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1 ***Exophiala atacamensis* sp. nov. and *E. crusticola* from**
2 **the Atacama Desert, northern Chile**

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35

36 In the course of a taxonomic survey on hyphomycetes from the Atacama Desert, four strains of slow-
37 growing, cycloheximide-tolerant dematiaceous fungi were obtained from soil samples. These isolates presented a
38 blastic conidiogenous apparatus and yeast-like budding cells typical of the genus *Exophiala*. DNA sequence
39 analyses of the internal transcribed spacer region and partial large subunit ribosomal RNA gene revealed the
40 presence of a novel species, *Exophiala atacamensis*, and a new record, *E. crusticola*. *Exophiala atacamensis* is
41 phylogenetically distant from other members of *Exophiala* and is morphologically characterized by the production
42 of annellidic conidiogenous cells, aseptate conidia in slimy masses, yeast-like budding cells, and abundant brown,
43 meristematic, thick-walled bodies. This study reports *E. crusticola* for the first time in the Southern Hemisphere.

44 Key Words: Black yeasts, Chaetothyriales, Herpotrichiellaceae, phylogeny, taxonomy. – 1 new species.

45

46 The fungal genus *Exophiala* (Chaetothyriales, Eurotiomycetes) currently includes about 65
47 species. They are characterized by the production of yeast-like budding cells, dematiaceous
48 mycelium, annellidic conidiogenous cells and aseptate or transversely septate conidia in slimy
49 masses (de Hoog & Hermanides-Nijhoff 1977; Crous et al. 2018a, 2019). Identification of
50 species in this genus is difficult due to the existence of aggregates of genetically close,
51 morphologically similar taxa (de Hoog et al. 2006; Zeng et al. 2008; Maciá-Vicente et al. 2016).
52 In addition, *Exophiala* species often show a high degree of pleomorphism in culture and
53 sometimes produce phialophora-like, cladophialophora-like or meristematic synanamorphs
54 (Crous et al. 2007; Borman et al. 2017; de Hoog et al. 2020). Considering the high
55 morphological plasticity of *Exophiala* spp., DNA sequence analyses are required for reliable
56 species-level identification (Zeng et al. 2007; Li et al. 2011; Wen et al. 2016).

57 The type species of *Exophiala*, *E. salmonis*, and most members of this genus are allied to
58 the Herpotrichiellaceae (de Hoog et al. 2011, 2020). However, a few species belong in other
59 families of Chaetothyriales, such as Chaetothyriaceae and Trichomeriaceae (Gueidan et al. 2014;
60 Madrid et al. 2016). Within Herpotrichiellaceae, *Exophiala* spp. do not form a distinct clade, but
61 they are often associated with other hyphomycete genera, such as *Fonsecaea*, *Phialophora*,
62 *Rhinochrysiella*, and *Veronaea* (Arzanlou et al. 2007; Crous et al. 2007; Réblová et al. 2013,
63 2016). *Exophiala*-like asexual morphs have been linked to certain species of the ascomycete
64 genus *Capronia* (de Hoog et al. 1994; Untereiner 1995), but this genus is also polyphyletic
65 (Untereiner et al. 2011). Members of *Capronia* s.l. are associated with multiple hyphomycete
66 genera (Müller et al. 1987; Untereiner 1997, 2000) but no DNA sequence data or strains of the

67 type species, *Capronia sexdecimspora*, are available (Untereiner et al. 2011). Therefore, it is
68 difficult to apply unitary nomenclature in this generic complex and a certain degree of polyphyly
69 is currently accepted in *Capronia* and its anamorphs (Untereiner & Naveau 1999; Gueidan et al.
70 2014).

71 *Exophiala* species occur in diverse habitats including soil, living or dead plant material,
72 water, river sediments, rocks and humid surfaces in indoor spaces (Papendorf 1969; de Hoog &
73 Hermanides-Nijhoff 1977; Matos et al. 2002; Crous et al. 2007; Döğen et al. 2013). They are
74 also associated with numerous animal hosts, where they may occur as mere colonizers or as
75 opportunistic pathogens causing a broad spectrum of superficial and invasive, often life-
76 threatening infections (de Hoog et al. 2003, 2005, 2011; Revankar & Sutton 2010; Seyedmousavi
77 et al. 2013; Woo et al. 2013). Furthermore, numerous *Exophiala* species occur in habitats with
78 scarce water and nutrients (Ruibal et al. 2008; Hallmann et al. 2013), high concentrations of
79 heavy metals or toxic aromatic hydrocarbons (Prenafeta-Boldú et al. 2001; Seyedmousavi et al.
80 2011), wide temperature fluctuations and intense exposure to UV radiation (Bates et al. 2006;
81 Isola et al. 2013). Some of these extremotolerant species are currently under study as potential
82 bioremediation agents for pollutants such as arsenic, and gasoline-derived volatile compounds
83 (Prenafeta-Boldú et al. 2006; Badali et al. 2011; Seyedmousavi et al. 2011).

84 In spite of the clinical relevance and biotechnological potential of *Exophiala*, no thorough
85 assessment of the biodiversity of this genus has been carried out in Chile. Only scarce
86 publications exist and they report only five species, i.e. *E. exophialae*, *E. jeanselmei*, *E. lecanii-*
87 *corni*, *E. pisciphila* and *E. salmonis* (Piontelli et al. 1984; Uijthof et al. 1997; Silva et al. 2004).
88 Considering the vast geographical territory of this country, its diversity of climates and rich flora

89 and fauna, we suspect that many more species remain to be found. In the present study, we
90 addressed the phylogenetic placement and species identities of four *Exophiala* strains obtained
91 from desert soil in northern Chile.

92

93 **Materials and methods**

94

95 **Sample collection and isolation**

96 Soil samples were collected in areas of the Atacama Desert near Calama (altitude 2400
97 m.a.s.l.). Samples were placed into polyethylene bags and kept at room temperature until
98 processed. Approximately 1 g of each sample was diluted in 9 mL of sterile water and a 500 μ L
99 aliquot of the mix was spread on the surface of plates with malt extract agar (MEA; Merck,
100 Germany) supplemented with cycloheximide at a final concentration of 0.1 mg/mL.
101 Cycloheximide was added in order to inhibit the growth of fast-growing molds, while favouring
102 the isolation of tolerant organisms, such as chaetothyrionalean fungi (Madrid et al. 2016). The
103 plates were incubated at 25 °C in the dark and observed weekly. Pure cultures of soilborne
104 *Exophiala* species were obtained by transferring fragments of slow-growing, strongly melanized
105 colonies growing on the primary cultures to MEA plates, with the aid of a sterile dissection
106 needle. MEA plates were incubated at 25 °C for 14 days in the dark and then DNA extraction
107 and subculturing for morphological studies were performed. Strains were preserved in the
108 Chilean Type Culture Collection (CCCT), Universidad de la Frontera, Temuco, Chile and in the
109 working collection of the main author (HM).

110

111 Phenotypic characterization

112 Colony morphology was studied on MEA and oatmeal agar (OA; Difco, USA) after 21
113 days at 25 °C in the dark. The ability to grow at 37 °C was also tested on both media.

114 Microscopic morphology was studied from slide cultures on MEA at 25 °C after 14 days.

115 Photomicrographs were obtained from lactophenol cotton blue mounts using a Zeiss Axioskop 2
116 Plus light microscope.

117

118 DNA sequence analyses

119 DNA was extracted directly from colonies on MEA using the PrepMan Ultra sample
120 preparation reagent (Applied Biosystems, Foster City, California) following the manufacturer's
121 instructions. The internal transcribed spacer region (ITS) and a fragment of the large subunit
122 rRNA gene (LSU) were sequenced with the primer pairs ITS5/ITS4 and LR0R/LR5 as described
123 by White et al. (1990) and Vilgalys and Hester (1990), respectively. Purification and Sanger
124 sequencing of PCR products were carried out at Macrogen USA (Rockville, Maryland).

125 Consensus sequences were obtained from the complementary sequences of each strain using the
126 SeqTrace software (Stucky 2012). BLAST searches (Altschul et al. 1990) were performed with
127 the ITS and LSU sequences of the strains studied in order to compare them with those of species
128 deposited in GenBank. For molecular species-level identification, percent identities of only the
129 ITS locus were considered, because it offers a higher resolution than the relatively conserved
130 LSU gene. LSU sequences were obtained as a complementary barcode useful at the level of

131 genus, family and higher taxonomic ranks (Iwen et al. 2002; Schoch et al. 2012). If the identity
132 of the ITS sequence of a studied strain to its closest match was $\geq 99\%$, they were considered
133 conspecific (Zeng et al. 2007; Madrid et al. 2016).

134 An ITS-based phylogeny reconstruction (Fig.1) was performed to show the relationships
135 between Chilean isolates obtained in this study and other *Exophiala* spp. currently represented in
136 GenBank. The type species of *Exophiala*, *E. salmonis* is a member of Herpotrichiellaceae, and
137 therefore the ingroup only included species belonging in that family. Excluded species include *E.*
138 *encephalarti* and *E. placitae*, which belong in Trichomeriaceae, and *E. eucalyptorum*, which
139 resides in Chaetothyriaceae. ITS sequences were aligned with the MUSCLE webserver
140 (<http://www.ebi.ac.uk/Tools/msa/muscle/>, Edgar 2004) and then adjusted manually with a text
141 editor. After excluding ambiguous regions, an alignment of 403 bp. was obtained. Phylogeny
142 reconstructions were performed with the maximum likelihood method with MEGA X (Kumar et
143 al. 2018), using the best DNA substitution models chosen by that software. The statistical
144 support for the groupings was assessed by bootstrap analysis of 1000 replicates. The DNA
145 sequences and alignments generated during this study were deposited in GenBank (Table 1) and
146 TreeBASE (study accession URL:
147 <http://purl.org/phylo/treebase/phyloids/study/TB2:S25910>), respectively.

148

149 **Results and discussion**

150

151 *Molecular study*

152 BLAST searches allowed us to identify three out of the four studied strains to species level.
153 Isolates CCCT 19.109, CCCT 19.110, and CCCT 19.111 showed 99.82–100% sequence
154 identities to the ITS region of the ex-type strain of *Exophiala crusticola*, CBS 119970 (GenBank
155 AM048755), and clustered with that strain in the ITS tree (Fig. 1). On the other hand, all the
156 closest matches of strain CCCT 19.114 showed relatively low ITS percent identities. These
157 included *Exophiala* sp. IFM 64156 (GenBank accession LC317596, 96.60% identical), *Veronaea*
158 *botryosa* CBS 126027, CBS 127264 and CBS 127265 (GenBank MH863891, MH864499, and
159 MH864500, respectively, 91.31–91.43% identical), and *Exophiala dermatitidis* CBS 125841
160 (GenBank MH863897, 89% identical). In the ITS tree (Fig. 1) CCCT 19.114 grouped with
161 *Exophiala* sp. IFM 64156 with 85% bootstrap support, but a considerable genetic distance
162 separated the strains, clearly indicating that they represent different taxa.

163

164 Taxonomy

165 Strain CCCT 19.114 shows morphological features which do not match any of the
166 described species of *Exophiala*. Its unique phylogenetic position and considerable genetic
167 distance from other members of this genus support the proposal of a novel species.

168 ***Exophiala atacamensis* Madrid, Gené, Quijada, Cantillo & R. Gacitúa sp. nov.** – Figs. 1, 2.

169 MycoBank no.: MB835461

170 Diagnosis. – Distinguished from other *Exophiala* species by the combination of thick-walled meristematic bodies,
171 and an inability to grow at 40 °C.

172 Holotypus. – CHILE, El Loa Province, Atacama Desert, near Calama, isolated from soil, Sep 2015, H. Madrid (SGO
173 168422 holotype, a dried culture on MEA; ex-type cultures CCCT 19.114 and HM 132).

174

175 Description. – Colonies after 21 days at 25 °C attaining 13–15 mm on MEA, and 14–17
176 mm on OA, velvety, on both media mid grey to mid olivaceous grey, flat to convex, with an
177 entire to lobulated, olivaceous black margin, sometimes umbonate with a glabrous, olivaceous
178 black, moist center; reverse olivaceous black. No growth observed at 37 °C. Vegetative hyphae
179 septate, branched, light olivaceous to mid olivaceous brown, smooth and thin-walled, 1–3 µm
180 wide, with moniliform segments showing swollen cells up to 6 µm wide and abundant
181 intercalary, lateral and terminal chlamydospore-like cells commonly evolving into mid
182 olivaceous brown, subglobose meristematic bodies up to 13 µm wide. Conidiophores
183 micronematous to semimacronematous, often reduced to conidiogenous cells, pale olivaceous to
184 pale olivaceous brown. Conidiogenous cells blastic, terminal or intercalary, mostly flask-shaped
185 or subcylindrical to fusiform, but sometimes also subglobose to ellipsoid, 5–18 × 2–5 µm often
186 with a narrow, (sub)apical or lateral, subcylindrical annellated extension 1–3.5 × 1–1.5 µm.
187 Conidia mostly guttuliform to clavate, aseptate, light olivaceous to light olivaceous brown,
188 smooth-walled, 2–7 × 1.5–4 µm. Yeast cells subglobose to subcylindrical, light olivaceous to
189 light olivaceous brown, smooth-walled, 3–6 × 2.5–3.5 µm, often forming short chains. Sexual
190 morph not observed.

191

192 Etymology. – The name refers to the place where this fungus was collected, the Atacama
193 Desert in northern Chile.

194 Habitat. – In desert soil

195 Notes. – *Exophiala atacamensis* is superficially similar to two *Exophiala* species
196 producing meristematic bodies in culture, i.e. *E. dermatitidis* and *E. phaeomuriformis*. These
197 species, however, are able to grow at 40 °C (de Hoog et al. 2020) and are phylogenetically
198 distant from *E. atacamensis* (Fig. 1). Furthermore, *E. dermatitidis* sometimes produces
199 phialophora-like phialides with conspicuous collarettes (de Hoog et al. 1994) which were not
200 observed in *E. atacamensis*, and the thallus of *E. phaeomuriformis* lacks hyphae (Matos et al.
201 2003). Meristematic bodies are also produced by certain *Exophiala* species causing
202 chromoblastomycosis in humans, such as *E. spinifera* and *Exophiala* aff. *pisciphila*. However,
203 these structures were reported only in infected tissues, not in culture (Padhye et al. 1996, Garzón
204 et al. 2018) and both fungi are phylogenetically distant from *E. atacamensis* (Fig. 1).

205

206

Discussion

207 This is the first study to provide conclusive, DNA sequence-based identifications of
208 Chilean *Exophiala* strains, with the proposal of a novel species, *E. atacamensis*, and a new
209 record, *E. crusticola*. The closest known relative of *E. atacamensis* is *Exophiala* sp. IFM 64156,
210 a clinical strain isolated from scalp, preserved at the Medical Research Center of Chiba
211 University (Chiba, Japan). In the phylogenetic study (Fig. 1), both fungi formed a clade with
212 significant statistical support, but branch lengths clearly indicate that they represent different
213 species. Molecular data suggest that IFM 64156 might represent another novel species, however,
214 further studies would be necessary to propose it formally. The ITS sequence of that strain was
215 submitted directly to GenBank in 2017 and heretofore, it has not been included in any published

216 study. Considering that the genus *Exophiala* includes opportunistic pathogens affecting a wide
217 spectrum of animal hosts (de Hoog et al. 2011, Seyedmousavi et al. 2013), it would be
218 interesting to perform experimental pathogenicity studies with *E. atacamensis*. Infections in
219 humans, nevertheless, are unlikely considering the inability of this fungus to grow at 37°C (de
220 Hoog et al. 2020).

221 *Exophiala crusticola* was originally described from biological soil crusts in arid areas of
222 the USA (Bates et al. 2006). Biological soil crusts are microbial communities formed by algae,
223 bacteria, bryophytes and fungi which occur in arid environments with scarce vascular plant
224 cover. In such places, these organisms form a consolidated crust which protect soil against
225 erosion (Warren et al. 2019, 2021). Like other filamentous fungi, *E. crusticola* was hypothesized
226 to contribute to the development of these formations by entwining soil particles with its hyphae
227 and gluing them with extracellular polysaccharides. In such communities, this fungus was
228 supposed to occur as a saprobe subsisting on organic compounds released by cyanobacteria by
229 leaching due to continued cycles of wetting and drying (Bates et al. 2006). After its original
230 description, *E. crusticola* has been reported only three times, i.e. from creosoted railway sleepers
231 in Turkey (Gümral et al. 2014), from gypsum soil in semi-arid steppes in Spain (Muriel et al.
232 2022), and from sites contaminated with aromatic hydrocarbons in Italy (Isola et al. 2021). This
233 study presents the first report of this species from the southern hemisphere.

234 Heretofore, five *Exophiala* species had been reported from Chile i.e., *Exophiala*
235 *exophialae*, *E. jeanselmei*, *E. lecanii-corni*, *E. pisciphila* and *E. salmonis*. These species,
236 reported from miscellaneous clinical and environmental sources, were originally identified
237 relying entirely on phenotypic features (Piontelli et al. 1984, Uijthof et al. 1997, Silva et al.

238 2004). Unfortunately, only two strains from those reports were preserved, *E. pisciphila* CBS
239 217.79 and *E. salmonis* 665.76, isolated from soil and *Araucaria* wood, respectively. ITS
240 sequence analyses carried out by Uijthof et al. (1997) concluded that Chilean strains are
241 genetically very different from the respective ex-type strains, both of which are pathogenic to
242 fish (Carmichael 1966, McGinnis & Ajello 1974). Unfortunately, the ITS sequences of CBS
243 217.79 and CBS 665.76 are not available in GenBank for comparison. An unidentified *Exophiala*
244 species was isolated from decaying trunks of the cactus *Eulychnia iquiquensis* in northern Chile
245 (Santiago et al. 2018) but, apparently, no strains were preserved and no DNA sequence data is
246 available. An additional ‘*Exophiala* sp.’ strain, 15LV1, was isolated by Pulshen et al. (2015)
247 from volcanic soil collected in the Atacama Desert. That strain shows 99.59% and 99.37%
248 identity to the ITS sequences of the ex-type strains of *Phaeoannellomyces elegans* and *Exophiala*
249 *sideris*, CBS 122.95 and CBS 128771, respectively. The former taxon is the type species of
250 *Phaeoannellomyces*, a poorly known clinically relevant genus implicated in different forms of
251 phaeohyphomycosis (Engleberg et al. 1987). This genus is characterized by the production of
252 dematiaceous yeast cells and blastic, mainly annellidic conidiogenous cells (McGinnis et al.
253 1985). These characteristics and its phylogenetic affinities to the Herpotrichiellaceae suggest that
254 *Phaeoannellomyces* might be a putative synonym of *Exophiala*. Further studies are required to
255 test this hypothesis and to determine whether *E. sideris* and *P. elegans* are synonyms. In such
256 case, it would be necessary to reallocate *P. elegans* to *Exophiala* as ‘*E. elegans*’ and this might
257 be the appropriate name for strain 15LV1.

258 Considering the vast geographical area of Chile, its diversity of climates, flora and fauna,
259 high level of endemism, and scarcity of taxonomic studies including *Exophiala* species (Piontelli

260 et al. 1984, Silva et al. 2004, Pulshen et al. 2015, Santiago et al. 2018), probably many more
261 members of this genus remain to be discovered in this country.

262

263

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494 *Biology* **123**: 151–158.
- 495
- 496 **Fig. 1** Maximum likelihood tree constructed with the ITS sequences of *Exophiala* spp. isolated
497 during this study and related reference strains. Branch lengths are proportional to distance.

498 Bootstrap values $\geq 70\%$ are shown near the internodes. *Knufia tsuneda* was used as outgroup.
499 Isolates obtained during this study appear in bold type. ^T, ex-type strain. GenBank accession
500 numbers of ITS sequences are given in parenthesis after strain numbers.

501 **Fig. 2** *Exophiala atacamensis* (CCCT 19.114). **a** Colony on MEA after 21 d at 24°C. **b-f**
502 Conidiophores, conidiogenous cells and conidia. **g** Moniliform hypha. **h** Chlamydospore-like
503 cells evolving into meristematic bodies. **i** Yeast cells. Scale bars **b** 10 μm **c-i** 5 μm .

Table 1. Strains included in the molecular study, their origins and GenBank accession no.

Species name	Isolate no.	Country and source/host	Genbank accession no		References
			ITS	LSU	
<i>Exophiala abietophila</i>	CBS 145038 ^T	Norway, bark of <i>Abies alba</i>	MK442581		Crous et al. (2019)
<i>Exophiala alcalophila</i>	CBS 520.82 ^T	Japan, soil	JF747041		de Hoog et al. (2011)
<i>Exophiala angulospora</i>	CBS 482.92 ^T	Japan, water from drinking well	JF747046		de Hoog et al. (2011)
<i>Exophiala aquamarina</i>	CBS 119918 ^T	USA, skin of <i>Phycodures eques</i> (leafy seadragon)	JF747054		de Hoog et al. (2011)
<i>Exophiala asiatica</i>	CBS 122847 ^T	China, tonsil tissue of a human patient with disseminated infection	EU910265		Li et al. (2011)
<i>Exophiala atacamensis</i>, sp. nov.	CCCT 19.114^T (= HM 132)	Chile, desert soil	MT137540	MT137544	This study
<i>Exophiala attenuata</i>	CBS 101540 ^T	Colombia, soil	AF549446		Vitale & de Hoog (2002)
<i>Exophiala bergeri</i>	CBS 353.52 ^T	Canada, skin of human patient with chromoblastomycosis	EF551462		Zeng & de Hoog (2008)
<i>Exophiala bonariae</i>	CBS 139957 ^T	Italy, surface of marble funerary monument	JX681046		Isola et al. (2013)
<i>Exophiala brunnea</i>	CBS 587.66 ^T	South Africa, leaf litter of <i>Acacia karroo</i>	JF747062		de Hoog et al. (2011)
<i>Exophiala cancerae</i>	CBS 120420 ^T	Brazil, diseased mangrove crab (<i>Ucides cordatus</i>)	JF747064		de Hoog et al. (2011)

Table 1 cont.

<i>Exophiala capensis</i>	CBS 128771 ^T	South Africa, leaf of <i>Phaenocoma prolifera</i>	JF499841		Crous & Groenewald (2011)
<i>Exophiala castellanii</i>	CBS 158.58 ^T	Sri Lanka, human	KF928458		Attili-Angelis et al. (2014)
<i>Exophiala crusticola</i>	CBS 119970 ^T	USA, biological soil crust	AM048755		Bates et al. (2006)
	CCCT 19.109 (= HM 136)	Chile, desert soil	MT137541	MT137545	This study
	CCCT 19.110 (=HM 135)	Chile, desert soil	MT137543	MT137547	This study
	CCCT 19.111 (= HM 134)	Chile, desert soil	MT137542	MT137546	This study
<i>Exophiala dermatitidis</i>	CBS 207.35 ^T	Japan, human	AF050269		Untereiner & Naveau (1999)
<i>Exophiala dopicola</i>	CBS 537.94 ^T	USA, litter of <i>Pinus taeda</i>	MH862483		Vu et al. (2019)
<i>Exophiala equina</i>	CBS 119.23 ^T	Italy, subcutaneous infection in a horse	JF747094		de Hoog et al. (2011)
<i>Exophiala eucalypticola</i>	CBS 143412 ^T	Australia, <i>Eucalyptus obliqua</i> leaf litter	MH107891		Crous et al. (2018)
<i>Exophiala exophialae</i>	CBS 668.76 ^T	Uruguay, straw in an armadillo burrow	AY156973		Vitale & de Hoog (2002)
<i>Exophiala halophila</i>	CBS 121512 ^T	USA, axillary skin, human	JF747108		de Hoog et al. (2011)
<i>Exophiala heteromorpha</i>	CBS 232.33 ^T	Sweden, wood pulp	AY857524		Prenafeta-Boldú et al. (2006)
<i>Exophiala hongkongensis</i>	CBS 131511 ^T	China, big toe nail infection, human	JN625231		Woo et al. (2013)

Table 1 cont.

<i>Exophiala italica</i>	MFLUCC 16-0245 ^T	Italy, dead branch of <i>Cytisus scoparius</i>	KY496744	Tibpromma et al. (2017)
<i>Exophiala jeanselmei</i>	CBS 664.76	N/A, human	AF050271	Untereiner & Naveau (1999)
<i>Exophiala lacus</i>	CBS 117497 ^T	The Netherlands, lake water	JF747110	de Hoog et al. (2011)
<i>Exophiala lecanii-corni</i>	CBS 123.33 ^T	N/A, <i>Lecanium corni</i>	AY857528	Prenafeta-Boldú et al. (2006)
<i>Exophiala lignicola</i>	CBS 144622 ^T	Ukraine, decorticated trunk of <i>Quercus</i> sp.	MK442582	Crous et al. (2019)
<i>Exophiala macquariensis</i>	CBS 144232 ^T	Australia, soil polluted with aromatic hydrocarbons	MF619956	Zhang et al. (2019)
<i>Exophiala mansonii</i>	CBS 101.67 ^T	Sweden, <i>Populus tremula</i>	AF050247	Untereiner & Naveau (1999)
<i>Exophiala mesophila</i>	CBS 402.95 ^T	Germany, silicone seal in shower room	MH862536	Vu et al. (2019)
<i>Exophiala moniliae</i>	CBS 520.76 ^T	Russia, twig of <i>Quercus</i> sp.	KF881967	Li et al. (2017)
<i>Exophiala nidicola</i>	CBS 138589 ^T	Spain, nest of a bird	MG701055	Crous et al. (2018b)
<i>Exophiala nigra</i>	CBS 546.82	N/A, N/A	EF551550	Zeng & de Hoog (2008)
<i>Exophiala nishimurae</i>	CBS 101538 ^T	Venezuela, culture contaminant	AY163560	de Hoog et al. (2003)
<i>Exophiala oligosperma</i>	CBS 265.49 ^T	France, honey	KP132067	Irinyi et al. (2015)

Table 1 cont.

<i>Exophiala opportunistica</i>	CBS 109811 ^T	Germany, drinking water at waterstation	JF747123	de Hoog et al. (2011)
<i>Exophiala palmae</i>	CMRP 1196 ^T	Brazil, decaying shell of babassu (<i>Attalea speciosa</i>) coconut	KY680434	Nascimento et al. (2017)
<i>Exophiala phaeomuriformis</i>	CBS 131.88 ^T	N/A, cutaneous phaeohyphomycosis in a human patient	AJ244259	de Hoog et al. (1999)
<i>Exophiala pisciphila</i>	CBS 537.73 ^T	USA, systemic mycosis in channel catfish (<i>Ictalurus punctatus</i>)	AF050272	Untereiner & Naveau (1999)
<i>Exophiala polymorpha</i>	CBS 138920 ^T	USA, subcutaneous lesion in a human patient	KP070763	Yong et al. (2015)
<i>Exophiala psychrophila</i>	CBS 191.87 ^T	Norway, Atlantic salmon (<i>Salmo salar</i>) in fish farm	JF747135	de Hoog et al. (2011)
<i>Exophiala radicans</i>	CBS 140402 ^T	Germany, root of pennycress (<i>Thlaspi perfoliatum</i>)	KT099204	Maciá-Vicente et al. (2016)
<i>Exophiala salmonis</i>	CBS 157.67 ^T	Canada, brain infection of cutthroat trout (<i>Oncorhynchus clarkii</i>)	AF050274	Untereiner & Naveau (1999)
<i>Exophiala sideris</i>	CBS 121818 ^T	The Netherlands, berry of <i>Sorbus aucuparia</i>	HQ452311	Seyedmousavi et al. (2011)
<i>Exophiala</i> sp.	GMG_C6	United Kingdom, coastal soil	FJ439580	Unpublished (direct submission)
<i>Exophiala</i> sp.	IFM 64156	Japan, scalp	LC317596	Unpublished (direct submission)
<i>Exophiala spinifera</i>	CBS 899.68 ^T	USA, nasal granuloma in a human patient	AY156976	Vitale & de Hoog (2002)

Table 1 cont.

<i>Exophiala tremulae</i>	UAMH 10998 ^T	Canada, roots of <i>Populus tremuloides</i>	FJ665274	Crous et al. (2011)
<i>Exophiala xenobiotica</i>	CBS 118157 ^T	Venezuela, oil sludge	DQ182587	de Hoog et al. (2006)
<i>Knufia tsuneda</i>	FMR 10621 ^T	Spain, soil	HG003669	Crous et al. (2013)
<i>Veronaea botryosa</i>	CBS 126027	Brazil, leaf of babassu palm	MH863891	Vu et al. (2019)
	CBS 127264	Mexico, disseminated phaeohyphomycosis in a human patient	MH864499	Vu et al. (2019)
	CBS 127265	Mexico, face tissue from a human patient	MH864500	Vu et al. (2019)
	CBS 254.57 ^T	Italy, sansa olive slag	JF747143	de Hoog et al. (2011)
<i>Veronaea compacta</i>	CBS 268.75 ^T	South Africa, soil	EU041819	Arzanlou et al. (2007)
<i>Veronaea japonica</i>	CBS 776.83 ^T	Japan, dead bamboo culm	EU041818	Arzanlou et al. (2007)

Strains and DNA sequences generated in this study appear in bold type. CBS, CBS-KNAW Fungal Biodiversity Centre, Utrecht, The Netherlands; CCCT, Chilean Type Culture Collection, Universidad de la Frontera, Temuco, Chile; FMR, Faculty of Medicine collection, Reus, Spain; CMRP, Microbiological Collections of the Paraná Network, Federal University of Paraná, Curitiba, Brazil; GMG, Geoff M. Gadd, Geomicrobiology Group, School of Life Sciences, University of Dundee, Dundee, United Kingdom; MFLUCC, Mae Fah Luang University Culture Collection, Chiang Rai, Thailand; UAMH, University of Alberta Microfungus Collection and Herbarium, Devonian Botanic Garden, Edmonton, Canada.