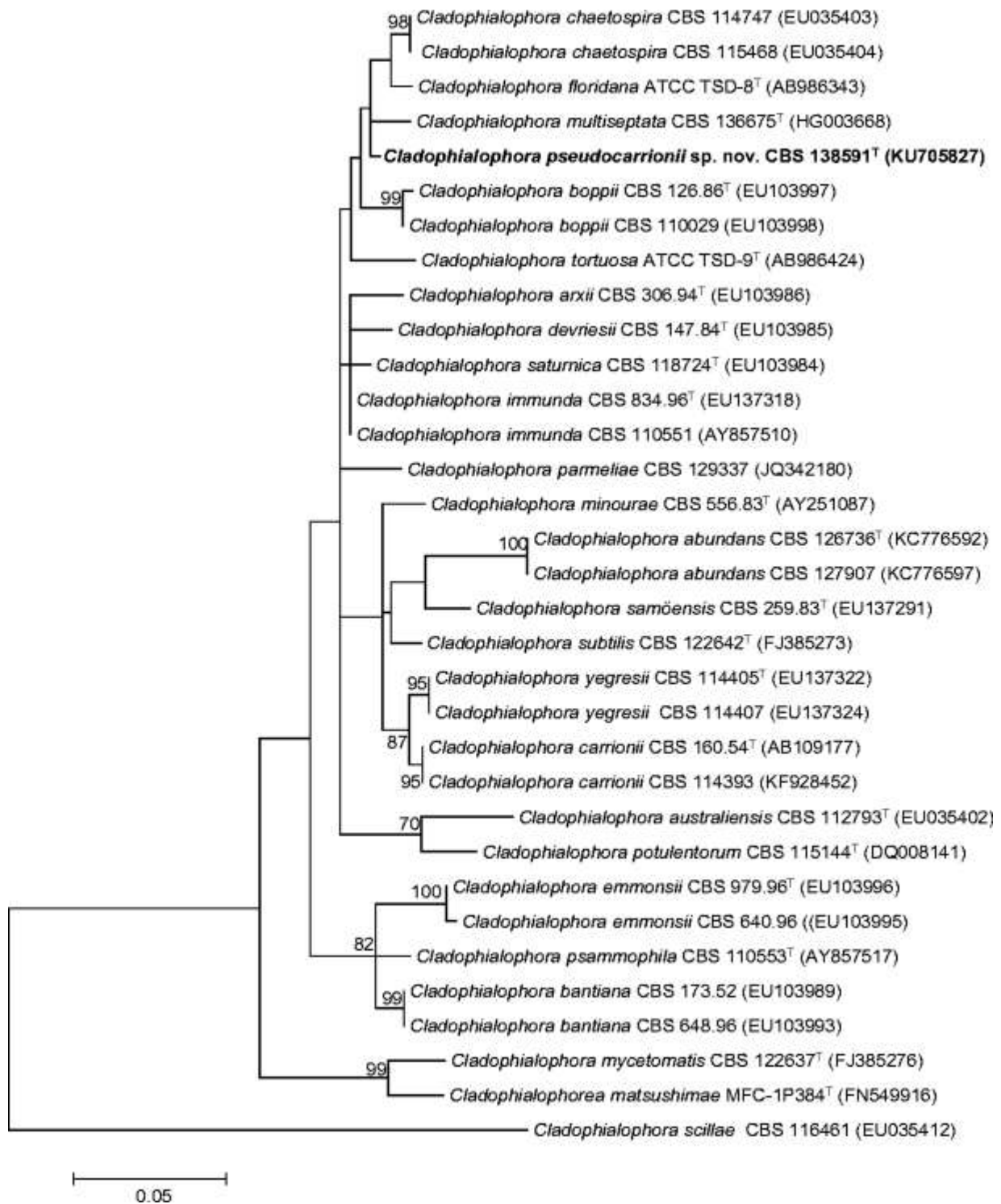


Fig. 2. Maximum likelihood tree constructed with partial sequences of the ITS region of *Cladophialophora* spp. Branch lengths are proportional to distance. Bootstrap values $\geq 70\%$ are shown near the internodes. The ingroup includes all species of this genus belonging to Herpotrichiellaceae for which DNA sequences are available at GenBank. *Cladophialophora scillae*, a species related to Cyphellophoraceae (Gueidan et al. 2014), was used as outgroup. ^T ex-type strain

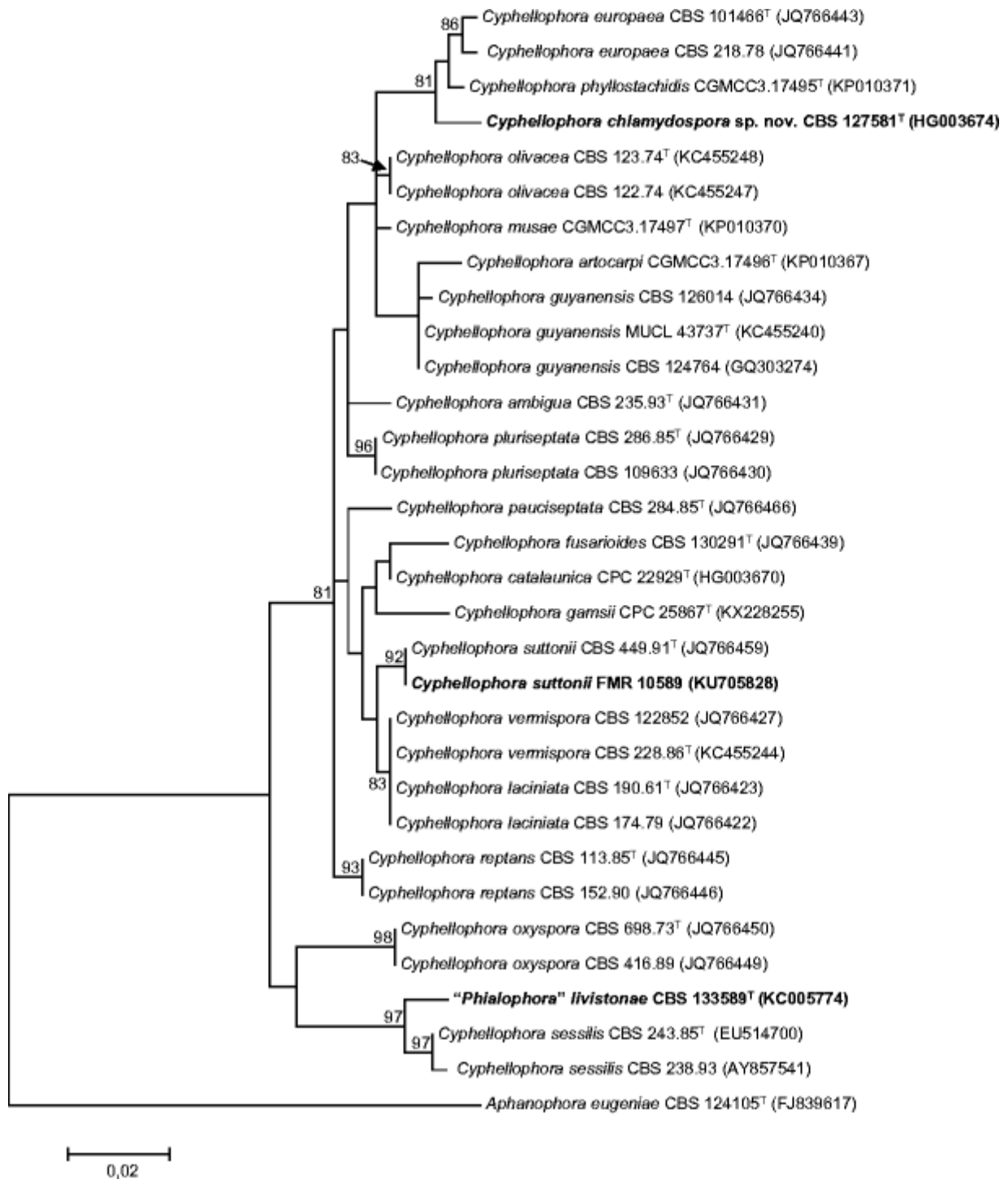


Fig. 3. Maximum likelihood tree constructed with partial sequences of the ITS region of *Cyphellophora* spp. Branch lengths are proportional to distance. Bootstrap values $\geq 70\%$ are shown near the internodes. The ingroup includes all species of this genus for which DNA sequences are available at GenBank. *Aphanophora eugeniae* was used as outgroup. ^T ex-type strain

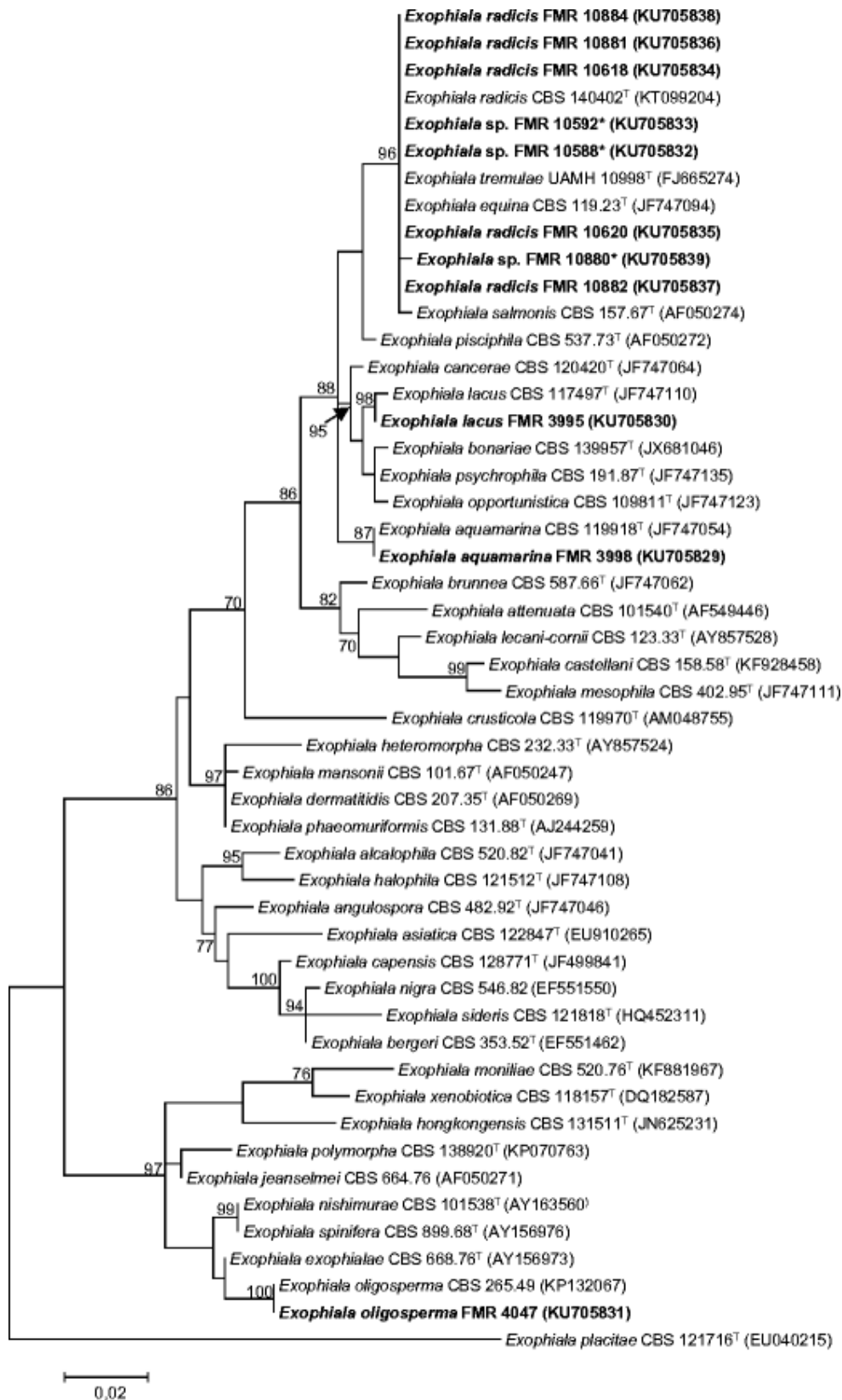


Fig. 4. Maximum likelihood tree constructed with partial sequences of the ITS region of *Exophiala* spp. Branch lengths are proportional to distance. Bootstrap values ≥ 70 % are shown near the internodes. The ingroup includes all species of this genus belonging to Herpotrichiellaceae for which DNA sequences are available at GenBank. *Exophiala placitae*, a species related to Trichomeriaceae (R blova et al. 2013; Gueidan et al. 2014), was used as outgroup. ^T ex-type strain; * *Exophiala* strains requiring data from additional loci for a definitive species-level identification

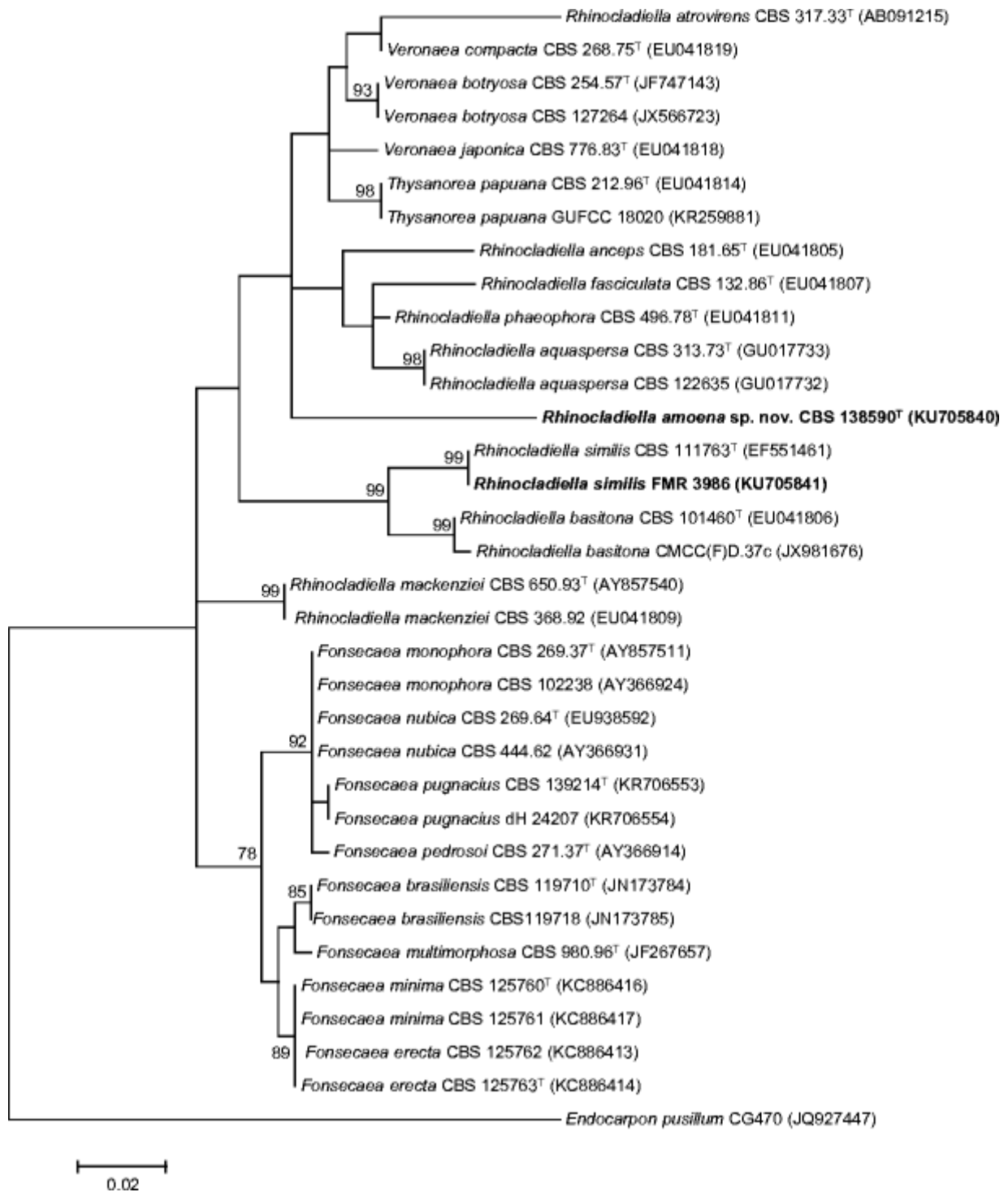


Fig. 5. Maximum likelihood tree constructed with partial sequences of the ITS region of *Rhinocladia* spp. and morphologically similar genera in Chaetothyriales. Branch lengths are proportional to distance. Bootstrap values $\geq 70\%$ are shown near the internodes. The ingroup includes all species of this genus for which DNA sequences are available at GenBank. *Endocarpon pusillum* (Verrucariaceae, Gueidan et al. 2014) was used as outgroup. ^T ex-type strain

Table 1. Strains included in the phylogenetic studies, their origins and EMBL accession no. (^T ex-type strain)

Taxon	Isolate no.	Substrate	Geographical origin	EMBL accession #		References
				ITS	LSU	
Ant-associated unidentified Chaetothyriales	T221_Tm15	<i>Azteca brevis</i> Forel ant carton	Costa Rica		KF614892	Nepel et al. (2014)
Ant-associated unidentified Chaetothyriales	T223_Tm14	<i>Azteca brevis</i> Forel ant carton	Costa Rica		KF614884	Nepel et al. (2014)
Ant-associated unidentified Chaetothyriales	T230_Tm1	<i>Azteca brevis</i> Forel ant carton	Costa Rica		KF614885	Nepel et al. (2014)
<i>Aphanophora eugeniae</i> (Crous & Alfenas) Réblová & Unter.	CBS 124105 ^T	Living leaves of <i>Eugenia uniflora</i> L.	Guaiba, Rio Grande do Sul, Brazil	FJ839617	FJ839652	Crous et al. (2009)
<i>Camptophora hylomeconis</i> (Crous, de Hoog & H.D. Shin) Réblová & Unter. Chaetothyriales sp.	CBS 113311 ^T	Leaves of <i>Hylomecon vernalis</i> Maxim.	Yangpyeong, Gyeonggi, South Korea		EU035415	Crous et al. (2007b)
(= <i>Cyphellophora chlamydospora</i> Madrid, Hern.-Restr., Cano, Gené, Guarro & V. Silva, sp. nov.)	CBS 127581 (= FMR 10878)	Soil	Castellvell del Camp, Tarragona, Spain	HG003674	HG003675	This study
<i>Chaetothyrium agathis</i> Hongsanan & K.D. Hyde	MFLUCC 12 C0113	Leaf of <i>Agathis</i> sp.	Mount Makiling, Laguna, Philippines		KP744480	Liu et al. (2015)
<i>Cladophialophora abundans</i> P. Feng, V.A. Vicente, M.J. Najafz., A.H.G. Gerrits van den Ende, B. Stielow, H. Badali, W.A. Boeger & de Hoog	CBS 126736 ^T	Thorn of <i>Smilax campestris</i> Griseb.	Bacabeira, Maranhão, Brazil	KC776592	KC812100	Feng et al. (2014)
	CBS 127907	Soil from mangrove environment	Acupi, Bahia, Brazil	KC776597		Feng et al. (2014)
<i>Cladophialophora arxii</i> Tintelnot	CBS 306.94 ^T	Tracheal abscess, human	Germany	EU103986		Badali et al. (2009)
<i>Cladophialophora australiensis</i> Crous & A.D. Hocking	CBS 112793 ^T	Sports drink	Australia	EU035402		Crous et al. (2007a, b)
<i>Cladophialophora bantiana</i> (Sacc.) de Hoog, Kwon-Chung & McGinnis	CBS 173.52	Brain abscess, human	USA	EU103989		Badali et al. (2009)
	CBS 648.96	Liver of a dog	Barbados	EU103993		Badali et al. (2009) ITS: Badali et al. (2009),
<i>Cladophialophora boppii</i> (Borelli) de Hoog, Kwon-Chung & McGinnis	CBS 126.86 ^T	Skin lesion, human	Brazil	EU103997	FJ358233	LSU: Gueidan et al. (2008)
	CBS 110029	Facial skin, human	Dordrecht, Netherlands	EU103998		Badali et al. (2009) ITS: Abliz et al. (2004a)
<i>Cladophialophora carrionii</i> (Trejos) de Hoog, Kwon-Chung & McGinnis	CBS 160.54 ^T	Chromoblastomycosis, human	Australia	AB109177	FJ358234	LSU: Gueidan et al. (2008)
	CBS 114393	Chromoblastomycosis, human	Falcón State, Venezuela	KF928452		Attili-Angelis et al. (2014)
	CBS 491.70	Roots of <i>Picea abies</i> (L.) Karst.	Denmark		EU035405	Crous et al. (2007a, b)
<i>Cladophialophora chaetospora</i> (Grove) Crous & Arzanlou	CBS 114747	Decaying bamboo	Yunnan, Jiliang, China	EU035403		Crous et al. (2007a, b)
	CBS 115468	Bamboo wood	Yunnan, Jiliang, China	EU035404		Crous et al. (2007a, b)
<i>Cladophialophora devriesii</i> (A.A. Padhye & Ajello) de Hoog, Kwon-Chung & McGinnis	CBS 147.84 ^T	Granulomatous lesion, human	Grand Cayman Island	EU103985		Badali et al. (2009)

Taxon	Isolate no.	Substrate	Geographical origin	EMBL accession #		References
				ITS	LSU	
<i>Cladophialophora emmonsii</i> (A.A. Padhye, McGinnis & Ajello) de Hoog & A.A. Padhye	CBS 979.96 ^T	Subcutaneous lesion, human	Virginia state, USA	EU103996		Badali et al. (2009)
	CBS 640.96	Subcutaneous lesion, cat	Unknown	EU103995		Badali et al. (2009)
<i>Cladophialophora floridana</i> Obase, Douhan, Y. Matsuda, & M.E. Sm.	ATCC TSD-8 ^T	Sclerotium of <i>Cenococcum geophilum</i> Fr.	Gainesville, Florida, USA	AB986343	AB986343	Obase et al. (2016)
<i>Cladophialophora immunda</i> Badali, M.M. Satow, Prenafeta-Boldú, & de Hoog	CBS 834.96 ^T	Subcutaneous ulcer, human	Atlanta, Georgia, USA	EU137318		De Hoog et al. (2007)
	CBS 110551	Gasolin station soil	Apeldoorn, Netherlands	AY857510		Prenafeta-Boldú et al. (2006)
<i>Cladophialophorea matsushimae</i> Koukol	MFC-1P384 ^T	Decaying petioles of palm tree	Momón River, Peru	FN549916	FN400758	Koukol (2010)
<i>Cladophialophora minourae</i> (Iwatsu) Haase & de Hoog	CBS 556.83 ^T	Decaying wood	Shiroi, Chiba, Japan	AY251087		Braun et al. (2003)
<i>Cladophialophora multiseptata</i> Madrid, Cano, Najafz., de Hoog, C. Silvera & Crous	CBS 136675 ^T	Soil	Carrascal de la Font Roja Natural Park, Alicante, Spain	HG003668	HG003671	Crous et al. (2013)
<i>Cladophialophora mycetomatis</i> Badali, de Hoog & Bonifaz	CBS 122637 ^T	Mycetoma, human	Jicaltepec, Mexico	FJ385276		Badali et al. (2008)
	CBS 454.82	Culture contaminant	Netherlands		KC809991	Feng et al. (2014)
<i>Cladophialophora parmeliae</i> (Etayo & Diederich) Diederich & Untereiner	CBS 132232	<i>Hypotrachyna</i> sp.	Azores		JX081671	Lawrey et al. (2013)
	CBS 129337	<i>Hypotrachyna imbricatula</i> (Zahlbr.) Hale	Azores	JQ342180		Lawrey et al. (2013)
<i>Cladophialophora potulentorum</i> Crous & A.D. Hocking	CBS 115144 ^T	Apple juice drink	Australia	DQ008141		Crous et al. (2007a, b)
<i>Cladophialophora psammophila</i> Badali, Prenafeta-Boldú, Guarro & de Hoog	CBS 110553 ^T	Gasolin-polluted soil	Bennekom, Netherlands	AY857517		Prenafeta-Boldú et al. (2006)
<i>Cladophialophora pucciniophila</i> M.J. Park & H.D. Shin	KACC 43957 ^T	Rust telia of <i>Puccinia polygoni-amphibii</i> Pers.	Bongmyeong-ri, Gangwon, Korea		JF263534	Park and Shin (2011)
<i>Cladophialophora samöensis</i> Badali, de Hoog & Padhye	CBS 259.83 ^T	Chromoblastomycosis, human	Samoa	EU137291	KC809992	ITS: de Hoog et al. (2007),
						LSU: Feng et al. (2014)
<i>Cladophialophora saturnica</i> Badali, Carvalho, Vicente, Attili-Angelis D, Kwiatkowski, Gerrits van den Ende & de Hoog.	CBS 118724 ^T	Interdigital skin lesion, human	Curitiba, Paraná, Brazil	EU103984		Badali et al. (2009)
<i>Cladophialophora scillae</i> (Deighton) Crous, U. Braun & K. Schub.	CBS 116461 ^T	Leaf lesions of <i>Scilla peruviana</i> L.	Manurewa, Auckland, New Zealand	EU035412		Crous et al. (2007a, b)
<i>Cladophialophora</i> sp. (= <i>Cladophialophora pseudocarrionii</i> Madrid, Hern.-Restr., Gené, Cano & Guarro, sp. nov.)	CBS 138591 (= FMR 12062)	Soil	Hayedo de la Tejera Negra National Park, Guadalajara, Spain	KU705827	KU705844	This study
<i>Cladophialophora subtilis</i> Badali & de Hoog	CBS 122642 ^T	Ice tea	Utrecht, Netherlands	FJ385273		Badali et al. (2008)
<i>Cladophialophora tortuosa</i> Obase, Douhan, Y. Matsuda, & M.E. Sm.	ATCC TSD-9 ^T	Sclerotium of <i>Cenococcum geophilum</i> Fr.	Gainesville, Florida, USA	AB986424	AB986424	Obase et al. (2016)

Taxon	Isolate no.	Substrate	Geographical origin	EMBL accession #		References
				ITS	LSU	
<i>Cladophialophora yegresii</i> de Hoog, Nishikaku, Zeppenfeldt, Ruibal & Gerrits van den Ende	CBS 114405 ^T	<i>Stenocereus griseus</i> (Haw.) Buxb.	Falcón State, Venezuela	EU137322	KC809994	ITS: de Hoog et al. (2007)
	CBS 114407	<i>Stenocereus griseus</i> (Haw.) Buxb.	Falcón State, Venezuela	EU137324		LSU: Feng et al. (2014) de Hoog et al. (2007)
<i>Cyphellophora ambigua</i> (P. Feng & de Hoog) Réblová & Unter.	CBS 235.93 ^T	Human toe nail	Delft, Netherlands	JQ766431	JQ766480	Feng et al. (2012)
<i>Cyphellophora artocarpi</i> G.Y. Sun & Liu Gao	CGMCC3.17496 ^T	Twig of <i>Artocarpus heterophyllus</i> Lam.	Haikou, Hainan, China	KP010367	KP122930	Gao et al. (2015)
<i>Cyphellophora catalaunica</i> Madrid, Gené, Guarro & Crous	CPC 22929 ^T	River sediments	Pals beach, Girona, Spain	HG003670	HG003673	Crous et al. (2013)
<i>Cyphellophora europaea</i> (de Hoog, Maysen & Haase) Réblová & Unter.	CBS 101466 ^T	Foot of human patient	Dordrecht, Netherlands	JQ766443	KC455259	ITS: Feng et al. (2012) LSU: Réblová et al. (2013)
	CBS 218.78	Finger nail	Rotterdam, Netherlands	JQ766441		Feng et al. (2012) ITS: Feng et al. (2012)
<i>Cyphellophora fusarioides</i> (B. Sutton & C.K. Campb.) Decock	CBS 130291 ^T	Human bronchial lavage fluid	Israel	JQ766439	KC455252	LSU: Réblová et al. (2013)
<i>Cyphellophora gamsii</i> Crous	CPC 25867 ^T	Leaf litter	Chiang Mai, Thailand	KX228255	KX228307	Crous et al. (2016)
	CBS 124764	<i>Eucalyptus</i> sp.	Australia	GQ303274		Cheewangkoon et al. (2009)
<i>Cyphellophora guyanensis</i> Decock & G. Delgado	CBS 126014	Tucum palm	Brazil	JQ766434		Feng et al. (2012)
	MUCL 43737 ^T	Dead leaf of undetermined angiosperm	Matouri, Cayenne area, French Guyana	KC455240	KC455253	Réblová et al. (2013)
	CBS 174.79	Foot skin, human	Unknown	JQ766422		Feng et al. (2012)
<i>Cyphellophora laciniata</i> G.A. de Vries	CBS 190.61 ^T	Skin, human	Basel, Switzerland	JQ766423	FJ358239	ITS: Feng et al. (2012) LSU: Gueidan et al. (2008)
	CGMCC3.17497 ^T	Fruit of <i>Musa basjoo</i> Siebold & Zucc. ex Linuma	Zhanjiang, Guangdong, China	KP010370	KP122932	Gao et al. (2015)
<i>Cyphellophora olivacea</i> (W. Gams) Réblová & Unter.	CBS 122.74	Moist wall paper	Kiel-Kitzeberg, Germany	KC455247	KC455260	Réblová et al. (2013)
	CBS 123.74 ^T	Stem of <i>Chamaerops humilis</i> L.	Baarn, Netherlands	KC455248		Réblová et al. (2013)
	CBS 416.89	Floor of swimming pool	Germany	JQ766449		Feng et al. (2012)
<i>Cyphellophora oxyspora</i> (W. Gams) Réblová & Unter.	CBS 698.73 ^T	<i>Clerodendron</i> sp., decaying leaf	Peradeniya Botanical Garden, Sri Lanka	JQ766450	KC455262	ITS: Feng et al. (2012) LSU: Réblová et al. (2013)
	CBS 284.85 ^T	Skin of hand, human	Roermond, Limburg, Netherlands	JQ766466	JQ766515	Feng et al. (2012)
<i>Cyphellophora phyllostachidis</i>	CGMCC3.17495 ^T	Twig of <i>Phyllostachys</i> sp.	Haikou, Hainan, China	KP010371	KP122933	Gao et al. (2015)

Taxon	Isolate no.	Substrate	Geographical origin	EMBL accession #		References
				ITS	LSU	
G.Y. Sun & Liu Gao						
<i>Cyphellophora pluriseptata</i> G.A. de Vries, Elders & Luykx	CBS 286.85 ^T	Foot skin of human patient	Roermond, Netherlands	JQ766429	KC455255	ITS: Feng et al. (2012) LSU: Réblová et al. (2013)
	CBS 109633	Human skin	Giessen, Germany	JQ766430		Feng et al. (2012)
<i>Cyphellophora reptans</i> de Hoog	CBS 113.85 ^T	Food stuffs	Uppsala, Sweden	JQ766445	JQ766493	Feng et al. (2012)
	CBS 152.90	Toe nail, human	Noord-Holland, Netherlands	JQ766446		Feng et al. (2012)
<i>Cyphellophora sessilis</i> (de Hoog) Réblová & Unter.	CBS 238.93	Biological filter for styrene-containing fumes	Delft, Netherlands	AY857541		Prenafeta-Boldú et al. (2008)
	CBS 243.85 ^T	Resin of <i>Picea abies</i> (L.) H. Karst.	Baarn, Netherlands	EU514700	EU514700	Untereiner et al. (2008) ITS: Feng et al. (2012),
<i>Cyphellophora suttonii</i> (Ajello, A.A. Padhye & M. Payne) Decock	CBS 449.91 ^T	Subcutaneous tissue of a dog	USA	JQ766459	KC455256	LSU: Réblová et al. (2013)
	FMR 10589	Soil	Tarragona, Tarragona, Spain	KU705828	KU705845	This study
<i>Cyphellophora vermisporea</i> A. Walz & de Hoog	CBS 228.86 ^T	Root of <i>Tritichum aestivum</i> L.	Monheim, Germany	KC455244	KC455257	Réblová et al. (2013)
	CBS 122852	Skin of foot, human	Netherlands	JQ766427		Feng et al. (2012)
<i>Endocarpon pusillum</i> Hedw.	CG470	Unknown	Unknown	JQ927447		Weerakoon et al. (2012)
<i>Exophiala alcalophila</i> Goto & Sujiy.	CBS 520.82 ^T	Soil	Wako-shi, Saitama, Japan	JF747041		de Hoog et al. (2011)
<i>Exophiala angulospora</i> Iwatsu, Udagawa & T. Takase	CBS 482.92 ^T	Water from drinking well	Yokohama-shi, Kanagawa, Japan	JF747046		de Hoog et al. (2011)
<i>Exophiala aquamarina</i> de Hoog, Vicente, Najafz., Harrak, Badali, Seyedm. & Nyaoke	CBS 119918 ^T	Leafy seadragon, skin	Boston, Massachusetts, USA	JF747054		de Hoog et al. (2011)
	FMR 3998	River sediments	Ebro River mouth, Riumar beach, Tarragona, Spain	KU705829	KU705846	This study
<i>Exophiala asiatica</i> D.M. Li, R.Y. Li, de Hoog & D.L. Wang	CBS 122847 ^T	Wound infection of tonsils, human	China	EU910265		Li et al. (2011)
<i>Exophiala attenuata</i> Vitale & de Hoog	CBS 101540 ^T	Soil	Colombia	AF549446		Vitale and de Hoog (2002)
<i>Exophiala bergeri</i> Haase & de Hoog	CBS 353.52 ^T	Skin infection, human	Canada	EF551462		Zeng and de Hoog (2008)
<i>Exophiala bonariae</i> D. isola & L. Zucconi	CBS 139957 ^T	Surface of marble funerary monument	Cagliari, Sardinia, Italy	JX681046		Isola et al. (2013)
<i>Exophiala brunnea</i> Papendorf	CBS 587.66 ^T	Leaf litter of <i>Acacia karroo</i> Hayne	Potchefstroom, North West Province, South Africa	JF747062		de Hoog et al. (2011)
<i>Exophiala cancerae</i> de Hoog, V.A. Vicente, Najafz., Harrak, Badali, Seyedm. & Boeger	CBS 120420 ^T	Diseased mangrove crab (<i>Ucides cordatus</i> L.)	Goiana City, Pernambuco, Brazil	JF747064		de Hoog et al. (2011)
<i>Exophiala capensis</i> Crous	CBS 128771 ^T	Leaf of <i>Phaenocoma prolifera</i> (L.) D. Don	Fernkloof Nature Reserve, Western Cape Province, South Africa	JF499841		Crous and Groenewald (2011)
<i>Exophiala castellani</i> Iwatsu, Nishim. & Miyaji	CBS 158.58 ^T	Human	Sri Lanka	KF928458		Attili-Angelis et al. (2014)
<i>Exophiala crusticola</i> S.T. Bates, G.S.N. Reddy & García-	CBS 119970 ^T	Biological soil crust	Colorado Plateau, USA	AM048755		Bates et al. (2006)

Taxon	Isolate no.	Substrate	Geographical origin	EMBL accession #		References
				ITS	LSU	
Pichel						ITS: Untereiner and Naveau (1999)
<i>Exophiala dermatitidis</i> (Kano) de Hoog	CBS 207.35 ^T	Human	Osaka, Kansai, Japan	AF050269	KJ930160	LSU: Li et al. (2017)
	CBS 119.23 ^T	Subcutaneous infection, horse	Pavia, Pavia, Italy	JF747094		de Hoog et al. (2011)
<i>Exophiala equina</i> (Pollacci) de Hoog, V.A. Vicente, Najafz., Harrak, Badali & Seyedm.	CBS 160.89	Root of <i>Hordeum vulgare</i> L.	Noordoostpolder, Flevoland, Netherlands		KF928494	Attili-Angelis et al. (2014)
	CBS 116009	Lung tissue of Galapagos tortoise	Chicago, Illinois, USA		KF928497	Attili-Angelis et al. (2014)
<i>Exophiala exophialae</i> (de Hoog) de Hoog	CBS 668.76 ^T	Straw in an armadillo burrow	Uruguay	AY156973		Vitale and de Hoog (2002)
<i>Exophiala halophila</i> de Hoog, V.A. Vicente, Najafz., Harrak, Badali & Seyedm.	CBS 121512 ^T	Axillary skin, human	San Antonio, Texas, USA	JF747108		de Hoog et al. (2011)
<i>Exophiala heteromorpha</i> (Nannf.) de Hoog & Haase	CBS 232.33 ^T	Wood pulp	Sweden	AY857524		Prenafeta-Boldú et al. (2006)
<i>Exophiala hongkongensis</i> P.C. Woo, A.H. Ngan, C.C. Tsang, I.W. Ling, J.F. Chan, S.Y. Leung, K.Y. Yuen & S.K. Lau	CBS 131511	Big toe nail infection, human	Hong Kong, China	JN625231		Woo et al. (2013)
<i>Exophiala jeanselmei</i> (Langeron) McGinnis & A.A. Padhye	CBS 664.76	Human	Unknown	AF050271		Untereiner and Naveau (1999)
	CBS 117497 ^T	Lake water	Loosdrecht, North Holland, Netherlands	JF747110		de Hoog et al. (2011)
<i>Exophiala lacus</i> de Hoog, V.A. Vicente, Najafz., Harrak, Badali & Seyedm.	FMR 3995	River sediments	Muga River mouth, Ampuriabrava, Girona, Spain	KU705830	KU705847	This study
<i>Exophiala lecani-cornii</i> (Benedek & G. Specht) Haase & de Hoog	CBS 123.33 ^T	<i>Lecanium corni</i> Bouché	Unknown	AY857528		Prenafeta-Boldú et al. (2006)
<i>Exophiala mansonii</i> (Castell.) de Hoog	CBS 101.67 ^T	<i>Populus tremula</i> L.	Sweden	AF050247		Untereiner and Naveau (1999)
<i>Exophiala mesophila</i> Listeman & Freiesl.	CBS 402.95 ^T	Silicon seal in shower room of a hospital	Hamburg, Germany	JF747111		de Hoog et al. (2011)
<i>Exophiala moniliae</i> de Hoog	CBS 520.76 ^T	Twig of <i>Quercus</i> sp.	St. Petersburg, Northwestern Federal District, Russia	KF881967		Li et al. (2017)
<i>Exophiala nigra</i> (Issatsch.) Haase & de Hoog	CBS 546.82	Unknown	Former USSR	EF551550		Zeng and de Hoog (2008)
<i>Exophiala nishimurae</i> Vitale & de Hoog	CBS 101538 ^T	Culture contaminant	Venezuela	AY163560		de Hoog et al. (2003)
<i>Exophiala opportunistica</i> de Hoog, V.A. Vicente, Najafz., Harrak, Badali & Seyedm.	CBS 109811 ^T	Drinking water at waterstation	Germany	JF747123		de Hoog et al. (2011)
	CBS 265.49	Honey	Ille et Villaine, Brittany, France	KP132067		Irinyi et al. (2015)
<i>Exophiala oligosperma</i> Calendron ex de Hoog & Tintelnot	CBS 725.88 ^T	Cerebral phaeohyphomycosis	Frankfurt-am-Main, Hesse, Germany		KF928486	Attili-Angelis et al. (2014)
	FMR 4047	River sediments	Besòs River, Sant Adrià del Besòs, Barcelona, Spain	KU705831	KU705848	This study
<i>Exophiala phaeomuriformis</i> (Matsumoto, A.A. Padhye, Ajello & McGinnis) Matos, Haase & de Hoog	CBS 131.88 ^T	Cutaneous phaeohyphomycosis, human	Japan	AJ244259		de Hoog et al. (1999b)

Taxon	Isolate no.	Substrate	Geographical origin	EMBL accession #		References
				ITS	LSU	
<i>Exophiala pisciphila</i> McGinnis & Ajello	CBS 537.73 ^T	Systemic mycosis in channel catfish	Central Alabama, USA	AF050272		Untereiner and Naveau (1999)
<i>Exophiala polymorpha</i> Guarro, Sandoval-Denis, Deanna A. Sutton & Wiederhold	CBS 138920 ^T	Subcutaneous lesion, human	USA	KP070763		Yong et al. (2015)
<i>Exophiala placitae</i> Crous & Summerell	CBS 121716 ^T	Leaf of <i>Eucalyptus placita</i> L.A.S. Johnson & K.D. Hill	Bimbadeen Lookout, New South Wales, Australia	EU040215		Crous et al. (2007a)
<i>Exophiala psychrophila</i> O.A. Pedersen & Langvad	CBS 191.87 ^T	<i>Salmo salar</i> L.	Norway	JF747135		de Hoog et al. (2011)
	CBS 140402 ^T	Root of <i>Microthlaspi perfoliatum</i> (L.) F.K. Mey	Near Buchen, Baden-Württemberg, Germany	KT099204	KT723448	Maciá-Vicente et al. (2016)
	FMR 10618	Soil	Near Besande, León, Spain	KU705834	KU705851	This study
<i>Exophiala radialis</i> Maciá-Vicente, Glynou & M. Piepenbr.	FMR 10620	Soil	Olleros de Alba, León, Spain	KU705835	KU705852	This study
	FMR 10881	Soil	Sierra de Monegros, Teruel, Spain	KU705836	KU705853	This study
	FMR 10882	Soil	Fuente de Matahombres, Teruel, Spain	KU705837	KU705854	This study
	FMR 10884	Soil	Puerto de San Rafael, Teruel, Spain	KU705838	KU705855	This study
<i>Exophiala salmonis</i> J.W. Carmich.	CBS 157.67 ^T	Cerebral infection, <i>Oncorhynchus clarkii</i> Richardson	Calgary, Alberta, Canada	AF050274	AY213702	ITS: Untereiner and Naveau (1999) LSU: Rakeman et al. (2005)
<i>Exophiala</i> sp.	FMR 10588	Soil	La Mussara, Tarragona, Spain	KU705832	KU705849	This study
<i>Exophiala</i> sp.	FMR 10592	Soil	Vigaña d'Arcéu, Belmonte de Miranda, Spain	KU705833	KU705850	This study
<i>Exophiala</i> sp.	FMR 10880	Soil	Mora de Rubielos, Teruel, Spain	KU705839	KU705856	This study
<i>Exophiala sideris</i> Seyedm. & de Hoog	CBS 121818 ^T	Berry of <i>Sorbus aucuparia</i> L.	Netherlands	HQ452311		Seyedmousavi et al. (2011)
<i>Exophiala spinifera</i> (H.S. Nielsen & Conant) McGinnis	CBS 899.68 ^T	Nasal granuloma, human	USA	AY156976		Vitale and de Hoog (2002)
<i>Exophiala tremulae</i> W. Wang	UAMH 10998 ^T	Roots of <i>Populus tremuloides</i> Michx	Lamont, Alberta, Canada	FJ665274	JF951155	Crous et al. (2011)
<i>Exophiala xenobiotica</i> de Hoog, J.S. Zeng, HARRAK & Deanna A. Sutton	CBS 118157 ^T	Oil sludge	San Tomé, Anzoategui, Venezuela	DQ182587		de Hoog et al. (2006)
<i>Fonsecaea brasiliensis</i> V.A. Vicente, Najafz., C.H.W. Klaassen & de Hoog	CBS 119710 ^T	<i>Scylla serrata</i> Forsskål (mangrove crab)	Brazil	JN173784		Vicente et al. (2012)
	CBS 119718	<i>Scylla serrata</i> Forsskål (mangrove crab)	Brazil	JN173785		Vicente et al. (2012)
<i>Fonsecaea erecta</i> V.A. Vicente, Najafz., Sun & de Hoog	CBS 125762	Leaf of <i>Orbignya phalerata</i> Mart.	Fortaleza, Maranhao, Brazil	KC886413		Vicente et al. (2014)
	CBS 125763 ^T	Spine of <i>Smilax</i> sp.	Bacabeira, Maranhao, Brazil	KC886414		Vicente et al. (2014)
<i>Fonsecaea monophora</i> (M. Moore & F.P. Almeida) de Hoog, V.A. Vicente & D. Attili	CBS 269.37 ^T	Chromoblastomycosis, human	South Africa	AY857511		Prenafeta-Boldú et al. (2006)
	CBS 102238	Soil	Tibagi river, Paraná, Brazil	AY366924		de Hoog et al. (2004)
<i>Fonsecaea minima</i> V.A.	CBS 125760 ^T	Leaf of <i>Orbignya speciosa</i>	Icatu, Maranhao,	KC886416		Vicente et al.

Taxon	Isolate no.	Substrate	Geographical origin	EMBL accession #		References
				ITS	LSU	
Vicente, Najafz., Sun & de Hoog		(Mart. ex Spreng.) Barb.Rodr.	Brazil			(2014)
	CBS 125761	Leaf of palm tree	Icatu, Maranhao, Brazil	KC886417		Vicente et al. (2014)
<i>Fonsecaea multimorphosa</i> Najafz., V.A. Vicente, Sun, Meis & de Hoog	CBS 980.96 ^T	Brain abscess, cat	Queensland, Australia	JF267657		Najafzadeh et al. (2011)
<i>Fonsecaea nubica</i> Najafz., Sun, V.A. Vicente, L. Xi, Van den Ende & de Hoog	CBS 269.64 ^T	Chromoblastomycosis, human	Cameroon	EU938592		Najafzadeh et al. (2010)
	CBS 444.62	Chromoblastomycosis, human	Paramaribo, Suriname	AY366931		de Hoog et al. (2004)
<i>Fonsecaea pedrosoi</i> (Brumpt) Negronei	CBS 271.37 ^T	Human	South America (unknown country)	AY366914		de Hoog et al. (2004)
<i>Fonsecaea pugnacius</i> R.R. Gomes, V.A. Vicente, C.M.P.S. Azevedo & de Hoog	CBS 139214 ^T	Skin lesion, human	Cidelândia, Maranhão, Brazil	KR706553		de Azevedo et al. (2015)
	dH 24207	Brain tissue, human	Cidelândia, Maranhão, Brazil	KR706554		de Azevedo et al. (2015)
<i>Phaeoemoniella prunicola</i> Damm & Crous	CBS 120876 ^T	Necrotic wood of <i>Prunus persica</i> (L.) Stokes	Mookgopong, Limpopo, South Africa		GQ154614	Damm et al. (2010)
<i>"Phialophora" livistonae</i> Crous & Summerell						
(= <i>Cyphellophora livistonae</i> (Crous & Summerell) Madrid & Hern.-Restr., comb. nov.)	CBS 133589 ^T	Leaf of <i>Livistona humilis</i> R.Br.	Litchfield National Park, Northern Territory, Australia	KC005774	KC005796	Crous et al. (2012b)
<i>Phialophora verrucosa</i> Medlar	MUCL 9760	Human	Brazil		EF413615	Geiser et al. (2006)
<i>Rhinocladiella anceps</i> (Sacc. & Ellis) S. Hughes	CBS 181.65 ^T	Soil under <i>Thuja plicata</i> Donn ex D. Don	Campbellville, Ontario, Canada	EU041805	EU041862	Arzanlou et al. (2007)
						ITS: Badali et al. (2010)
<i>Rhinocladiella aquaspersa</i> (Borelli) Schell, McGinnis & Borelli	CBS 313.73 ^T	Chromoblastomycosis, human	Mexico	GU017733	AB100677	LSU: Abliz et al. (2004b)
	CBS 122635	Chromoblastomycosis, human	Mexico City, Mexico	GU017732		Badali et al. (2010)
<i>Rhinocladiella atrovirens</i> Nannf.	CBS 317.33 ^T	Pine wood	Sweden	AB091215		Abliz et al. (2003)
	CBS 264.49	Honey	Ille et Villaine, Brittany, France		EU041869	Arzanlou et al. (2007)
<i>Rhinocladiella basitona</i> (de Hoog) Arzanlou & Crous	CBS 101460 ^T	Subcutaneous lesion, human	Hamamatsu, Shizuoka, Japan	EU041806	EU041863	Arzanlou et al. (2007)
	CMCC(F)D.37c	Lesion on facial skin, human	China	JX981676		Cai et al. (2013)
<i>Rhinocladiella fasciculata</i> (V. Rao & de Hoog) Arzanlou & Crous	CBS 132.86 ^T	Decaying wood	Thirathahalli, Karnataka, India	EU041807	EU041864	Arzanlou et al. (2007)
						ITS: Prenafeta-Boldú et al. (2006)
<i>Rhinocladiella mackenziei</i> (C.K. Campb. & Al-Hedaithy) Arzanlou & Crous	CBS 650.93 ^T	Cerebral phaeohyphomycosis, human	Saudi Arabia	AY857540	AF050288	LSU: Untereiner and Naveau (1999)
	CBS 368.92	Brain abscess, Human	Haifa, Haifa district, Israel	EU041809		Arzanlou et al. (2007)
<i>Rhinocladiella phaeophora</i> Veerkamp & W. Gams	CBS 496.78 ^T	Maize field soil	Near Villavicencio, Meta, Colombia	EU041811	EU041868	Arzanlou et al. (2007)
<i>Rhinocladiella similis</i> de Hoog	CBS 111763 ^T	Cutaneous ulcer, human	Minas Gerais, Brazil	EF551461		Zeng and de

Taxon	Isolate no.	Substrate	Geographical origin	EMBL accession #		References
				ITS	LSU	
& Calig.	CBS 126848	Enugu, Anambra, Nigeria	Soil		KU752195	Hoog (2008) This study
	FMR 3986	River sediments	Muga River mouth, Ampuriabrava, Girona, Spain	KU705841	KU705858	This study
<i>Rhinocladiella</i> sp.	CBS 138590^T (= FMR 12063)	Submerged twig	Ordesa y Monte Perdido National Park, Huesca, Spain	KU705840	KU705857	This study
(= <i>Rhinocladiella amoena</i> Hern.-Restr., Madrid, Gené, Cano & Guarro, sp. nov.)						
<i>Veronaea botryosa</i> Cif. & Montemart.	CBS 254.57 ^T	Sansa olive slag	Pisa, Tuscany, Italy	JF747143		de Hoog et al. (2011)
	CBS 127264	Disseminated phaeohyphomycosis, human	Cuatla, Morelos, Mexico	JX566723		Bonifaz et al. (2013)
<i>Veronaea compacta</i> Papendorf	CBS 268.75 ^T	Soil	Kosi Bay, KwaZulu- Natal, South Africa	EU041819		Arzanlou et al. (2007)
<i>Veronaea japonica</i> Arzanlou, W. Gams & Crous	CBS 776.83 ^T	Dead bamboo culm	Kyoto, Japan	EU041818		Arzanlou et al. (2007)
<i>Thysanorea papuana</i> (Aptroot) Arzanlou, W. Gams & Crous	CBS 212.96 ^T	Stipe of undetermined plant	Foothill of Finisterre range, Madang, Papua New Guinea	EU041814		Arzanlou et al. (2007)

ATCC American Type Culture Collection, Bethesda, Maryland, USA, CBS CBS-KNAW Fungal Biodiversity Centre, Utrecht, The Netherlands, CG Cécile Gueidan, Natural History Museum, Department of Botany, London, United Kingdom, CGMCC China General Microbiological Culture Collection, Beijing, China, CMCC China Medical Culture Collection, National Institute for the Control of Pharmaceutical and Biological Products, Beijing, China, CPC Pedro Crous Working Collection, housed at CBS, dH Sybren de Hoog Working Collection, housed at CBS, FMR Faculty of Medicine collection, Reus, Spain, KACC Korean Agricultural Culture Collection, National Academy of Agricultural Science, Seoul, Korea, MFC Matsushima Fungus Collection, Kobe, Japan, MUCL Mycothèque de L'Université Catholique de Louvain, Faculté des Sciences Agronomiques, Louvain-la-Neuve, Belgium, UAMH University of Alberta Microfungus Collection and Herbarium, Devonian Botanic Garden, Edmonton, Canada

Results

Molecular and morphological study

BLAST searches allowed us to identify 10 out of the 16 studied strains to species level. They belong to *Cyphellophora suttonii* ($n = 1$), *Exophiala aquamarina* ($n = 1$), *E. radialis* ($n = 5$), *E. lacus* ($n = 1$), *E. oligosperma* ($n = 1$) and *Rhinocladiella similis* ($n = 1$). All of those strains had ITS sequence identities $\geq 99\%$ to the ex-type or representative strains of each of those species, and clustered with them in LSU and ITS phylogenies (Figs. 1, 3, 4, 5). The only species for which no reference LSU sequences were available in GenBank were *E. aquamarina* and *E. lacus*, and these species were represented only by strains from Spain in the LSU tree (Fig. 1). The ex-type strains of both species, however, were included in an ITS tree of *Exophiala* spp. (Fig. 4). Three strains, i.e. FMR 10588, FMR 10592, and FMR 10880 showed 99% ITS sequence identities to the ex-type strains of both *E. radialis* (CBS 140402, GenBank KT099204) and *E. tremulae* (UAMH 10998, GenBank FJ665274). We decided to keep these FMR strains provisionally as "*Exophiala* sp." (Table 1; Figs. 1, 4), and in a future study more loci will be analyzed to determine their final identifications. In the *Exophiala* ITS tree (Fig. 4), these strains, *E. equina*, *E. radialis*, *E. salmonis* and *E. tremulae* could not be properly separated. This was probably caused by the loss of informative sites located within ambiguously aligned positions which had to be excluded from the analysis. A higher level of resolution might be obtained in an ITS tree including only those species and very closely

related ones, but such phylogenetic analysis was considered unnecessary since identifications of *Exophiala* spp. in this paper are mainly based on ITS percent identities revealed by BLAST search results. Strains CBS 127581, CBS 138590, and CBS 138591 showed ITS identities ≤ 97 % to known members of the Chaetothyriales, suggesting that they might represent novel taxa.

Strain CBS 127581 did not sporulate on OA or PCA, but produced some chlamydospores on MEA. The closest matches for its ITS sequence were *Cyphellophora europaea* CBS 101466, ex-type (GenBank EU514698) and other strains of the same species, 91–92 % identical, and *C. phyllostachydis* CGMCC3.17495, ex-type (GenBank KP010371), 91 % identical. Strain CBS 138590 produced melanized, sympodial, denticulate conidiophores and aseptate conidia typical of the genus *Rhinocladiella* (Arzanlou et al. 2007), but its morphological features did not match any of the currently accepted species (see “Taxonomy”). The closest match in a BLAST search with its ITS sequence, however, was *Exophiala dermatitidis* CBS 207.35, ex-type (GenBank AF050269) and other strains, 83–84 % identical. Strain CBS 138591 produced acropetal, branched chains of elongate, olivaceous brown blastic conidia from undifferentiated to moderately differentiated conidiophores, resembling members of *Cladophialophora* (Badali et al. 2008). BLAST searches revealed that its closest relatives are *C. chaetospira* CBS 491.70 (GenBank EU035405) and other strains, 96–97 % identical, and *C. parmeliae* CBS 129337 (GenBank JQ342180), 95 % identical.

The best substitution models chosen by MEGA 6 were K2+G+I for the general LSU, the *Cladophialophora* ITS and the *Exophiala* ITS datasets, and K2+G for the *Cyphellophora* ITS and *Rhinocladiella* ITS datasets. In the LSU phylogenetic tree (Fig. 1), strain CBS 127581 appeared within a clade with 100 % bootstrap support (bs) which represents the genus *Cyphellophora*. The strain appeared as a novel lineage clearly separated from other species of this genus. In the *Cyphellophora* ITS tree (Fig. 3), strain CBS 127581 grouped with *C. europaea* and *C. phyllostachydis* with 81 % bs, but also appeared as a clearly distinct taxon, separated from these species by a considerable genetic distance. The ex-type strain of *Phialophora livistonae* (CBS 133589), included in the phylogenetic analyses, clustered with the *Cyphellophora* clade, which is quite distant from the type species of the genus *Phialophora*, *P. verrucosa* (Fig. 1). LSU and ITS-based phylogenies proved that the *Rhinocladiella* sp. strain CBS 138590 is clearly distinct from all members of that genus and similar fungi sequenced so far (Figs. 1, 5). In the LSU tree, it clustered with low support with three strains of unidentified Chaetothyriales associated with ant galleries from a study by Nepel et al. (2014). In the LSU tree, the *Cladophialophora* sp. strain CBS 138591 grouped with 94 % bs with *Cladophialophora parmeliae*, and both species were separated by relatively short branch lengths. Their morphological features, however, are remarkably different (see section Taxonomy). In the *Cladophialophora* ITS tree (Fig. 2), strain CBS 138591 grouped with *C. chaetospira*, *C. floridana*, and *C. multiseptata*, with low bs., but appeared as a clearly different species. Molecular and morphological data justify the proposal of three novel species of *Cyphellophora*, *Rhinocladiella* and *Cladophialophora*, based on strains CBS 127581, CBS 138590 and CBS 138591, respectively, as well as a new combination for *Phialophora livistonae* in *Cyphellophora*.

Taxonomy

Cladophialophora pseudocarrionii Madrid, Hern.-Restr., Gené, Cano & Guarro, sp. nov.,
Fig. 6

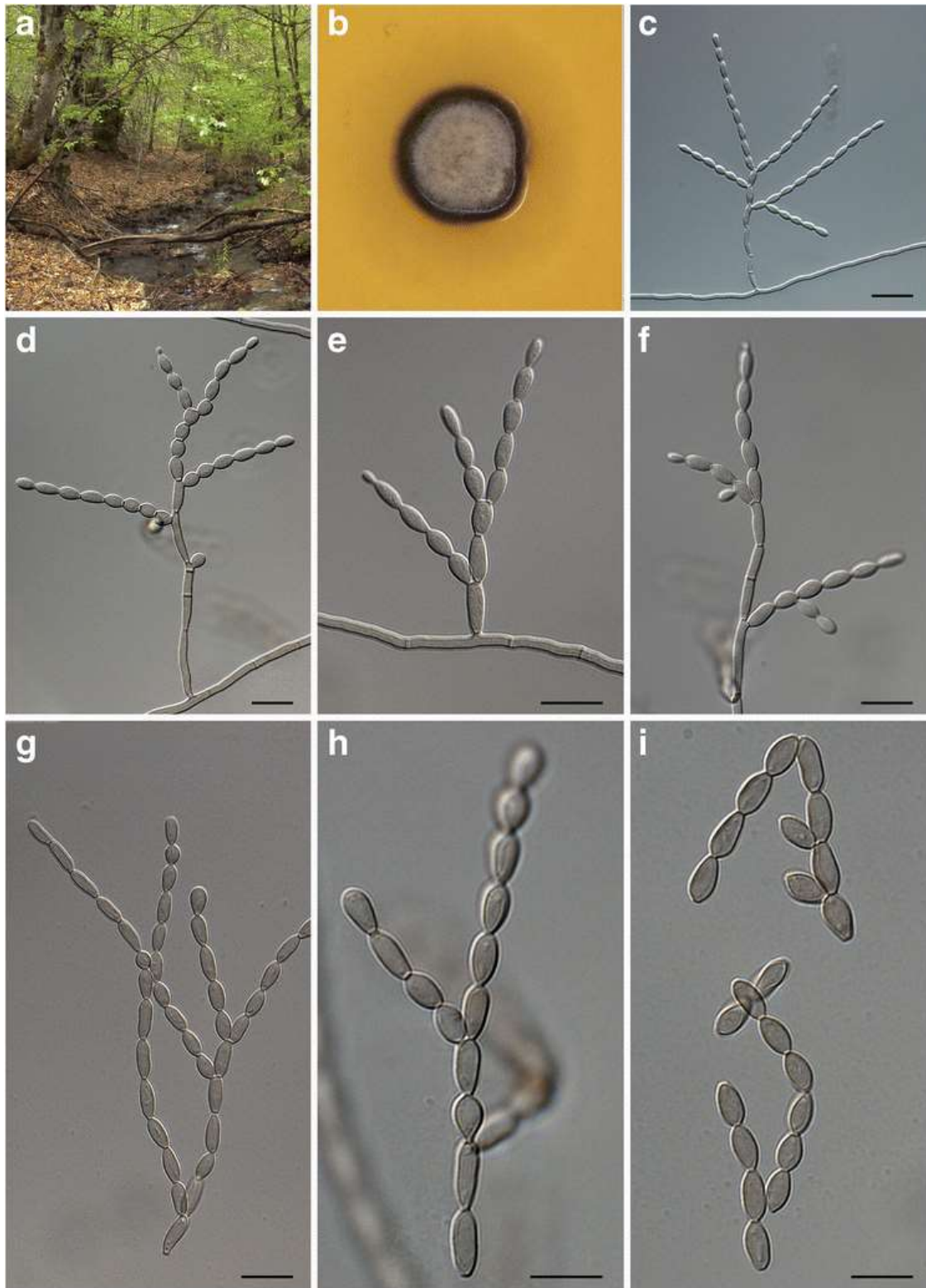


Fig. 6. *Cladophialophora pseudocarrionii* (CBS 138591). **a** Sampling area in Hayedo de la Tejera Negra Natural Park. **b** Colony on MEA after 14 d at 24 °C. **c–f** Conidiophores, conidiogenous cells and conidia. **g–i** Conidial chains. Scale bars (c) 20 µm, (d–i) 10 µm

MycoBank:MB815961

Etymology: the name refers to the morphological similarity between this fungus and the generic type, *C. carrionii*

Colonies after 14 days at 24 °C attaining 6 mm on MEA and 8–9 mm on OA, cottony, olivaceous gray and elevated at the center, glabrous and fuscous black toward the periphery, with an entire margin and hyaline exudates; reverse black. Vegetative hyphae septate, branched, subhyaline to light olivaceous brown, smooth- and thin-walled, 2–3 µm wide. Conidiophores micronematous to semimacronematous, sometimes reduced to conidiogenous cells, pale olivaceous brown. Conidiogenous cells subcylindrical, 7.5–19 × 2–3 µm. Conidia in acropetal, branched, strongly coherent chains, mostly ellipsoid to fusiform, aseptate (very rarely 1-septate), subhyaline to pale brown, smooth-walled, 5.5–9.5 × 2–4.5 µm; ramoconidia 4–15 × 3–4 µm. Chlamydo-spores and sexual morph not observed. Optimum growth temperature 24 °C, minimum below 6 °C, maximum between 24 and 30 °C.

Material examined: SPAIN. Guadalajara Province, Hayedo de la Tejera Negra Natural Park, isolated from soil, May 2011, M. Hernández Restrepo, J. Guarro & J. Mena Portales (CBS H-21836 holotype, a dried culture on MEA; ex-type cultures CBS 138591 and FMR 12062).

Notes: This new species is morphologically very different from its closest relatives, *C. parmeliae* and *C. chaetospora*. *Cladophialophora parmeliae* is a sporodochium-forming species which produces 1-septate, verrucose conidia which frequently remain attached to each other laterally, forming strongly flexuous chains (Diederich et al. 2013). *Cladophialophora chaetospora*, on the other hand, clearly differs from the new species in producing chains of much longer conidia (20–45 × 3–5 µm) with 1–3 septa (Crous et al. 2007b).

Cladophialophora pseudocarrionii more closely resembles the type species of the genus, *C. carrionii*, and its closest relative, *C. yegresii*, by the ability to produce repeatedly branched chains of aseptate, ellipsoid to fusiform conidia. *Cladophialophora carrionii* and *C. yegresii*, however, tolerate higher temperatures (both species can grow at 37 °C; de Hoog et al. 2007). Furthermore, a phialidic synasexual stage occasionally produced by *C. carrionii* (de Hoog et al. 2000), was not observed in *C. pseudocarrionii*.

Cyphellophora chlamydo-spore Madrid, Hern.-Restr., Cano, Gené, Guarro & V. Silva, sp. nov.
Fig. 7

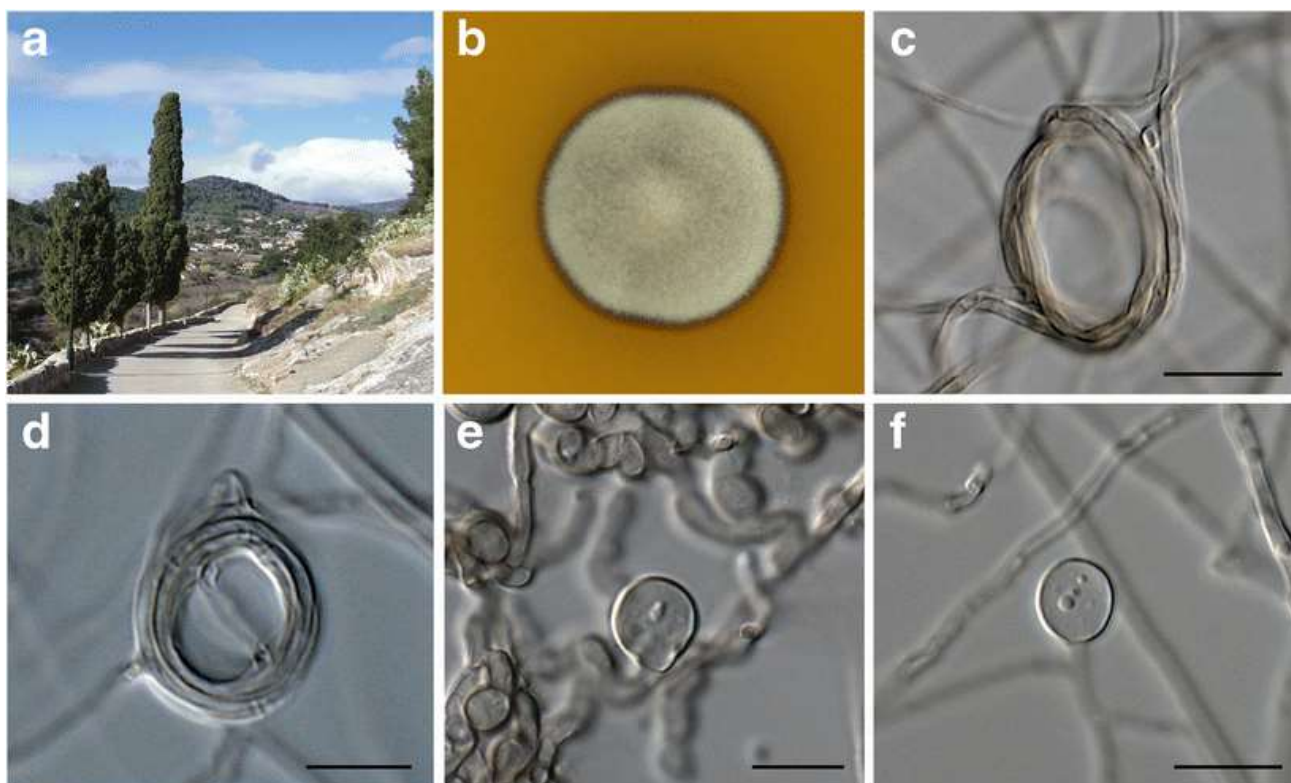


Fig. 7. *Cyphellophora chlamydospora* (CBS 127581). **a** Sampling area in Castellvell del Camp. **b** Colony on MEA after 14 d at 24 °C. **c, d** Hyphal coils. **e, f** Chlamydospores. Scale bars (**c–f**) 10 μm

MycoBank:MB809813

Etymology: The name refers to the chlamydospores produced by the fungus in culture

Colonies after 14 days at 24 °C attaining 21 mm on MEA and 23 mm on OA, velvety, gray, with an olivaceous black, entire margin; reverse olivaceous black. Vegetative hyphae septate, branched, straight to flexuous, pale olivaceous to pale olivaceous brown, smooth- and thin-walled, 1.5–4 μm wide, forming strands and coils, with anastomoses, often appearing irregular and constricted at the septa, especially in cultures at 30 °C.

Chlamydospores mostly subglobose, aseptate, pale olivaceous to pale olivaceous brown, smooth-walled, 6.5–13.5 μm wide. Conidia, yeast cells and sexual morph not observed. Optimum growth temperature 24 °C, minimum below 6 °C, maximum between 30 and 36 °C.

Material examined: SPAIN. Tarragona Province, Castellvell del Camp, isolated from soil, February 2010, H. Madrid (CBS H-21629 holotype, a dried culture on MEA; ex-type cultures CBS 127581 and FMR 10878).

Notes: *Cyphellophora chlamydospora* is an atypical member of this genus by its inability to produce conidia on common mycological media (Feng et al. 2012). However, in spite of its poor morphology, it was possible to place it in the genus *Cyphellophora* based on DNA sequence analyses. In this strain, chlamydospores were abundant at 30 °C, but were less frequent at lower temperatures, suggesting that thermal stress might stimulate their production when approaching the maximum tolerated. None of the species currently accepted in *Cyphellophora* has been reported to produce chlamydospores in culture

(Matsushima 1987; de Hoog et al. 2000; Decock et al. 2003; Cheewangkoon et al. 2009; Feng et al. 2012; Réblová et al. 2013; Gao et al. 2015; Crous et al. 2016). Hyphal coils were abundant in *C. chlamydospora*, but these are also produced by many other species of *Cyphellophora* as well as other genera of Chaetothyriales (Feng et al. 2012; Crous et al. 2007b, 2013), and are morphologically very variable, indicating that they are not taxonomically informative.

As previously mentioned, a species originally described in *Phialophora*, *P. livistonae*, proved to belong in *Cyphellophora*, and clustered with 100 and 97 % bs with *C. sessilis* in LSU and ITS-based phylogenetic analyses (Figs. 1 and 3, respectively). Both species are similar in producing abundant intercalary phialides and elongate, rather short and non-falcate conidia. They differ, however, in conidial size, i.e. 4–10 × 2–3.5 µm in *P. livistonae* and about 3 × 1.8 µm in *C. sessilis* (de Hoog et al. 1999a; Crous et al. 2012a). *Phialophora livistonae* is transferred to *Cyphellophora* and the following new combination is proposed:

Cyphellophora livistonae (Crous & Summerell) Madrid & Hern.-Restr., comb. nov. –
Mycobank:MB809814

≡ *Phialophora livistonae* Crous & Summerell, Persoonia 29: 169 (2012)

Rhinocladiella amoena Hern.-Restr., Madrid, Gené, Cano & Guarro, sp. nov. Fig. 8

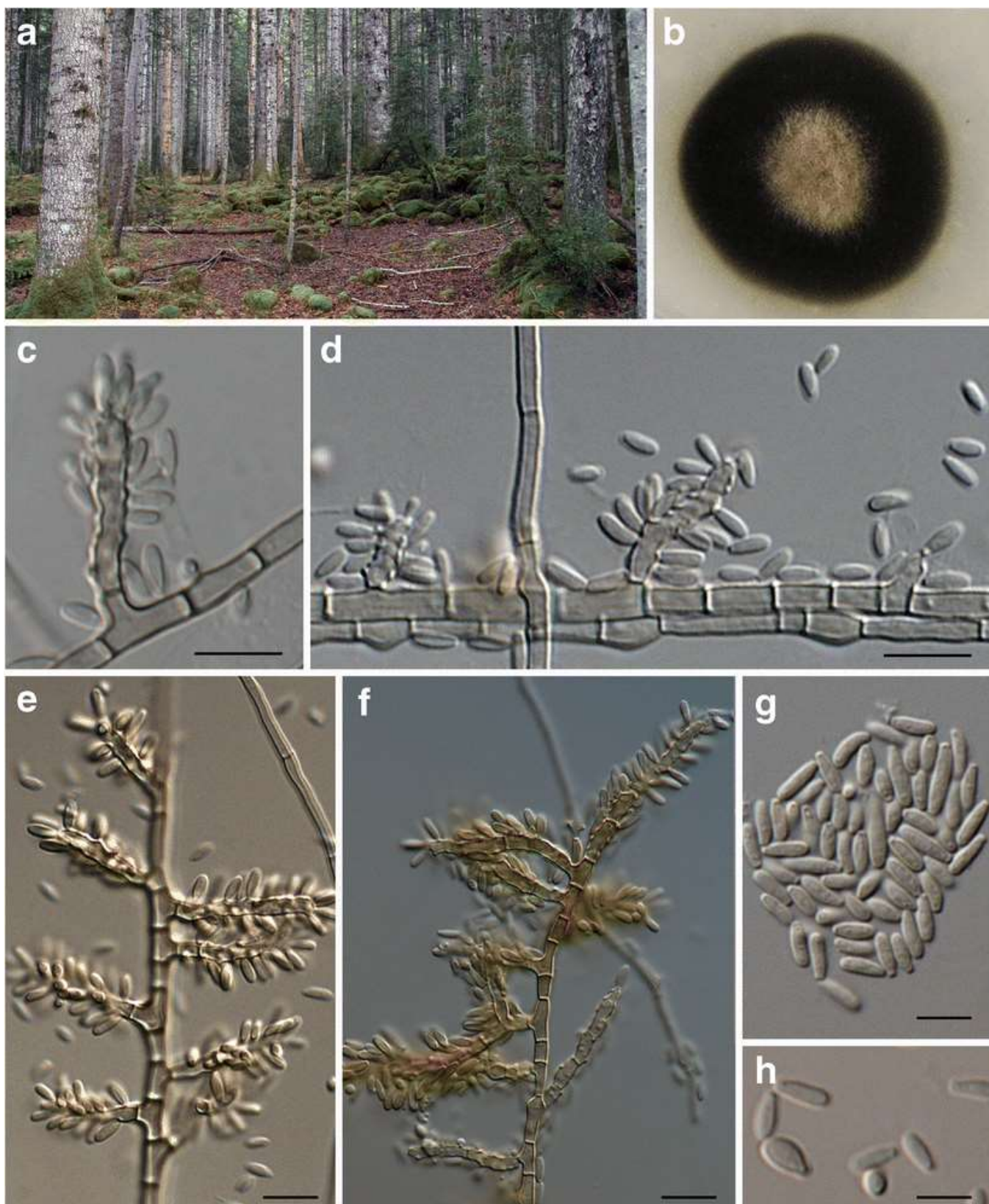


Fig. 8. *Rhinocladiella amoena* (CBS 138590). **a** Sampling area in Ordesa y Monte Perdido National Park. **b** Colony on OA after 14 days at 24 °C. **c–f** Conidiophores, conidiogenous cells and conidia. **g, h** conidia. Scale bars (**c–f**) 10 μ m, (**g, h**) 5 μ m

MycoBank:MB815962

Etymology: The name derives from Latin “*amoenus*”, meaning “delightful”

Colonies after 14 days at 24 °C attaining 6 mm on MEA and 13–16 mm on OA, dry, cottony and grayish sepia at the center, glabrous and fuscous black at the periphery, with an entire margin; reverse black. Vegetative hyphae septate, branched, subhyaline, smooth- and thin-walled, 1–2.5 µm wide. Conidiophores semimacronematous to macronematous, simple to profusely branched, light to dark olivaceous brown, rather thick-walled, up to 43 µm long and 3 µm wide. Conidiogenous cells mostly terminal, cylindrical, olivaceous-brown, 4.5–20 × 1.5–3 µm, producing conidia sympodially on numerous small denticles. Conidia obovoid, subcylindrical to narrowly clavate, aseptate, pale olivaceous, 3–6 × 1–2 µm, with an obtuse apex and a truncate base with an inconspicuous scar. Chlamydo-spores, yeast cells and sexual morph not observed. Optimum growth temperature 24 °C, minimum between 6 and 12 °C, maximum between 30 and 36 °C.

Material examined: SPAIN. Huesca Province, Ordesa y Monte Perdido National Park, isolated from a submerged twig, 26 March 2011, M. Hernández-Restrepo & J. Capilla (CBS H-21835 holotype, a dried culture on MEA; ex-type cultures CBS 138590 and FMR 12063).

Notes: This fungus is superficially similar to other *Rhinocladiella* species with branched conidiophores, such as *R. anceps*, *R. atrovirens*, *R. basitona* and *R. similis*. However, they can be distinguished by conidial morphology and size, i.e. subglobose to ellipsoidal and 2.5–3.8 × 1.8–2.5 µm in *R. anceps*, short-cylindrical and 3.7–5.5 × 1.2–1.8 µm in *R. atrovirens*, guttuliform to clavate and 3.5–4.5 × 2.2 µm in *R. basitona*, and cylindrical, 4–7 × 1.5 µm in *R. similis* (de Hoog and Hermanides-Nijhof 1977; de Hoog et al. 2003). Furthermore, the yeast cells that are often produced in culture by *R. anceps*, *R. atrovirens* and *R. similis* (de Hoog and Hermanides-Nijhof 1977; de Hoog et al. 2000, 2003) were not observed in *R. amoena*.

Discussion

Most of the best-known hyphomycetous genera in the Chaetothyriales are polyphyletic within the order (Crous et al. 2007b; Gueidan et al. 2014). Traditionally, they have been defined by morphological features (de Hoog et al. 2000), which later proved to have emerged many times in separate, often relatively distant, phylogenetic groups (Arzanlou et al. 2007; Crous et al. 2007b; Badali et al. 2008; Najafzadeh et al. 2011). One of such genera is *Cladophialophora*, defined by the production of globose to elongate, acropetal, usually branched chains of blastic, melanized conidia with inconspicuous scars (Badali et al. 2008; Bensch et al. 2012). The generic type, *C. carrionii*, belongs in Herpotrichiellaceae, but many other species are related to other chaetothyrialean families, such as Epibryaceae, Chaetothyriaceae and Trichomeriaceae (Gueidan et al. 2014). Even outside the Chaetothyriales, species of the genus *Fusicladium* (Venturiaceae, Pleosporales) may show morphological features which closely resemble those of *Cladophialophora* (Crous et al. 2007b; Koukol 2010). The new species described in this paper, however, is related to members of the Herpotrichiellaceae (Fig. 1) and can undoubtedly be considered a member of *Cladophialophora* s. str.

The genus *Cyphellophora* originally included dematiaceous, phialidic chaetothyrialean fungi with falcate, septate conidia (de Vries 1962; de Hoog et al. 2000; Decock et al. 2003). Conidial morphology was the main difference between this genus and *Phialophora*, which typically produces aseptate, mostly globose to ellipsoid conidia (Schol-Schwarz 1970; Gams 2000). Phylogenetic studies revealed that typical *Cyphellophora* species formed a paraphyletic group which also included certain members of *Phialophora* with non-falcate conidia (Feng et al. 2012). Two species with atypical morphology, i.e. *C. eugeniae* and *C. hylomeconis* (Crous et al. 2007b), clustered outside that group and were later transferred to the segregate genera *Aphanophora* and *Camptophora*, respectively. In culture, *Aphanophora* produces setae and subcylindrical to cylindrical conidia with constrictions at the septa, whereas *Camptophora* produces fusiform to falcate conidia with a tendency to anastomose and undergo microcyclic sporulation (Réblová et al. 2013). With the reallocation of those atypical species and the inclusion of genetically related members of *Phialophora*, the genus *Cyphellophora* was redelimited to become a monophyletic entity (Réblová et al. 2013). In our study, one new *Cyphellophora* species, *C. chlamydospora*, was proposed and *C. suttonii* is reported for the first time from Europe, isolated from garden soil in Catalonia. The latter species was originally described as an agent of subcutaneous phaeohyphomycosis in a dog in USA (Ajello et al. 1980) and was later reported from a human infection in the same country (Perfect and Schell 1996) and from soil in Brazil (Nunes et al. 1999). However, the identity of the strains from human and soil have not been confirmed molecularly. In the present study, one more *Phialophora* s.l. species, *P. livistonae*, was transferred to *Cyphellophora* based on DNA sequence data (Figs. 1, 3). Since the type species of *Phialophora*, *P. verrucosa*, is a member of Herpotrichiellaceae (de Hoog et al. 1999a), many other *Phialophora* s.l. species related to different taxonomic groups have been reallocated to other genera, such as *Cadophora* (Helotiales), *Gaeumannomyces* (as “*Harpophora*”, Magnaporthaceae), *Phaeoacremonium* (Togniniaceae), *Pleurostomophora* (Pleurostomataceae) and others (Crous et al. 1996; Gams 2000; Harrington and McNew 2003; Vijaykrishna et al. 2004; Réblová et al. 2013). Despite these advances in the taxonomy of *Phialophora* s.l., many species have been described without a proper molecular study (e.g. Millar 1990; Jiang and Wang 2010; Wu and Zhang 2011) and their phylogenetic placement still needs to be assessed.

The *Cyphellophora* clade, which is strongly supported, shows a considerable degree of genetic diversity and appeared clearly separated from the accepted families of Chaetothyriales (Feng et al. 2012; Réblová et al. 2013). Therefore, it was considered by Réblová et al. (2013) to be a distinct, monotypic family, the Cyphellophoraceae. However, in the phylogenetic analysis by Gueidan et al. (2014), two species of *Cladophialophora* s.l., i.e. *C. hostae* and *C. scillae*, formed a sister group to the *Cyphellophora* clade and were also included in the Cyphellophoraceae. These species, which form cladosporoid, acropetal chains of holoblastic conidia (Crous et al. 2007b), are morphologically and phylogenetically clearly distinct from the core of the genus *Cyphellophora*, in which only phialidic conidiogenesis has been described (Feng et al. 2012; Réblová et al. 2013), and evidently should not be transferred to this genus. *Cladophialophora hostae* and *C. scillae* should be kept, at least provisionally, under the broad, polyphyletic current concept of *Cladophialophora*.

Rhinocladiella includes dematiaceous hyphomycetes with more or less differentiated, sympodial conidiophores with a denticulate rachis and aseptate, usually elongate conidia, but *Exophiala*-like yeast stages are observed in several species of this genus (de Hoog and Hermanides-Nijhof 1977). Species of *Rhinocladiella* appear in different clades of Chaetothyriales, sometimes in association with genera such as *Exophiala* and the sexual morph *Capronia* (Arzanlou et al. 2007; Crous et al. 2007b; Pratibha and Prabhugaonkar 2015). Strain CBS 138590 fits well in the current concept of *Rhinocladiella*, but its morphological and phylogenetic features clearly indicate that it is a novel taxon. In this paper, we also report *R. similis*, which is a relatively poorly-known species described originally from a cutaneous ulcer in a patient from Brazil (de Hoog et al. 2003). The CBS fungal collection (<http://www.cbs.knaw.nl/Collections/>) also includes strains of *R. similis* from bathroom surfaces, bronchial wash and soil, from different geographic regions. The only chaetothyrialean genus with which *Rhinocladiella* might be confused is *Veronaea*, but species of the latter genus typically have 1-septate conidia (de Hoog and Hermanides-Nijhof 1977). *Thysanorea* is also superficially similar, but produces both micronematous and macronematous conidiophores, the latter ones with a dark brown, thick-walled stalk and a head formed by a complex system of branches. The conidiogenous cells of *Thysanorea* have denticles much more prominent than those of *Rhinocladiella* and, as in *Veronaea*, its conidia are septate (Arzanlou et al. 2007; Pratibha and Prabhugaonkar 2015). Many hyphomycetous genera outside Chaetothyriales produce a conidial apparatus similar to that of *Rhinocladiella*, e.g. *Myrmecridium* (Myrmecridiaceae, Sordariomycetes), *Pseudoramichloridium* (Teratosphaeriaceae, Capnodiales), *Radulidium* (incertae sedis, Sordariomycetes), *Ramichloridium* (Mycosphaerellaceae, Capnodiales), *Rhodoveronaea* (Annulatasaceae, Sordariomycetes), and *Veronaeopsis* (close to Venturiaceae, Pleosporales), probably reflecting convergent evolution (Arzanlou et al. 2007; Cheewangkoon et al. 2009).

During the present study, four *Exophiala* spp. were identified, i.e. *E. aquamarina*, *E. lacus*, *E. oligosperma*, and *E. radialis*, isolated from soil and river sediments (Table 1). *Exophiala aquamarina* was previously known only from Canada and USA, associated with infections in a number of fish hosts, including leafy and weedy seadragons, winter flounder, little tunny, lumpfish and sand lance. It causes necrotic skin lesions which may progress to systemic infections with angio- and osteotropism, but apparently not neurotropism (de Hoog et al. 2011; Seyedmousavi et al. 2013). Its presence in Europe raises concern about its possible role in phaeohyphomycosis in fishes in this continent, considering its broad range of hosts and its ability to cause aquarium outbreaks (de Hoog et al. 2011). An uncultured *Exophiala* sp. with 98 % identity to the ex-type strain of *E. aquamarina* (CBS 119918) in the 18S rDNA gene was reported as one of the main fungi colonizing a marble monument in Germany (Hallmann et al. 2013). In that study, the fungus was identified as *E. aquamarina* but, taking into account its terrestrial habitat and that 18S is a relatively conserved gene (Iwen et al. 2002), almost certainly the fungus on marble represents a different but related taxon. *Exophiala radialis* was recently described as an endophyte of the brassicaceous host *Microthlaspi perfoliatum* in Bulgaria, France and Germany, and was also isolated from other plant materials in different European countries. That fungus was also isolated from samples of human skin and nails, but its role in disease has not been properly demonstrated (Maciá-Vicente et al. 2016). Remarkably, this fungus was recovered from soil samples collected in different Spanish regions (Table 1), probably representing a widespread species in this

country. *Exophiala lacus* was recently described from shallow freshwater in a lake in The Netherlands (de Hoog et al. 2011). The fungus was only known from the ex-type strain, CBS 117497, and no infections by this organism have been reported so far. During our study, the known distribution of this species was expanded to Spain, but it has not been reported outside Europe. *Exophiala oligosperma* has a widespread, transoceanic geographical distribution and is associated with a broad clinical spectrum, which includes brain abscesses, disseminated infections, onychomycosis, rhinosinusitis, and other clinical manifestations (de Hoog et al. 2003; Kan et al. 2013; Woo et al. 2013; Wen et al. 2016). In Spain, a case of subcutaneous infection in a renal transplant recipient was published by González-López et al. (2007). In the environment, *E. oligosperma* has been isolated from various substrates, including pasteurized ice tea, drinking water networks, plastic, and the floor of a steam bath (Najafzadeh et al. 2013). However, as far as we know, our study is the first one to report this species from an aquatic environment, i.e. river sediments (Table 1).

The order Chaetothyriales is an ecologically and clinically important group of fungi, of which still little is known. Further work and the collaboration of the global mycological community are necessary to generate a more complete knowledge about their biodiversity, habitats, distribution and the role they play in different ecosystems.

Acknowledgments

We are indebted to Drs. Mohammad Javad Najafzadeh and Sybren de Hoog, CBS-KNAW Fungal Biodiversity Centre (Utrecht, The Netherlands) for comparing ITS sequences of the *Exophiala* strains included in this study with the black yeasts DNA sequence database of that institution. This work was supported by the Spanish Ministry of Economy and Competitiveness, grant CGL2011-27185.

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