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ORIGINAL ARTICLE

Five novel *Curvularia* species (*Pleosporaceae*, *Pleosporales*) isolated from fairy circles in the Namib desert

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Abstract
The Namib Desert (Namibia) is home to fairy circles which are barren, circular to almost-circular patches of land surrounded by grasses. During a survey of the fungi associated with the most common grass species, *Stipagrostis ciliata* (*Poaceae*), and its rhizospheric soils associated with these fairy circles, *Curvularia* was commonly isolated (80 strains). *Curvularia* is a cosmopolitan fungal genus that occurs in diverse geographical locations and on a wide range of substrates, but particularly on foliar plants. *Curvularia* strains were identified based on multilocus sequence comparisons of their internal transcribed spacer rDNA region (ITS), and the partial gene regions of glyceraldehyde-3-phosphate dehydrogenase (*GAPDH*) and translation elongation factor 1-alpha (*TEF1*). The strains belonged to 13 species, including the discovery of five novel *Curvularia* species. The aim of this paper was to report on the identified species and to formally describe and name the new species as *C. deserticola, C. gobabebensis, C. maraisii, C. namibensis*, and *C. stipagrostidicola.*

Keywords *Bipolaris* · Fungal diversity · Phylogeny · Plant pathogen · Taxonomy · 5 new taxa

Introduction

Deserts provide a harsh habitat for lifeforms due to the high salinity and acidity of the soils, fluctuating temperatures, low precipitation, and high UV irradiation (Makhalanyane et al. 2015; Whitford and Wade 2002). One of the oldest and driest deserts on earth is the Namib, where a phenomenon known as Fairy Circles occurs.

Fairy circles are barren, circular to almost circular patches surrounded at their edges by healthy grass (*Poaceae*) species (Albrecht et al. 2001). These unusual circles in Namibia were first documented by Tinley (1971) and have puzzled scientists for over 50 years, with many hypotheses as to their origin and maintenance. These hypotheses include factors such as termite activity and plant self-organization due to water stress (Albrecht et al. 2001; Getzin et al. 2021, 2022). Ramond et al. (2014) suggested that a soil-borne microbial plant pathogen could be the cause of Namibian fairy circles. Later, van der Walt et al. (2016) further pursued the microbial phytopathogen hypothesis by analysing the fungal composition of fairy circles in the dunes and gravel plains of the Namib Desert and adjacent soils using a metabarcoding high-throughput sequencing (HTS) approach. They discovered 57 fairy circle-specific fungal operational taxonomic units (OTUs), which they hypothesized might play a role in the formation and maintenance of the fairy circles.

The genus *Curvularia* [MB#7847] was described by Boedjin (1933) and is currently classified in the family *Pleosporaceae* (order *Pleosporales*, class *Dothidiomycetes*) together with *Alternaria* [MB#7106], *Bipolaris* [MB#7375], *Exserohilum* [MB#8241], *Stemphylium* [MB#10081] and others (Ferdinandez et al. 2021). *Curvularia* currently contains 232 described species (https://www.mycobank.org), of which Marin-Felix et al. (2020) recognised 105 based on DNA sequence data. *Curvularia* species can be saprophytes, endophytes, or human pathogens, and are found in a variety of habitats including air, indoor environments, soil, water, or plant material (Almaguer et al. 2012; Dransfield 1966; Manamgoda et al. 2015; Marin-Felix et al. 2017; Verma et al. 2013). For example, *C. hominis* [MB#806054], *C. lunata* [MB#269889] and *C. spicifera* [MB#278597] can cause infections in humans and animals (Barde and Singh 1983;

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Carter and Boudreaux 2004; Manamgoda et al. 2012; Rai et al. 2021; Rinaldi et al. 1987), while *C. lunata* causes a leaf spot disease on maize (*Zea mays*) (Manamgoda et al. 2012).

Curvularia species are dematiaceous and characterised by their curved conidia which arise from the unevenly enlarged intermediate cells of these distoseptate spores (Marin-Felix et al. 2020). However, some species also produce straight conidia. These features are similar to those observed in the closely related *Bipolaris* (Manamgoda et al. 2012). The sexual morphs of these genera were previously classified as *Cochliobolus* [MB#1158], but this state is rarely observed in nature and is difficult to induce in culture, and its species were thus incorporated into both *Bipolaris* and *Curvularia* (Manamgoda et al. 2014). Due to the difficulty in distinguishing these fungi using morphological characters, species recognition in these genera relies on multi-locus sequence analyses of the internal transcribed spacer rDNA region (ITS), and the partial gene regions of glyceraldehyde-3-phosphate dehydrogenase (*GAPDH*) and translation elongation factor 1 alpha (*TEF1*) (Manamgoda et al. 2012; Marin-Felix et al. 2017, 2020; Tan et al. 2018).

During a survey aimed at characterising the cultural fungal communities associated with *Stipagrostis ciliata* and its rhizosphere soils collected from fairy circles in the Namib Desert, *Curvularia* was among the most frequently isolated fungi. Here, we report on *Curvularia* species identified, introduce five new species, and compare them with existing species using morphological characters and phylogenetic analyses based on ITS, *GAPDH*, and *TEF1*.

Materials and methods

Sampling, isolations, and preservations

The strains included in this study were isolated from the tissue of *Stipagrostis ciliata* and associated rhizosphere soils collected in the fairy circles or so-called reverse circles of the Namib Desert. Three sites were sampled in Namibia, namely "Mirabib" (-23.479167, 15.335000), "Far East" (-23.732500, 15.775000) and an area known as the "Reverse" region (-23.545167, 15.234333). In the "Reverse" region, there were patches of vegetation surrounded by bare ground. Grass and associated rhizosphere soils were sampled at the edges of the fairy circles and in the areas between the circles. Samples were also taken from an area without fairy circles in the Mirabib region.

Stipagrostis ciliata tissue was surface disinfested with 2% sodium hypochlorite (bleach) for 3 min, with 70% ethanol for 30 s and then rinsed in distilled water for 10 s and air-dried on sterile paper towel. The surface disinfested material and soil samples were plated directly onto Malt Extract Agar (MEA) (20 g/L malt extract, 20 g/L Difco agar) supplemented with 0.4 mg 50 ppm Streptomycin. The plates were incubated for 1–3 wks at 19 – 21 °C. Isolates were purified on quarter strength Potato Dextrose Agar (12 g/L Difo Agar, 10 g/L Potato Dextrose Agar) supplemented with 2 mL 100 ppm Chloramphenicol. These were incubated for a further 1 – 3 wks for culture preservation and DNA extraction. The isolates obtained were accessioned in the CN collection (working culture collection of the Applied Mycology group) housed at the Forestry Agriculture and Biotechnology Institute (FABI) at the University of Pretoria (South Africa). Representative strains were accessioned in the CMW and CMW-IA culture collections also housed at FABI, and the CBS-KNAW culture collection of Westerdijk Institute in Utrecht (the Netherlands) (see Table 1).

DNA extractions, polymerase chain reaction (PCR) amplification, sequencing, identification, and phylogenetic analyses

Genomic DNA was extracted using the PrepMan™ Ultra Sample Preparation Reagent (Applied Biosystems, Foster City, CA, USA) according to the manufacturer's instructions and stored at -20 °C.

PCR amplification of the ITS, *GAPDH*, and *TEF1* loci was conducted using primer pairs and thermal cycle conditions as described in Table 2. Reactions were set up in 25 µL volumes as follows: 17.3 µL Milli-Q® water (Millipore Corporation), 2.5 µL 10 × FastStart™ Taq PCR reaction buffer with 20 mM $MgCl_2$ (Sigma-Aldrich, Roche Diagnostics), 2.5 µL of 100 mM of each deoxynucleotide (New England Biolabs®, Inc), 0.5 µL forward primer (10 µM), 0.5 µL reverse primer (10 µM), 0.5 µL 25 mM $MgCl_2$ (Sigma-Aldrich, Roche Diagnostics), 0.2 µL of 5 U/µL FastStart™ Taq DNA Polymerase (Sigma-Aldrich, Roche Diagnostics), and 1 µL template DNA. PCR products were prepared for sequencing using 2 µL ExoSAP-IT™ PCR clean-up reagent [1 U/µL FastAP™ Thermosensitive Alkaline Phosphatase (Thermo Fisher Scientific)], 20 U/µL Exonuclease I (Thermo Fisher Scientific)) and 5 µL PCR product. Reactions were incubated at 37 °C for 15 min, followed by 85 °C for 15 min, and stored at 4 °C until used.

Bidirectional sequencing was conducted in 96-well plates with each reaction having a total volume of 13 µL [7.4 µL Milli-Q® water, 2.1 µL 5 × BigDye™ Terminator v3.1 Sequencing buffer (Applied Biosystems, Foster City, CA, USA), 0.5 µL BigDye™ Terminator v3.1 Cycle Sequencing Ready Reaction Mix (Applied Biosystems, Foster City, CA, USA), 1 µL forward or reverse primer, and 2 µL ExoSap product]. Initial denaturation at 94 °C for 5 min was conducted, followed by 40 cycles of denaturation at 96 °C for 30 s, annealing at 50 °C for 10 s, and elongation at 60 °C for 4 min. Reactions were precipitated for Sanger sequencing using sodium acetate and ethanol.

Table 1 Strains included in this study including their location and GenBank accession numbers

Fungus species	Collection number	Sampling location	Substrate/Host	ITS	*GAPDH*	*TEF1*
Bipolaris zeae	BRIP 11512^T	Australia	*Zea mays*	KJ415538	KJ415408	KJ415454
Curvularia aeria	CBS 294.61^T	Brazil	Air	HE861850	HF565450	–
C. ahvazensis	CBS 144673^T	Iran	*Zinnia elegans*	KX139029	MG428693	MG428686
C. annellidiconidiophora	CGMCC 3.19352^T	China	*Saccharum officinarum*	MN215641	MN264077	MN263935
C. arcana	CBS 127224^T	Unknown	Unknown	MN688801	MN688828	MN688855
C. aurantia	USJCC-0096^T	Sri Lanka	*Zea mays*	OQ275217	OQ269628	OQ332409
C. australiensis	BRIP 12044^T	Australia	*Oryza sativa*	KJ415540	KJ415406	KJ415452
C. austriaca	CBS 102694^T	Austria	Nasal cavity of patient with sinusitis	MN688802	MN688829	MN688856
C. bannonii	**CMW-IA 6928 = CMW 58180 = CN021G8**	**Namibia: Far East**	***Stipagrostis ciliata***	**ON074888**	**ON355386**	**–**
C. bannonii	**CN024C4**	**Namibia: Far East**	***Stipagrostis ciliata***	**ON074977**	**ON355392**	**–**
C. bannonii	BRIP 16732^T	USA	*Jacquemontia tamnifolia*	KJ415542	KJ415404	KJ415450
C. beasleyi	BRIP 10972^T	Australia	*Chloris gayana*	MH414892	MH433638	MH433654
C. borreriae	CBS 859.73^T	Chile	Volcanic ash soil	LT631355	LT715838	–
C. brachyspora	CBS 186.50	India	Soil	KJ922372	KM061784	KM230405
C. buchloes	CBS 246.49^T	USA	*Buchloë dactyloides*	KJ909765	KM061789	KM196588
C. caricae-papayae	CBS 135941^T	India	*Carica papaya*	HG778984	HG779146	–
C. chlamydospora	UTHSC 07-2764^T	USA	Toe nail	HG779021	HG779151	–
C. clavata	BRIP 61680b	Australia	*Oryza rufipogon*	KU552205	KU552167	KU552159
C. coatesiae	BRIP 24261^T	Australia	*Litchi chinensis*	MH414897	MH433636	MH433659
C. dactyloctenii	BRIP 12846^T	Australia	*Dactyloctenium radulans*	KJ415545	KJ415401	KJ415447
C. deserticola	**CMW-IA 6933 = CMW 64024 = CBS 151411 = CN027A5**	**Namibia: Far East**	***Stipagrostis ciliata***	**ON075008**	**ON355400**	**ON355361**
C. deserticola	**CMW-IA 6929 = CMW 64022 = CN022I3**	**Namibia: Far East**	***Stipagrostis ciliata***	**ON074969**	**ON355389**	**–**
C. deserticola	**CMW 64023 = CN025B7**	**Namibia: Far East**	***Stipagrostis ciliata***	**ON074983**	**ON355398**	**ON355359**
C. deserticola	**CN025B5**	**Namibia: Far East**	***Stipagrostis ciliata***	**ON074982**	**ON355397**	**ON355358**
C. deserticola	**CMW-IA 6932 = CMW 58190 = CBS 151410 = CN025G1^T**	**Namibia: Far East**	***Stipagrostis ciliata***	**ON074985**	**ON355399**	**ON355360**
C. deserticola	**CMW-IA 6946 = CMW 64029 = CN037D9**	**Namibia: Far East**	**Soil**	**OR992658**	**ON355434**	**–**
C. deserticola	**CMW-IA 6937 = CMW 64025 = CBS 151412 = CN034A5**	**Namibia: Reverse**	**Soil**	**OR992659**	**ON355422**	**–**
C. determinata	CGMCC 3.19340^T	China	*Saccharum officinarum*	MN215653	MN264088	MN263947
C. eleusinicola	USJCC-0005^T	Sri Lanka	*Eleusine coracana*	MT262877	MT393583	MT432925
C. elliptiformis	CGMCC 3.19351^T	China	*Saccharum officinarum*	MN215656	MN264091	MN263950
C. ellisii	CBS 193.62^T	Pakistan	Air	JN192375	JN600963	JN601007
C. eragrostidicola	BRIP 12538^T	Australia	*Eragrostis pilosa*	MH414899	MH433643	MH433661
C. eragrostidis	CBS 189.48	Indonesia	*Sorghum* sp.	HG778986	HG779154	–
C. flexuosa	CGMCC 3.19447^T	China	*Saccharum officinarum*	MN215663	MN264096	MN263957
C. gladioli	CBS 210.79	Romania	*Gladiolus* sp.	HG778987	HG779123	–
C. gobabebensis	**CMW-IA 6921 = CMW 58191 = CBS 149139 = CN010F9**	**Namibia: Mirabib**	***Stipagrostis ciliata***	**ON332848**	**ON355373**	**ON355344**
C. gobabebensis	**CMW-IA 6925 = CMW 58192 = CBS 149140 = CN013C4^T**	**Namibia: Mirabib**	***Stipagrostis ciliata***	**ON074797**	**ON355381**	**ON355347**

Table 1 (continued)

Fungus species	Collection number	Sampling location	Substrate/Host	ITS	*GAPDH*	*TEF1*
C. gobabebensis	**CMW-IA 6926 = CMW 58193 = CBS 149141 = CN013F6**	**Namibia: Mirabib**	***Stipagrostis ciliata***	**ON074805**	**ON355383**	**ON355349**
C. graminicola	BRIP 23186^{T}	Australia	Unknown	JN192376	JN600964	JN601008
C. guangxiensis	CGMCC 3.19330^{T}	China	*Saccharum officinarum*	MN215667	MN264100	MN263961
C. gudauskasii	DAOM 165085	Tanzania	*Triticum aestivum*	–	AF081393	–
C. harveyi	BRIP 57412^{T}	Australia	*Triticum aestivum*	KJ415546	KJ415400	KJ415446
C. hawaiiensis	BRIP 11987^{T}	USA	*Oryza sativa*	KJ415547	KJ415399	KJ415445
C. homomorpha	CBS 156.60^{T}	USA	Air	JN192380	JN600970	JN601014
C. huamulaniae	BRIP 10936a^{T}	Australia	Air	OR130931	OR135531	OR135532
C. indica	CBS 550.74	Unknown	Soil	–	LT715837.1	–
C. intermedia	CBS 334.64	USA	*Avena versicolor*	HG778991	HG779155	–
C. khuzestanica	CBS 144736^{T}	Iran	*Atriplex lentiformis*	MH688044.1	MH688043.1	–
C. malina	CBS 131274^{T}	USA	*Zoysia matrella*	JF812154	KP153179	KR493095
C. manamgodae	CGMCC 3.19446^{T}	China	*Saccharum officinarum*	MN215677	MN264110	MN263971
C. maraisii	**CMW-IA 6927 = CMW 58194 = CBS 149142 = CN021G3**	**Namibia: Far East**	***Stipagrostis ciliata***	**ON074886**	**ON355385**	**ON355351**
C. maraisii	**CMW-IA 6951 = CMW 58195 = CBS 149143 = CN037F7^{T}**	**Namibia: Far East**	**Soil**	**OR471647**	**ON355439**	**OR486044**
C. mebaldsii	**CMW-IA 6956 = CMW 58185 = CN060G8**	**Namibia: Reverse**	***Stipagrostis ciliata***	**ON644443**	**ON661549**	**–**
C. mebaldsii	BRIP 12900^{T}	Australia	*Cynodon transvaalensis*	MH414902	MH433647	MH433664
C. microspora	GUCC 6272^{T}	China	*Hippeastrum striatum* leaf spot	MF139088	MF139106	MF139115
C. moringae	**CN010G6**	**Namibia: Mirabib**	***Stipagrostis ciliata***	**OM759877**	**–**	**–**
C. moringae	**CN010H3**	**Namibia: Mirabib**	***Stipagrostis ciliata***	**ON074750**	**–**	**–**
C. moringae	**CN010H5**	**Namibia: Mirabib**	***Stipagrostis ciliata***	**ON074752**	**–**	**–**
C. moringae	**CN011E9**	**Namibia: Mirabib**	***Stipagrostis ciliata***	**ON074770**	**–**	**–**
C. moringae	**CMW-IA 6924 = CMW 58186 = CN011F2**	**Namibia: Mirabib**	***Stipagrostis ciliata***	**ON074771**	**ON355378**	**ON355346**
C. moringae	**CN011H6**	**Namibia: Mirabib**	***Stipagrostis ciliata***	**ON074777**	**–**	**–**
C. moringae	**CN012B1**	**Namibia: Mirabib**	***Stipagrostis ciliata***	**ON074784**	**–**	**–**
C. moringae	**CN013B5**	**Namibia: Mirabib**	***Stipagrostis ciliata***	**ON074796**	**–**	**–**
C. moringae	**CN013E2**	**Namibia: Mirabib**	***Stipagrostis ciliata***	**ON074802**	**ON355382**	**ON355348**
C. moringae	**CN022A3**	**Namibia: Far East**	***Stipagrostis ciliata***	**ON074957**	**ON355387**	**ON355352**
C. moringae	**CN024B8**	**Namibia: Far East**	***Stipagrostis ciliata***	**ON074976**	**ON355391**	**ON355355**
C. moringae	**CN034A3**	**Namibia: Reverse**	**Soil**	**OR992648**	**ON355421**	**–**
C. moringae	**CN038C9**	**Namibia: Far East**	**Soil**	**ON332845**	**–**	**–**
C. moringae	**CN059H1**	**Namibia: Reverse**	***Stipagrostis ciliata***	**ON332834**	**ON355411**	**ON355366**
C. moringae	**CN060H6**	**Namibia: Reverse**	***Stipagrostis ciliata***	**ON332839**	**ON355416**	**–**
C. moringae	**CN060I1**	**Namibia: Reverse**	***Stipagrostis ciliata***	**ON332840**	**ON355417**	**ON355369**
C. moringae	**CN060I4**	**Namibia: Reverse**	***Stipagrostis ciliata***	**ON332841**	**ON355418**	**ON355370**
C. moringae	CBS 146828^{T}	Namibia	*Moringa ovalifolia*	MW175363	MW173105	–
C. namibensis	**CMW-IA 6973 = CMW 58196 = CBS 149144 = CN015H8^{T}**	**Namibia: Mirabib**	***Stipagrostis ciliata***	**ON074819**	**ON355384**	**ON355350**
C. namibensis	**CMW-IA 6930 = CMW 58197 = CN023D3**	**Namibia: Far East**	***Stipagrostis ciliata***	**ON074972**	**ON355390**	**ON355354**

Table 1 (continued)

Fungus species	Collection number	Sampling location	Substrate/Host	ITS	*GAPDH*	*TEF1*
C. namibensis	**CMW-IA 6931 = CMW 58198 = CBS 149145 = CN024D2**	**Namibia: Far East**	***Stipagrostis ciliata***	**ON074978**	**ON355393**	**ON355356**
C. namibensis	**CMW-IA 6934 = CMW 58199 = CN027A9**	**Namibia: Far East**	***Stipagrostis ciliata***	**ON075009**	**ON355401**	**ON355362**
C. namibensis	**CMW-IA 6935 = CMW 58200 = CN027C4**	**Namibia: Far East**	***Stipagrostis ciliata***	**ON075010**	**ON355402**	**ON355363**
C. namibensis	**CN034A7**	**Namibia: Reverse**	**Soil**	**OR992649**	**ON355424**	**–**
C. namibensis	**CN036F1 = CMW 58202**	**Namibia: Mirabib**	**Soil**	**OR992650**	**ON355428**	**–**
C. namibensis	**CMW-IA 6942 = CMW 58203 = CN036F6**	**Namibia: Mirabib**	**Soil**	**OR992651**	**ON355430**	**–**
C. namibensis	**CMW-IA 6943 = CMW 58204 = CN036G9**	**Namibia: Mirabib**	**Soil**	**ON332844**	**PP113003**	**–**
C. namibensis	**CMW-IA 6944 = CMW 58205 = CBS 149146 = CN036I5**	**Namibia: Mirabib**	**Soil**	**OR992652**	**ON355432**	**–**
C. namibensis	**CMW-IA 6945 = CMW 58206 = CN037D8**	**Namibia: Far East**	**Soil**	**OR992653**	**ON355433**	**–**
C. namibensis	**CMW-IA 6947 = CMW 58207 = CN037F2**	**Namibia: Far East**	**Soil**	**OR992654**	**ON355435**	**–**
C. namibensis	**CMW-IA 6948 = CMW 58208 = CN037F3**	**Namibia: Far East**	**Soil**	**OR992655**	**ON355436**	**–**
C. namibensis	**CMW-IA 6949 = CMW 58209 = CN037F5**	**Namibia: Far East**	**Soil**	**OR992656**	**ON355437**	**–**
C. namibensis	**CMW-IA 6950 = CMW 58210 = CN037F6**	**Namibia: Far East**	**Soil**	**OR992657**	**ON355438**	**–**
C. namibensis	**CMW-IA 6952 CMW 58211 = CBS 149147 = CN044C8**	**Namibia: Far East**	***Stipagrostis ciliata***	**ON074947**	**ON355408**	**ON355365**
C. namibensis	**CMW 58212 = CN060F9**	**Namibia: Reverse**	***Stipagrostis ciliata***	**ON332835**	**ON355412**	**–**
C. neergaardii	BRIP 12919^{T}	Ghana	*Oryza sativa*	KJ415550	KJ415397	KJ415443
C. nodosa	CPC 28800^{T}	Thailand	*Digitaria ciliaris*	MF490816	MF490838	MF490859
C. ovoidea	CBS 854.72	Unknown	Unknown	–	LT715842.1	–
C. pallescens	CBS 156.35^{T}	Indonesia	Air	KJ922380	KM083606	KM196570
C. pandanicola	MFLUCC 15-0746^{T}	Thailand	*Pandanus sp.*	MH275056	MH412748	MH412763
C. papendorfii	**CMW 58187 = CN013H2**	**Namibia: Mirabib**	***Stipagrostis ciliata***	**ON074810**	**–**	**–**
C. papendorfii	CBS 308.67^{T}	South Africa	*Acacia karroo*	KJ909774	KM083617	KM196594
C. patereae	CBS 198.87^{T}	Argentina	*Triticum durum*	MN688810	MN688837	MN688864
C. penniseti	CBS 528.70	Unknown	Unknown	MN688811	MN688838	–
C. perotidis	CBS 350.90^{T}	Australia	*Perotis rara*	JN192385	KJ415394	JN601021
C. prasadii	**CN011B8**	**Namibia: Mirabib**	***Stipagrostis ciliata***	**ON074762**	**ON355375**	**–**
C. prasadii	**CN012B3**	**Namibia: Mirabib**	***Stipagrostis ciliata***	**ON332852**	**ON355379**	**–**
C. prasadii	**CN012D4**	**Namibia: Mirabib**	***Stipagrostis ciliata***	**–**	**ON355380**	**–**
C. prasadii	**CN011G7**	**Namibia: Mirabib**	***Stipagrostis ciliata***	**ON074776**	**–**	**–**
C. prasadii	**CN036F4**	**Namibia: Mirabib**	**Soil**	**ON332830**	**ON355429**	**–**
C. prasadii	CBS 143.64^{T}	India	*Jasminum sambac*	KJ922373	KM061785	KM230408
C. pseudobrachyspora	CPC 28808^{T}	Thailand	*Eleusine indica*	MF490819	MF490841	MF490862
C. pseudoellisii	CBS 298.80^{T}	Sudan	*Sorghum bicolor*	MN688818	MN688845	MN688870
C. pseudointermedia	CBS 553.89^{T}	Brazil	Soil	MN688819	MN688846	MN688871

Table 1 (continued)

Fungus species	Collection number	Sampling location	Substrate/Host	ITS	*GAPDH*	*TEF1*
C. pseudolunata	**CMW 58188 = CN061A4**	**Namibia: Reverse**	***Stipagrostis ciliata***	**ON332842**	**ON355419**	**–**
C. pseudolunata	UTHSC 09-2092^{T}	USA	Human nasal sinus	HE861842	HF565459	–
C. richardiae	BRIP 4371^{T}	Australia	*Richardia brasiliensis*	KJ415555	KJ415391	KJ415438
C. rouhanii	**CN025B3**	**Namibia: Far East**	***Stipagrostis ciliata***	**ON074981**	**ON355396**	**ON355357**
C. rouhanii	**CN028H7**	**Namibia: Far East**	***Stipagrostis ciliata***	**ON074910**	**ON355404**	**–**
C. rouhanii	**CN022H5**	**Namibia: Far East**	***Stipagrostis ciliata***	**ON074966**	**ON355388**	**ON355353**
C. rouhanii	**CMW-IA 6920 = CMW 58189 = CN010F6**	**Namibia: Mirabib**	***Stipagrostis ciliata***	**OM759872**	**ON355372**	**–**
C. rouhanii	**CN010I9**	**Namibia: Mirabib**	***Stipagrostis ciliata***	**ON074755**	**ON355374**	**–**
C. rouhanii	**CN061A5**	**Namibia: Reverse**	***Stipagrostis ciliata***	**ON332843**	**ON355420**	**ON355371**
C. rouhanii	**CN034A6**	**Namibia: Reverse**	**Soil**	**OR992660**	**ON355423**	**–**
C. rouhanii	CBS 144674^{T}	Iran	*Syngonium vellozianum*	KX139030	MG428694	MG428687
C. sacchari-officinarum	CGMCC 3.19331^{T}	China	*Saccharum officinarum*	MN215705	MN264137.1	MN263998
C. saccharicola	CGMCC 3.19344^{T}	China	*Saccharum officinarum*	MN215701	MN264133	MN263994
C. siddiquii	CBS 196.62^{T}	Pakistan	Air	MN688823	MN688850	–
C. simmonsii	USJCC-0002^{T}	Sri Lanka	*Panicum maximum*	MN044753	MN053011	MN053005
C. spicifera	CBS 274.52	Spain	Soil	JN192387	JN600979	JN601023
C. sporobolicola	BRIP 23040b^{T}	Australia	*Sporobolus australasicus*	MH414908	MH433652	MH433671
C. stipagrostidicola	**CMW-IA 6922 = CMW 58213 = CN011D7**	**Namibia: Mirabib**	***Stipagrostis ciliata***	**ON074769**	**ON355376**	**ON355345**
C. stipagrostidicola	**CMW-IA 6923 = CMW 58219 = CN011D8**	**Namibia: Mirabib**	***Stipagrostis ciliata***	**–**	**ON355377**	**–**
C. stipagrostidicola	**CN034B7**	**Namibia: Reverse**	**Soil**	**OR992661**	**ON355425**	**–**
C. stipagrostidicola	**CMW-IA 6940 = CMW 58214 = CBS 149148 = CN034B8**	**Namibia: Reverse**	**Soil**	**OR992662**	**ON355426**	**–**
C. stipagrostidicola	**CMW-IA 6941 = CMW 58215 = CN034H8**	**Namibia: Reverse**	**Soil**	**OR992663**	**ON355427**	**–**
C. stipagrostidicola	**CMW-IA 6953 = CMW 58216 = CN044D1**	**Namibia: Far East**	***Stipagrostis ciliata***	**–**	**ON355409**	**–**
C. stipagrostidicola	**CMW-IA 6954 = CMW 58217 = CBS 149149 = CN060G3**	**Namibia: Reverse**	***Stipagrostis ciliata***	**ON332836**	**ON355413**	**–**
C. stipagrostidicola	**CN060G4**	**Namibia: Reverse**	***Stipagrostis ciliata***	**ON332837**	**ON355414**	**ON355367**
C. stipagrostidicola	**CMW-IA 6968 = CMW 58218 = CBS 149150 = CN060H5^{T}**	**Namibia: Reverse**	***Stipagrostis ciliata***	**ON332838**	**ON355415**	**ON355368**
C. subpapendorfii	CBS 656.74^{T}	Egypt	Soil	KJ909777	KM061791	KM196585
C. tanzanica	BRIP 71104^{T}	Tanzania	*Cyperus aromaticus*	MW396857	MW388669	–
C. tribuli	**CN043E2**	**Namibia: Far East**	***Stipagrostis ciliata***	**ON074929**	**ON355406**	**–**
C. tribuli	**CN043E6**	**Namibia: Far East**	***Stipagrostis ciliata***	**ON074931**	**ON355407**	**–**
C. tribuli	**CMW-IA 6936 = CMW 58221 = CN027E2**	**Namibia: Far East**	***Stipagrostis ciliata***	**ON075013**	**ON355403**	**–**
C. tribuli	**CN024H6**	**Namibia: Far East**	***Stipagrostis ciliata***	**–**	**ON355394**	**–**
C. tribuli	**CN024I3**	**Namibia: Far East**	***Stipagrostis ciliata***	**–**	**ON355395**	**–**
C. tribuli	**CN038E7**	**Namibia: Far East**	**Soil**	**ON332832**	**ON355440**	**–**
C. tribuli	**CN036G4**	**Namibia: Mirabib**	**Soil**	**ON332831**	**ON355431**	**–**
C. tribuli	**CN059G9**	**Namibia: Reverse**	***Stipagrostis ciliata***	**ON332833**	**ON355410**	**–**
C. tribuli	CBS 126975^{T}	South Africa	*Tribulus terrestris*	MN688825	MN688852	MN688875
C. trifolii	CBS 173.55	New Zealand	*Setaria glauca*	HG779023	HG779124	–

Table 1 (continued)

Fungus species	Collection number	Sampling location	Substrate/Host	ITS	*GAPDH*	*TEF1*
C. tsudae	ATCC 44764[T]	Japan	*Chloris gayana*	KC424596	KC747745	KC503940
C. variabilis	CPC 28815[T]	Thailand	*Chloris barbata*	MF490822	MF490844	MF490865
C. vidyodayana	USJCC–0029[T]	Sri Lanka	*Oryza sativa*	OQ275234	OQ269645	OQ332413
C. warraberensis	BRIP 14817[T]	Australia	*Dactyloctenium aegyptium*	MH414909	MH433653	MH433672
Exserohilum turcicum	CBS 690.71[T]	Germany	*Zea mays*	LT837487	LT882581	LT896618

[1]**ATCC**: American Type Culture Collection, Manassas, Virginia, USA; **BRIP**: Queensland Plant Pathology Herbarium, Brisbane, Australia; **CBS**: Westerdijk Fungal Biodiversity Institute, Utrecht, Netherlands; **CGMCC:** China General Microbiological Culture Collection, Chinese Academy of Sciences, Beijing, China; **CMW**: culture collection of the Forestry and Agricultural Biotechnology Institute (FABI) at the University of Pretoria; **CN**: working culture collection of the Applied Mycology Group, FABI, Univeristy of Preotria, Gauteng, South Africa; **CPC**: cultures of Pedro Crous, Westerdijk Fungal Biodiversity Institute; **DAOMC**: Plant Research Institute, Department of Agriculture, Ottowa, Canada; **GUCC**: culture collection at the Department of Plant Pathology, Agriculuture Collage, Guizhou University, China; **MFLUCC**: Mae Fah Luang University Culture Collection, Chiang Rai, Thailand; **USJCC** University of Jayewardenepura Culture Collection; **UTHSC**: Fungus Testing Laboratory, University of Texas Health Science Centre, San Antonio, Texas, USA

[T] Type

Sanger sequencing was conducted on an ABI PRISM™ 3500xl Auto-sequencer (Applied Biosystems, Foster City, CA, USA) at the Sanger Sequencing Facility of the University of Pretoria (Bioinformatics and Computational Biology Unit, v 19.8.22).

Forward and reverse sequences were obtained from SeqServe v 19.8.22 (Bioinformatics and Computational Biology Unit), hosted by the DNA Sanger Sequencing Facility. Contigs were assembled and manually reviewed in Geneious Prime® v 2023.2.1 (Biomatters Ltd., Auckland, New Zealand). BLASTn analysis was performed to compare obtained sequences against the NCBI (National Centre for Biotechnology Information, USA) GenBank nucleotide database to obtain preliminary identifications. The sequences for *Curvularia* were used in subsequent phylogenetic analyses. The newly generated sequences were deposited in GenBank with accession numbers listed in Table 1.

For phylogenetic analyses, a reference sequence database (Table 1) was compiled based on recent literature (Crous et al. 2020; Ferdinandez et al. 2021; Iturrieta-González et al. 2020; Kiss et al. 2020; Manamgoda et al. 2012; Marin-Felix et al. 2020). *Exserohilum turcicum* (CBS 690.71 [T]) and *Bipolaris zeae* (BRIP 11512[T]) were included as outgroups. Sequences were aligned in Geneious Prime® 2023.2.1 using the MAFFT v 7.450 plugin, selecting the L-INS-i algorithm (Katoh and Standley 2013), and then manually trimmed where appropriate. The datasets were partitioned to take into account gene regions, as well as introns and exons. For multi-gene phylogenies, alignments were concatenated in Geneious Prime. Maximum likelihood trees were calculated in IQtree v 2.1.3 (Nguyen et al. 2015), and support in nodes was calculated using a bootstrap analysis with 1000 replicates. Phylogenetic trees were visualised

Table 2 PCR reactions and primer details for loci

Locus	Annealing temp (°C)	Cycles	Primer	Primer Direction	Primer sequence (5'-3')	Reference
Internal transcribed spacer (ITS)	52	35	V9G	Forward	TTACGTCCCTGCCCTTTGTA	(de Hoog and van den Ende 1998)
			LS266	Reverse	GCATTCCCAAACAACTCGACTC	(Masclaux et al. 1995)
Glyceraldehyde-3-phosphate dehydrogenase (*GAPDH*)	52	30	GDP1	Forward	CAACGGCTTCGGTCGCATTG	(Berbee et al. 1999)
			GDP2	Reverse	GCCAAGCAGTTGGTTGTGC	(Berbee et al. 1999)
Translation elongation factor 1-alpha (*TEF1*)	54	30	EF1-983F	Forward	GCYCCYGGHCAYCGTGAYTTYAT	(Schoch et al. 2009)
			EF1-2218R	Reverse	ATGACACCRACRGCRACRGTYTG	(Schoch et al. 2009)

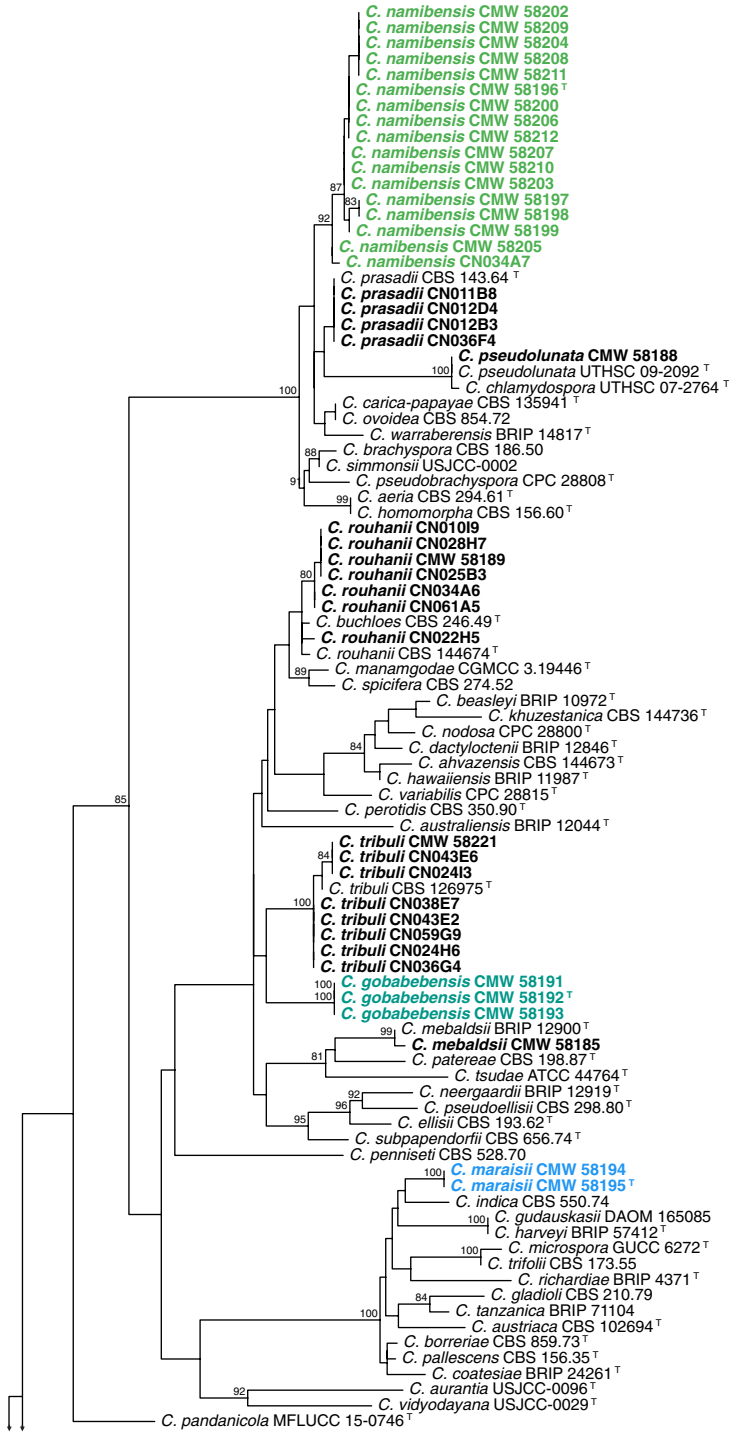

Fig. 1 Phylogenetic tree based on a maximum-likelihood approach of the concatenated data from *GAPDH* and *TEF1* loci from phylogenetically related *Curvularia* species. The tree was rooted to *Exserohilum turcicum* and *Bipolaris zeae*. The taxonomic novelties proposed in this study are represented in bold and highlighted, and additional strains included in this study are shown in bold. Bootstrap values above 80% are shown on the branch nodes.[T] Type

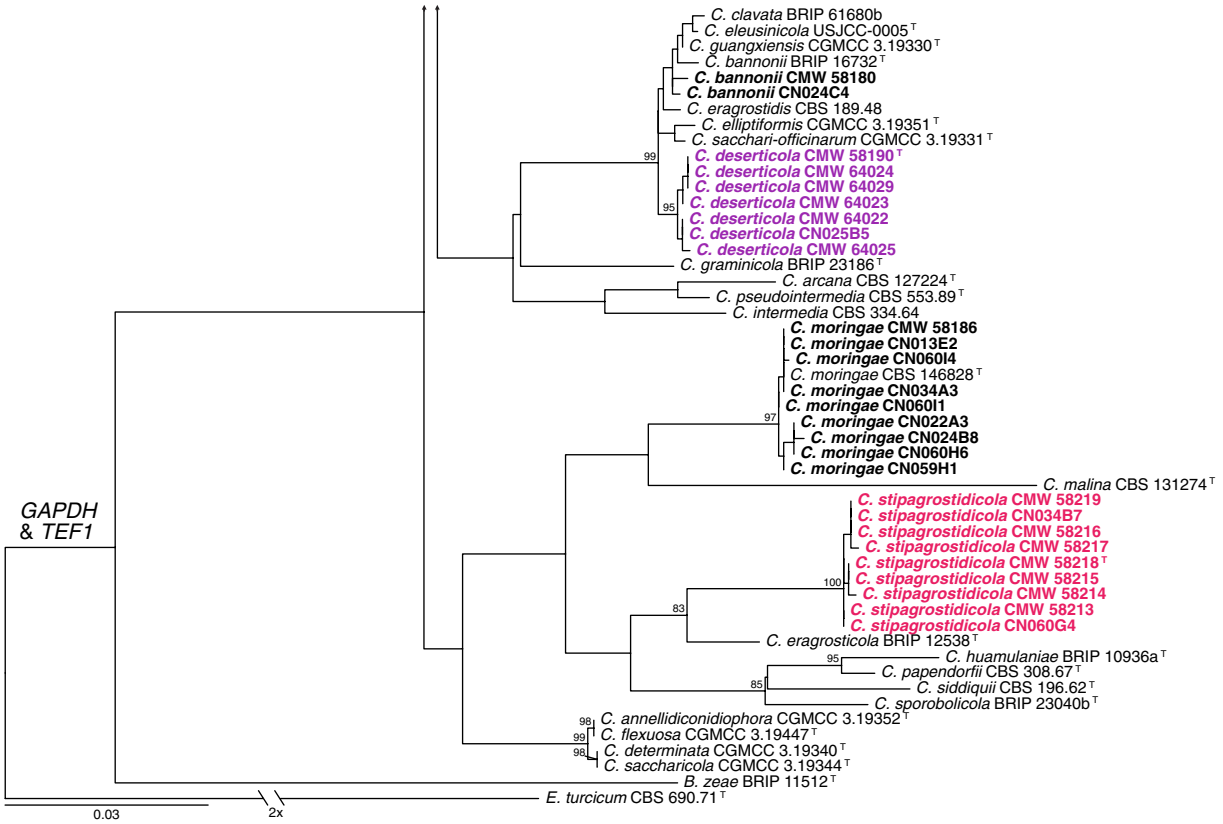

Fig. 1 (continued)

using TreeViewer v 2.2.0 and visually edited using Affinity Designer v 2.3.1 (Serif (Europe) Ltd, Nottingham, UK). The reference datasets, alignments, and tree files were uploaded to the University of Pretoria research data repository hosted on Figshare (https://doi.org/10.25403/UPresearchdata.25817800).

Morphology

Strains of novel species were inoculated onto 90 mm Petri dishes containing potato dextrose agar [PDA; 39% (w/v) BD Difco™ Potato Dextrose Agar], 2% malt extract agar [MEA; 20% (w/v) Malt Extract, 20% (w/v) Difco Agar], synthetic nutrient agar (SNA), oatmeal agar [OA; 30% (v/v) oatmeal extract, 20% (w/v) Difco Agar] and water agar [WA; 20% (w/v) Difco Agar] as described by Marin-Felix et al. (2020). One set of plates was incubated at 25 °C in complete darkness, and a second set for 7 d in a 12 h UV light and dark diurnal cycle (Marin-Felix et al. 2020). Colony diameters were measured in triplicate from colonies incubated in complete darkness. Colour names used in descriptions follow the colour charts in the Methuen Handbook of Colour (Kornerup and Wanscher 1967). Images of colonies were captured using a Sony Alpha a7 III camera equipped with a Sony FE 90 mm f/2.8 macro G OSS lens (Tokyo, Japan). Micromorphology was studied using a Zeiss AXIO Imager.A2 compound microscope equipped with an AxioCaM 512 color camera driven by Zen Blue v. 3.2 software (Carl Zeiss CMP GmbH, Göttingen, Germany). Microscopic specimens were prepared from colonies on WA using water as mounting fluid. At least 25 measurements of each character were made for representative strains of each species with NIS-Elements Basic Research software v 4.30.00 (Nikon Europe B.V.). The mean ($\bar{x}$) and standard deviation values for each structural element were calculated and the ranges expressed as follow: (minimum value) general range (maximum value). Photo plates were assembled using Affinity Photo v 2.3.1 (Serif (Europe) Ltd, Nottingham, UK).

Results

Identifications and phylogenetic analyses

Fungal isolations resulted in 80 *Curvularia* strains from which 173 new DNA sequences were generated for ITS ($n = 75$), *GAPDH* ($n = 70$), and *TEF1* ($n = 28$) (Table 1).


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h
i

◂**Fig. 2** *Curvularia deserticola*; **a** CMW 64023 Colony after incubation for 7 d on, from left to right, PDA in complete darkness, PDA exposed to a 12-h UV light diurnal cycle, MEA exposed to a 12-h UV light diurnal cycle, and OA exposed to a 12-h UV light diurnal cycle; **b** CMW 64023 Colony texture on PDA; **c** CMW 58190, **d, h** CMW 64023**, f, g** CMW 64025 Conidiophores and conidia; **e** CMW 64023 Chlamydospore; **i** CN025B5, CMW 64025 Conidia. Scale bars 10 µm

A total of 142 strains (62 reference and 80 from the current study) were included in the multi-locus sequence analyses. Alignments of the ITS, *GAPDH*, and *TEF1* datasets were 618, 552 and 828 bp long, respectively. The GTR + I + G nucleotide substitution model was applied to ITS, *GAPDH* (including introns and codons 1, 2 and 3), and *TEF1* (including codons 1, 2 and 3). Tree topologies for individual gene trees were not in conflict (Supplementary Figs. 1, 2 and 3), and thus, a concatenated phylogeny was used to display results (Fig. 1). The most suitable nucleotide substitution models for the concatenated phylogeny including *GAPDH* and *TEF1* was GTR + I + G.

Our strains were identified to 13 species, including: *C. bannonii* [MB#135463] (*n* = 2), *C. mebaldsii* [MB#825457] (*n* = 1), *C. moringae* [MB#837854] (*n* = 17), *C. papendorfii* [MB#329447] (*n* = 1), *C. prasadii* [MB#296253] (*n* = 5), *C. pseudolunata* [MB#806056] (*n* = 1), *C. rouhanii* [MB#823474] (*n* = 7), *C. tribuli* [MB#830062] (*n* = 8), and five that were phylogenetically distinct from other *Curvularia* species. These are described below in the Taxonomy section (Fig. 1).

Even though ITS performed relatively well as an identification marker for some clades, it was less informative in others and did not allow robust identifications (e.g. clade containing *C. buchloes*, *C. manamgodae*, *C. rouhanii* and *C. spicifera*). *GAPDH* and *TEF1* were useful in distinguishing species, but since *GAPDH* had a larger dataset available, it was more useful as an identification marker. The *TEF1* locus was less informative for some clades and did not allow for robust identification (e.g. clade containing *C. annellidiconidiophora, C. austriaca* [MB#830045]*, C. coatesiae* [MB#825452], *C. determinata, C. desertus, C. eleusinicola, C. flexuosa, C. graminicola, C. guangxiensis, C. homomorpha, C. maraisii, C. microspora* [MB#822544]*, C. namibensis, C. pallescens* [MB#273299]*, C. pandanicola, C. pseudointermedia, C. saccharicola, C. sacchari-officinarum, C. vidyodayana,* and *C. warraberensis*). However, our analyses showed that some species share very similar sequences making their identification difficult. For example, *C. bannonii* (BRIP 16732 ^{T}) and *C. guangxiensis* (CGMCC 3.19330 ^{T}) which have 2 bp differences in ITS, a single bp difference in *GAPDH*, and 4 bp difference in *TEF1*. Similarly, distinguishing between *C. pseudolunata* (UTHSC 09-2092 ^{T}) and *C. chlamydospora* [MB#806053] (UTHSC 07-2794 ^{T}) is difficult, as is differentiating *C. aeria* (CBS 294.61 ^{T}) and *C. homomorpha* (CBS 156.60 ^{T}) using ITS and *GAPDH*. Further work is needed to establish the inter- and intra-species relationships between these strains/species.

Taxonomy

Curvularia deserticola van Vuuren, M.J. Wingf., Yilmaz & Visagie, **sp. nov.** Figure 2

MycoBank MB#853988

Etymology. Latin, *deserticola*, refers to the arid desert environment in which this species occurs.

Typus. NAMIBIA, Far East region of the Namib desert, from *Stipagrostis ciliata* tissues from fairy circles, November 2019, coll. Neriman Yilmaz (holotype PRU(M) 4583, dried specimen in metabolically inactive state, ex-type strain CMW-IA 6932 = CMW 58190 = CBS 151410 = CN025G1).

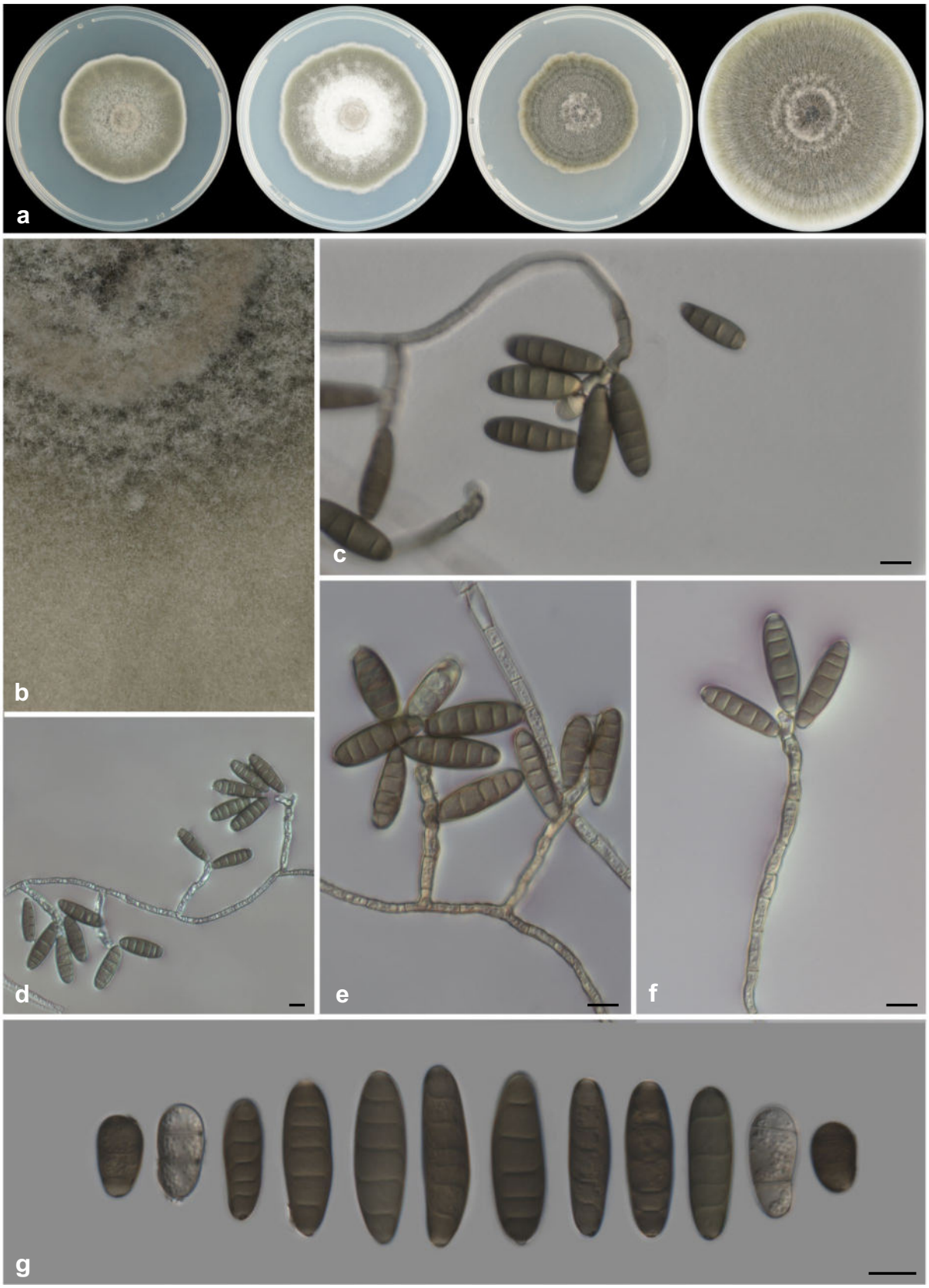
Aditional material examined. NAMIBIA, Erongo region, from *Stipagrotis ciliata* tissues and surrounding rhizosphere, CMW-IA 6933 = CMW 64024 = CBS 151411 = CN027A5, CMW-IA 6929 = CMW 64022 = CN022I3, CMW 64023 = CN025B7, CN025B5, CMW-IA 6946 = CMW 64029 = CN037D9, CMW-IA 6937 = CMW 64025 = CBS 151412 = CN034A5.

DNA barcodes. ITS = ON074985, *GAPDH* = ON355399 & *TEF1* = ON355360.

Conidiophores on WA. *Hyphae* subhyaline to pale brown, branched, septate, smooth, (1)3 − 6(7) µm wide. *Conidiophores* single or in small groups, semi-macronematous, septate, straight to flexuous, geniculate, branched, cell walls thicker than those of vegetative hyphae, mononematous, pale brown to brown, not swollen at the base, (24)90 − 115(180) × (3)4–5(7) µm. *Conidiogenous cells* smooth-walled, terminal or intercalary, proliferating sympodially, pale brown to brown with dark scars, size (4)4–6(13) × (3)4–6(19) µm. *Conidia* smooth-walled, ellipsoidal, straight, rarely curved, brown to dark brown, rounded at the apex, 3-distoseptate, sometimes 1 to 2-distoseptate, (11)15–19(24) × (6)9–12(15) µm, ($\bar{x}$ = 17.09 ± 2.53 × 10.03 ± 1.51 µm); *hila* not protuberant to slightly protuberant to flat, darkened and thickened, 1–4 µm wide. *Chlamydospores* borne intercalary, cylindrical, distoseptate, smooth, 6–7 × 10 µm.

Culture characteristics on PDA (25 ºC, 7 d). Cultures incubated in the dark: Colonies 84–85 mm, olive to silver, margins white, few aerial mycelia giving the colony a slightly cottony appearance, reverse olive brown to greenish grey at margin. *Cultures incubated in a 12-h diurnal UV light cycle*: Colonies 84–85 mm, olive, margin subhyaline to olive, few aerial mycelium, reverse olive brown.

Notes. Curvularia deserticola resides in a clade containing *C. bannonii, C. clavata, C. eleucinicola, C. elliptiformis,*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◂**Fig. 3** *Curvularia gobabebensis*; **a** CMW 58192 Colony after incubation for 7 d on, from left to right, PDA in complete darkness, PDA exposed to a 12-h UV light diurnal cycle, MEA exposed to a 12-h UV light diurnal cycle, and OA exposed to a 12-h UV light diurnal cycle; **b** CMW 58192 Colony texture on PDA; **c–e** CMW 58192, **f** CMW 58191 Conidiophores and conidia; **g** CMW 58192 Conidia. Scale bars 10 µm

C. eragrostidis, C. guangxiensis and *C. sacchari-officinarum* (Fig. 1). *Curvularia deserticola* has smaller conidia ((11)15–19(24)×(6)9–12(15) µm) than the closely related *C. banonnii* (24–34×13–17 µm) (Morgan-Jones 1988). *Curvularia deserticola* has 3 septa and non-protuberant hila as found in the closely related clade of species mentioned above. Similar to various species of *Curvularia*, *C. deserticola* occurs on a member of the *Poaceae* (Ferdinandez et al. 2021; Jain 1962; Raza et al. 2019). Examples include *C. clavata* on *Tripogon jacquemontii*, *C. eleusinicola on Eleusine coracana, C. elliptiformis* and *C. sacchari-officinarum on Saccharum officinarum,* and *C. eragrostidis Eragrostis chapelieri* (Ferdinandez et al. 2021; Jain 1962; Raza et al. 2019). *Curvularia deserticola* differs in at least 1 bp for ITS, 6 bp for *GAPDH*, and 1 bp for *TEF1* from other *Curvularia* species.

Curvularia gobabebensis van Vuuren, M.J. Wingf., Yilmaz & Visagie, **sp. nov.** Fig. 3.

MycoBank MB#853989

Etymology. Latin, *gobabebensis*, named for the Gobabeb research and training Centre in Namibia, in recognition of its contribution to research in the Namib desert.

Typus. NAMIBIA, Mirabib, from the roots of *Stipagrostis ciliata* in an area where no fairy circles occurred (-23.479230, 15.335000), November 2019, coll. Neriman Yilmaz (holotype PRU(M) 4565, dried specimen in metabolically inactive state, ex-type strain CMW-IA 6925 = CMW 58192 = CBS 149140 = CN013C4).

Aditional material examined. NAMIBIA, Erongo region, from *Stipagrotis ciliata* tissues and surrounding rhizosphere, CMW-IA 6921 = CMW 58191 = CBS 149139 = CN010F9, CMW-IA 6926 = CMW 58193 = CBS 149141 = CN013F6.

DNA barcodes. ITS = ON074797, *GAPDH* = ON355381 & *TEF1* = ON355347.

Conidiophores on WA. *Hyphae* subhyaline to pale brown, branched, septate, smooth, (3)4 – 5(8) µm wide. *Conidiophores* single or in small groups, semi- to macronematous, septate, straight to flexuous, geniculate towards the upper part, branched, cell walls thicker than those of vegetative hyphae, mononematous, pale brown to brown, not swollen at the base, (28)40 – 108(316) × (3)4–6(9) µm. *Conidiogenous cells* smooth-walled, terminal or intercalary, proliferating sympodially, pale brown to brown with dark scars, (5)8–12(18) × (3)4–6(8) µm. *Conidia* smooth-walled, ellipsoidal, straight, rarely curved, brown to dark brown, rounded at the apex, 5 distoseptate, sometimes 1–6 distoseptate, (13)34–36(45) × (8)10–11(14) µm ($\bar{x}$ = 32 ± 6.23 × 10.6 ± 0.95 µm); *hila* slightly protuberant, darkened and thickened, 1–3 µm wide. *Chlamydospores* not observed.

Culture characteristics on PDA (25 ºC, 7 d). Cultures incubated in the dark: Colonies 49–66 mm, greenish grey to dark green, margin greenish grey, aerial mycelium moderate giving the colony a slightly cottony appearance, reverse greenish grey to black. *Cultures incubated in a 12-h diurnal UV light cycle*: Colonies 55–70 mm, colony greenish grey to dark green, margin greenish grey, aerial mycelium moderate giving the colony a slightly cottony appearance, reverse greenish grey to black.

Notes. Curvularia gobabebensis is closely related to *C. tribuli* (Fig. 1). *Curvularia gobabebensis* differs from that species as it has mostly 5-distoseptate conidia (*vs* 1–4(6)-distoseptate) and longer conidia (34–36 *vs* 17–30 µm). *Curvularia gobabebensis* also grows more rapidly on PDA (49–66 *vs* 41–53 mm) and has greenish grey to dark green colonies compared to the olivaceous grey to olivaceous black colonies of *C. tribuli* (Marin-Felix et al. 2020). This new species has at least 1 bp difference for ITS, 9 bp for *GAPDH*, and 4 bp for *TEF1* from other *Curvularia* species.

Curvularia maraisii van Vuuren, M.J. Wingf., Yilmaz & Visagie, **sp. nov.** Fig. 4.

MycoBank MB#853991

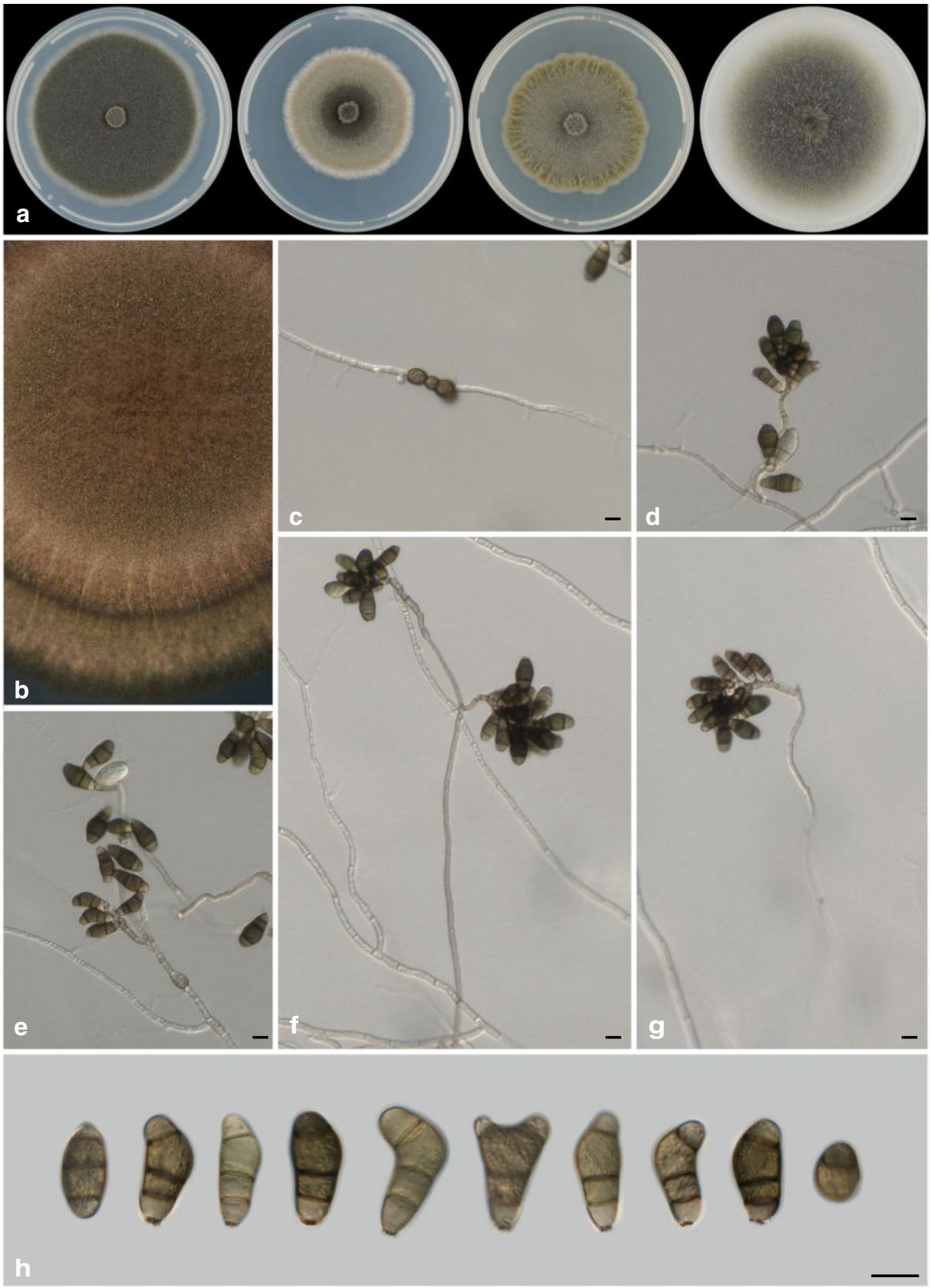
Etymology. Latin, *maraisii*, named for Dr Eugene Marais, an exceptional scientist and research manager based at the Gobabeb Reserch Centre.

Typus. NAMIBIA, Far East region of the Namib desert, from soil surrounding fairy circles, November 2019, coll. Neriman Yilmaz (holotype PRU(M) 4563, dried specimen in metabolically inactive state, ex-type strain CMW-IA 6951 = CMW 58195 = CBS 149143 = CN037F7).

Aditional material examined. NAMIBIA, Erongo region, from *Stipagrotis ciliata* tissues and surrounding rhizosphere, CMW-IA 6927 = CMW 58194 = CBS 149142 = CN021G3.

DNA barcodes. ITS = OR471647, *GAPDH* = ON355385 & *TEF1* = OR486044.

Conidiophores on WA. *Hyphae* hyaline to pale brown, branched, septate, smooth, (2)3–5(7) µm. *Conidiophores* single or in small groups, macronematous, septate, straight to flexuous, geniculate towards the apex, sometimes branched, cell walls thicker than those of vegetative hyphae, mononematous, pale brown to brown, tapers towards the base, apex often darker than base, (15)71–88(254) × (3)4–5(7) µm. *Conidiogenous cells* smooth-walled, terminal or intercalary, proliferating sympodially, pale brown to brown with dark scars (3)7–9(16) × (4)5–6(18) µm. *Conidia* ellipsoidal to curved, sometimes atypical and bifurcate (forking at the apex), the third cell from the base is often swollen unequally, asymmetrical, pale brown to dark brown, base and apex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◂**Fig. 4** *Curvularia maraisii*; **a** CMW 58195 Colony after incubation for 7 d on, from left to right, PDA in complete darkness, PDA exposed to a 12-h UV light diurnal cycle, MEA exposed to a 12-h UV light diurnal cycle, and OA exposed to a 12-h UV light diurnal cycle; **b** CMW 58194 Colony texture on PDA; **c** Chlamydospores CMW 58194; **d–g** Conidiophores and conidia CMW 58194; **h** CMW 58195 Conidia. Scale bars 10 µm

often paler, rounded at the apex, 3-distoseptate, sometimes 2- to 4-distoseptate, (12)24–29(33) × (6)10–12(16) µm ($\bar{x}$ = 26.99 ± 5.90 × 11.82 ± 2.51 µm); *hila* slightly protuberant, darkened and thickened, (2)3–4 µm. *Chlamydospores* borne intercalary in chains, spherical to ovoid, rough, (9)10–13(16) × (8)9–12(15) µm.

Culture characteristics on PDA (25 ºC, 7 d). Cultures incubated in the dark: Colonies 63–70 mm, dark green, margin hyaline and fimbriate, sporulation abundant, reverse greenish grey to black. *Cultures incubated in a 12-h diurnal UV light cycle*: Colonies 54–71 mm, colour dark green, margin hyaline and fimbriate, sporulation abundant, reverse greenish grey to black.

Notes. Curvularia maraisii strains resolve in a clade that has a poorly supported backbone, with *C. austriaca*, *C. borreriae* [MB#283049], *C. coatesiae*, *C. gladioli* [MB#125511], *C. gudauskasii* [MB#312389], *C. harveyi* [MB#329444], *C. indica* [MB#296247], *C. microspora, C. pallescens*, *C. richardiae* [MB#312391], *C. tanzanica* [MB#838305], and *C. trifolii* [MB#280637]. *C. maraisii* differs from *C. austriaca* in its slower growth on PDA (54–71 *vs* 75–90 mm) and in having dark green colonies compared to those of *C. austriaca* that are luteous to orange (Marin-Felix et al. 2020). The new species differs from *C. gudauskasii* in having mostly 3-distoseptate *vs* 4-septate conidia, and its conidiophores have a tyically tapered base and darker apex compared to those of *C. gudauskasii* that has a bulbous base and a paler apex (Morgan-Jones and Karr 1976). *Curvularia maraisii* differs from *C. harveyi* by growing faster on PDA (63–70 *vs* 57 mm), and in having colonies that are dark green *vs* grey-black to brownish black (Shipton 1966). The new species differs from *C. microspora* in having larger conidia ((12)24–29(45) × (6)10–12(19) *vs* (4.5)8.2–(11.5) × (2)3.8–(6) µm) (Liang et al. 2018). *Curvularia maraisii* differs from *C. richardiae* by its darker conidiophore apices and tapering basal cells compared to the more swollen basal cell of *C. richardiae. C. maraisii* also has dark green colonies compared to the grey to dark greyish brown to almost black colonies of *C. richardiae* (Alcorn 1971). *Curvularia maraisii* differs from *C. tanzanica* based on its curved *rather than* straight conidia, and its faster growth on PDA (54–71 *vs* 40 mm). The colonies of *C. maraisii* are dark green compared to the dark brown to black colonies of *C. tanzanica* colonies (Crous et al. 2021). *Curvularia maraisii* has at least 2 bp differences for ITS, 5 bp for *GAPDH*, and 4 bp for *TEF1* from other *Curvularia* species.

Curvularia namibensis van Vuuren, M.J. Wingf., Yilmaz & Visagie, **sp. nov.** Fig. 5.

MycoBank MB# 853992

Etymology. Latin, *namibensis*, name referring to the Namib desert.

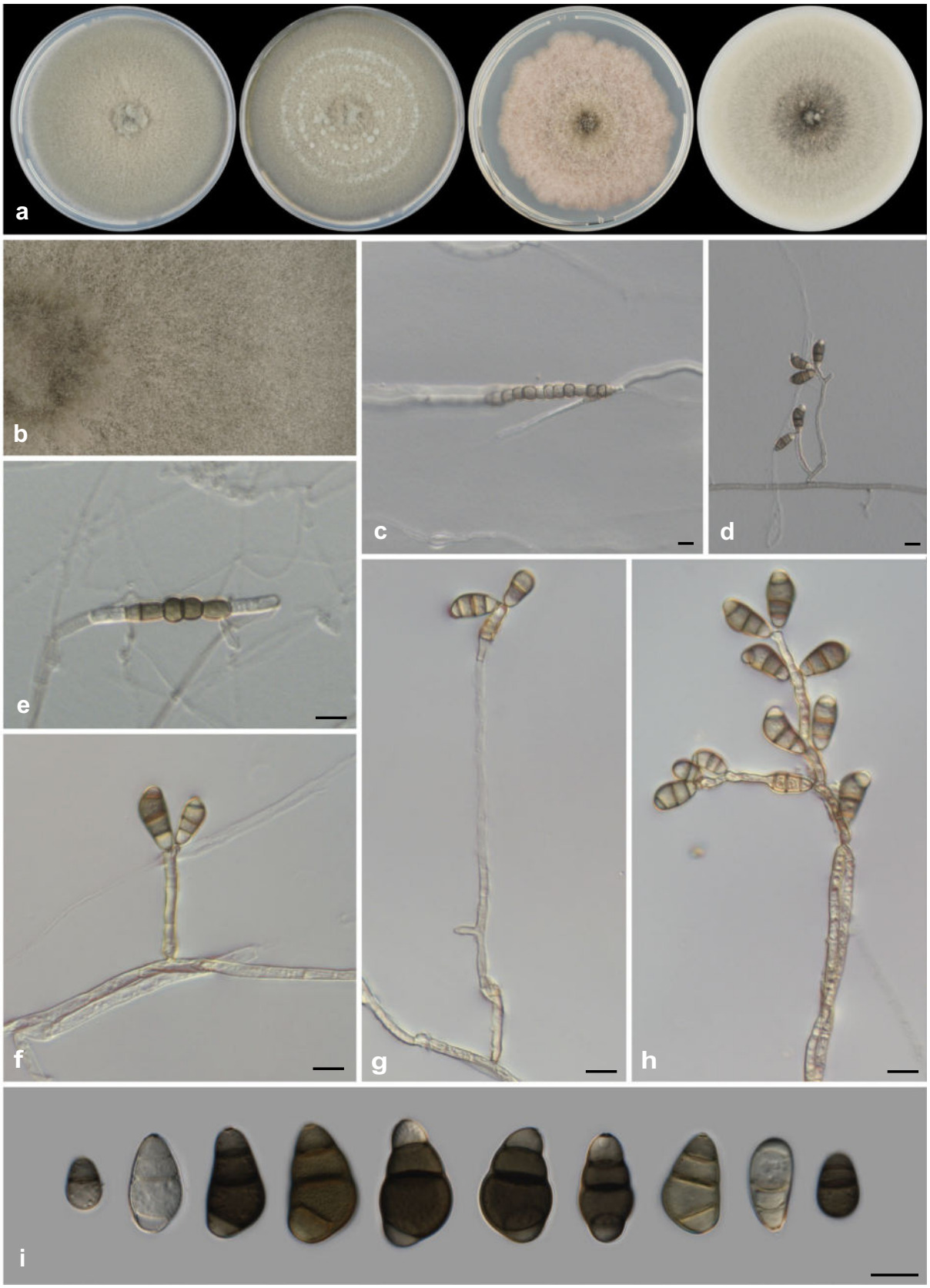
Typus. NAMIBIA, Mirabib, from the roots of *Stipagrostis* species in an area with no fairy circles present, November 2019, coll. Neriman Yilmaz (holotype PRU(M) 4562, dried specimen in metabolically inactive state, ex-type strain CMW-IA 6973 = CMW 58196 = CBS 149144 = CN015H8).

Aditional material examined. NAMIBIA, Erongo region, from *Stipagrotis ciliata* tissues and surrounding rhizosphere, CMW-IA 6930 = CMW 58197 = CN023D3, CMW-IA 6931 = CMW 58198 = CBS 149145 = CN024D2, CMW-IA 6934 = CMW 58199 = CN027A9, CMW-IA 6935 = CMW 58200 = CN027C4, CN034A7, CMW 58202 = CN036F1, CMW-IA 6942 = CMW 58203 = CN036F6, CMW-IA 6943 = CMW 58204 = CN036G9, CMW-IA 6944 = CMW 58205 = CBS 149146 = CN036I5, CMW-IA 6945 = CMW 58206 = CN037D8, CMW-IA 6947 = CMW 58207 = CN037F2, CMW-IA 6948 = CMW 58208 = CN037F3, CMW-IA 6949 = CMW 58209 = CN037F5, CMW-IA 6950 = CMW 58210 = CN037F6, CMW-IA 6952 = CMW 58211 = CBS 149147 = CN044C8, CMW 58212 = CN060F9.

DNA barcodes. ITS = ON074819, *GAPDH* = ON355384 & *TEF1* = ON355350.

Conidiophores on WA. *Hyphae* hyaline to pale brown, branched, septate, smooth walled, (1)4–5(8) µm. *Conidiophores* single or in small groups, macronematous, septate, straight to flexuous, geniculate at the upper part, sometimes branched, cell walls thicker than those of vegetative hyphae, mononematous, pale brown to brown, (13)51–88(284) × (2)4–5(7) µm. *Conidiogenous cells* smooth-walled, terminal or intercalary, proliferating sympodially, sometimes swollen, (5)7–10(25) × (3)4–5(9) µm. *Conidia* ellipsoidal to curved, the third cell from the base is often swollen unequally, asymmetrical, pale brown to dark brown, base and apex often paler, rounded at the apex, 3-distoseptate, sometimes 1-distoseptate, (12)20–24(29) × (8)10–12(17) µm ($\bar{x}$ = 21.65 ± 3.23 × 11.18 ± 1.53 µm); *hila* flat, darkened and thickened, 2–3 µm. *Chlamydospores* borne intercalary, spherical to cylindrical, smooth, (3)6–12(24) × (3)8–11(28) µm.

Culture characteristics on PDA (25 ºC, 7 d). Cultures incubated in the dark: Colonies 57–84 mm, colour nickel green to dull green, moderate aerial mycelia giving the colony a cottony appearance in the center, margin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◂**Fig. 5** *Curvularia namibensis*; **a** CMW 58197 Colony after incubation for 7 d on, from left to right, PDA in complete darkness, PDA exposed to a 12-h UV light diurnal cycle, MEA exposed to a 12-h UV light diurnal cycle, and OA exposed to a 12-h UV light diurnal cycle; **b** CMW 58197 Colony texture on PDA; **c** CMW 58211**, e** CMW 58205 Chlamydospores; **d** CMW 58211**, f, g** CMW 58197**, h** CMW 58211 Conidiophores and conidia; **i** CMW 58198 Conidia. Scale bars 10 µm

fimbriate and hyaline to white, reverse greenish grey to black. *Cultures incubated in a 12-h diurnal UV light cycle*: Colonies 38–84 mm, olive green to ivy green, moderate aerial mycelia giving the colony a cottony appearance in the center, margin fimbriate and hyaline to brown reverse greenish grey, grey or black.

Notes. Curvularia namibensis strains resolve in a clade with *C. caricae-papayae* [MB#329436]*, C. chlamydospora, C. ovoidea* [MB#296250], *C. prasadii, C. pseudolunata* and *C. warraberensis* [MB#825462] (Fig. 1). *Curvularia namibensis* differs from *C. prasadii* in having shorter conidiophores (51–88 *vs* 80–320 µm) (Mathur and Mathur 1959). *Curvularia warraberensis* has a more restricted growth than *C. namibensis* on PDA (6–7 *vs* 77 mm) and was described from *Dactyloctenium aegyptium*, a member of the *Poaceae* (Tan et al. 2018) *Curvularia namibensis* has at least 3 bp for *GAPDH* and 4 for *TEF1* from other *Curvularia* species, but no bp differences for ITS.

Curvularia stipagrostidicola van Vuuren, M.J. Wingf., Yilmaz & Visagie, **sp. nov.** Fig. 6.

MycoBank MB#853993

Etymology. Latin, *stipagrostidicola*, name refers to *Stipagrostis*, the genus of grass from which the holotype was isolated.

Typus. NAMIBIA, Far East, Mirabib and Reverse region, from shoots of *Stipagrostis* species on the margin of a vegetation patch, November 2019, coll. Neriman Yilmaz (holotype PRU(M) 4602, dried specimen in metabolically inactive state, ex-type strain (CMW-IA 6968 = CMW 58218 = CBS 149150 = CN060H5).

Aditional material examined. NAMIBIA, Erongo region, from *Stipagrotis ciliata* tissues and surrounding rhizosphere, CMW-IA 6922 = CMW 58213 = CN011D7, CMW-IA 6923 = CMW 58219 = CN011D8, CMW-IA 6939 = CMW 64028 = CN034B7, CMW-IA 6940 = CMW 58214 = CBS 149148 = CN034B8, CMW-IA 6941 = CMW 58215 = CN034H8, CMW-IA 6953 = CMW 58216 = CN044D1, CMW-IA 6954 = CMW 58217 = CBS 149149 = CN060G3, CMW-IA 6955 = CMW 64030 = CN060G4.

DNA barcodes. ITS = ON332838, *GAPDH* = ON355415 & *TEF1* = ON355368.

Conidiophores on WA. *Hyphae* hyaline to pale brown, branched, septate, smooth walled (3)5–7(8) µm. *Conidiophores* single or in small groups, semi-maronematous, septate, straight to flexous, geniculate towards upper part, sometimes branched, cell walls thicker than those of vegetative hyphae, mononematous, uniformly brown (30)62–97(226) × (4)5–7(9) µm. *Conidiogenous cells* smooth-walled, terminal or intercalary, proliferating sympodially, 4–11(31) × (4)6–8(13) µm. *Conidia* curved, uniformly pale brown to dark brown, 3-distoseptate, sometimes aseptate to 4-distoseptate (27)30–35(37) × (12)13–16(18) µm ($\bar{x}$ = 31.92 ± 2.51 × 14.77 ± 1.11 µm); *hila* flat, thickened and darkened 2–4 µm. *Chlamydospores* not observed.

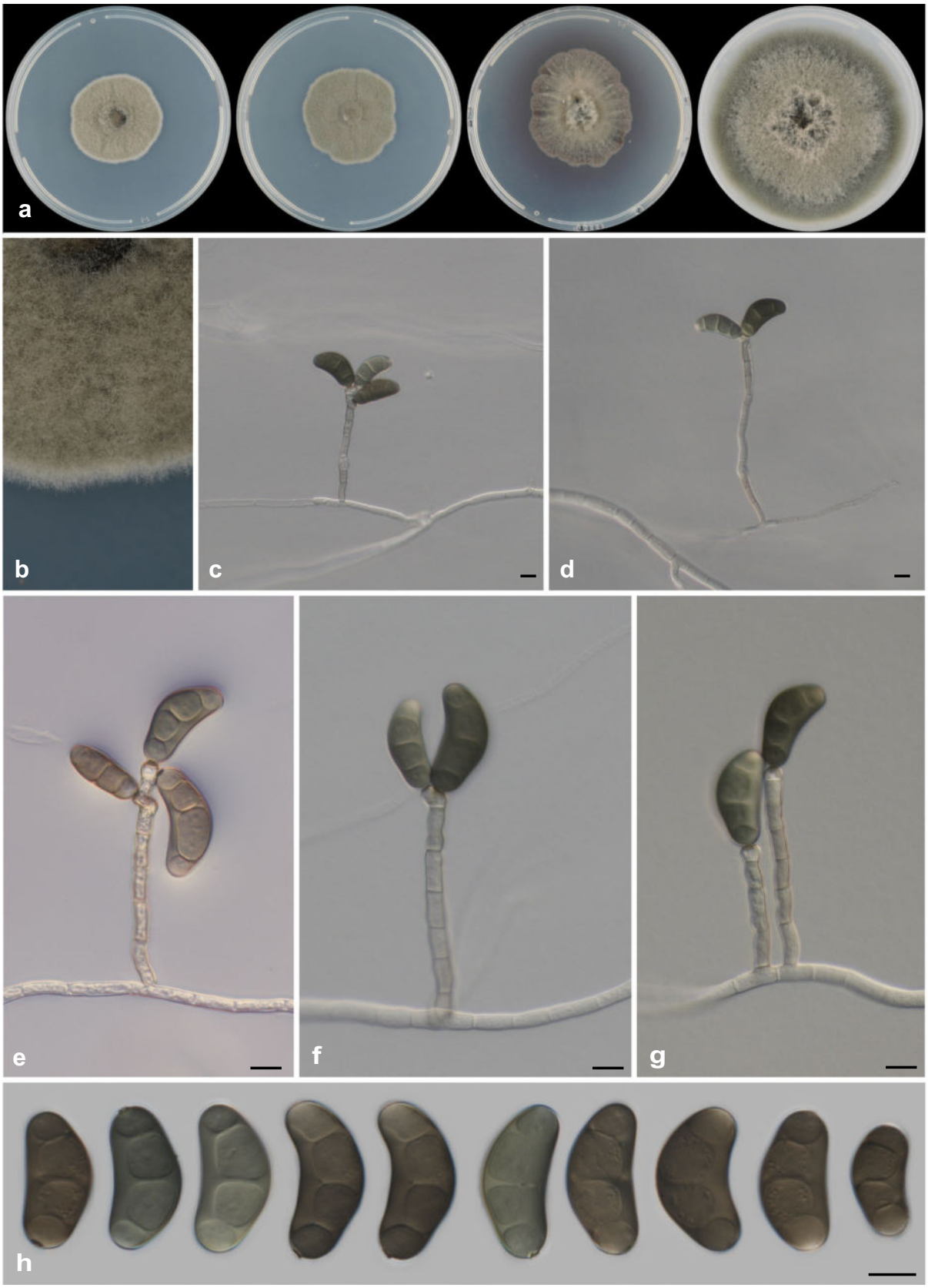
Culture characteristics on PDA (25 ºC, 7 d). Cultures incubated in the dark: Colonies 26–38 mm, colour greenish grey to olive, little to moderate aerial mycelia giving the colony a cottony appearance, margin hyaline to white and lobate, sulcation present reverse coal to black. *Cultures incubated in a 12-h diurnal UV light cycle*: Colonies 32–61 mm, greenish grey to olive, aerial mycelia sparse to moderate giving the colony a cottony appearance, margin hyaline to white and lobate reverse coal to black.

Notes. Curvularia stipagrostidicola is closely related to *C. eragrostidicola* [MB#827458] (Fig. 1). Compared to the new species, *C. eragrostidicola* has a more restricted growth on PDA (20 mm compared with 26–38 mm) after 7 d, while its conidia is paler towards the apex (Tan et al. 2018). *Curvularia stipagrostidicola* has at least 7 bp differences for ITS, 15 bp for *GAPDH* and 8 for *TEF1* from other *Curvularia* species.

Discussion

Our study represents the most extensive effort to document *Curvularia* species from Africa and specifically from Namibia. A total of 80 *Curvularia* strains were isolated from *S. ciliata* and its associated rhizosphere soils. Strains were identified as 13 species using gene sequences from the ITS, *GAPDH* and/or *TEF1*. Notably five of those species including *C. deserticola, C. gobabebensis, C. maraisii, C. namibensis* and *C. stipagrostidicola* were found to be new taxa.

Curvularia species have previously been reported from the Namib Desert. Eicker et al. (1982) surveyed rhizosphere soils associated with fairy circles in the Giribes Plain and reported isolating *Curvularia,* but they did not identify the species. Crous et al. (2020) described *Curvularia moringae* from *Moringa ovalifolia* (*Moringaceae*) collected from Namibia. In addition, *C. eragrostidis* [MB#296246] and *C. carica-papayae* were identified from *Stipagrostis sabulicola*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◂**Fig. 6** *Curvularia stipagrostidicola*; **a** CMW 58217 Colony after incubation for 7 d on, from left to right, PDA in complete darkness, PDA exposed to a 12-h UV light diurnal cycle, MEA exposed to a 12-h UV light diurnal cycle, and OA exposed to a 12-h UV light diurnal cycle; **b** CMW 58217 Colony texture on PDA; **c–f** CMW 58217, **g** CMW 58214 Conidiophores and conidia; **h** CMW 58217 Conidia. Scale bars 10 µm

plant litter in the Namib Sand Sea using a culture-dependent and culture-independent approach (Wenndt et al. 2021).

Members of the genus *Curvularia* cannot be reliably distinguished from the genus *Bipolaris* based on morphological characteristics alone (Marin-Felix et al. 2017, 2020; Tan et al. 2018). This is due to the many overlapping morphological characters; therefore, phylogenetic inference based on DNA sequence data is essential (Manamgoda et al. 2014). An ITS sequence is useful to assign strains to one of the two genera, but it is generally poor in distinguishing closely related species. This is evident from our ITS phylogeny (Supplementary Fig. 1), with a few to no base pair differences between, for example, *C. buchloes* [MB#622507], *C. manamgodae* [MB#556662], *C. rouhanii*, and *C. spicifera* strains. ITS, *GAPDH* and *TEF1* were recommended as useful identification and phylogenetic markers in *Curvularia* (Manamgoda et al. 2015). For our new species, *GAPDH* typically showed at least 3 bp differences, and *TEF1* showed 1 bp difference from close relatives. However, some clades appear problematic. In our opinion, species concepts for the genus have been applied narrowly, with undersampling further complicating this problem. In our study we isolated several species previously known only from a single isolate. The DNA sequences generated for these strains are thus important to capture infraspecies variation. In future, additional gene regions, as well as genomes, should be incorporated to achieve more robust species delineation. Additionally, a taxonomic revision will be necessary to evaluate species boundaries once deeper sampling has been achieved across various geographic locations and substrates.

Curvularia moringae and *C. namibensis* were the most frequently isolated species in this study, each including 17 strains isolated from grass and rhizosphere samples in the Far East, Mirabib and Reverse locations, respectively. This is the first report of *C. moringae* occurring in grasses and soil; previously only recovered from *Moringa ovalifolia* in the Namib Desert (Crous et al. 2020). Eight strains of *C. tribuli* were isolated from samples collected from the Far East, Mirabib and Reverse locations. This species was described by Marin-Felix et al. (2020) from punctureVine (*Tribulus terrestris*) leaves. We also isolated seven strains of *C. rouhanii* from samples collected from all three sampling sites. It was described from leaves of both the American Evergreen (*Syngonium vellozianum*) and *Eucalyptus* trees (Mehrabi-Koushki et al. 2018). To the best of our knowledge, this is the first report of these species from a member of *Poaceae*.

Of the new species described in this study, *C. gobabebensis* was found only in the tissues of *S. ciliata*, while others were also isolated from rhizosphere soils. In addition, *C. gobabebensis* was found exclusively in the Mirabib region, and not associated with fairy circles but rather isolated from the rhizosphere from an area not having fairy circles. *Curvularia maraisii* was only found in the Far East region. While these strains showed some association with specific substrates and locations in this study, the biology of these *Curvularia* species and their substrate associations, and distribution would be better understood through more extensive sampling.

It is becoming increasingly clear that fungi are well-adapted to living in extreme environments like deserts, which have high UV radiation, radically fluctuating temperatures, low rainfall, and often highly saline and/or acidic soils, by adopting a variety of lifestyles (Coleine et al. 2022; Makhalanyane et al. 2015; Porras-Alfaro et al. 2008; Whitford and Wade 2002). To inhabit these harsh environments, microorganisms usually have resistance mechanisms (Porras-Alfaro et al. 2008; Selbmann et al. 2021). The production of melanin, that protects microorganisms from harmful UV radiation, is one of these (Eisenman and Casadevall 2012; Gessler et al. 2014; Newsham 2011). Fungi can also have vegetative survival structures such as chlamydospores and/or ascomata (sexual states) that are often resistant to extreme temperatures (Manamgoda et al. 2012). In this regard, *Curvularia* species have cell walls that are melanised and/or produce chlamydospores (Bengyella et al. 2019; Kiss et al. 2020).

Identification of thirteen *Curvularia* species, including five new species, contributes to an expanding knowledge regarding species in this genus, including their distribution. It also provides a substantially increased database of reference sequence data available for the genus. Furthermore, the results of this study contribute to a better understanding of the diversity of fungi in the Namib Desert.

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Author Contributions All authors contributed to formal analyses and investigation. The original draft was composed by Nicole van Vuuren and reviewed and edited by Neriman Yilmaz, Michael Wingfield and Cobus Visagie. All authors read and approved the final manusacript.

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Data Availability Our data is already available at GenBank, culture collections and on FIgShare.

Declarations

Competing interests The authors have declared that no competing interests exist.

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