



# Multi-locus phylogeny of the genus *Curvularia* and description of ten new species

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## Abstract

*Curvularia* is a cosmopolitan genus that includes species associated with plants, animals and humans, several of which are of clinical significance. Some of these species are important pathogens of grasses, causing devastating diseases on cereal crops in the family Poaceae. In the present multi-locus study, ex-type and reference strains of *Curvularia*, as well as several strains deposited in the CBS culture collection of the Westerdijk Fungal Biodiversity Institute, were included. Based on ITS, *GAPDH* and *TEF1* sequences, as well as phenotypic data, ten new species are described and illustrated: *C. arcana*, *C. austriaca*, *C. canadensis*, *C. ellisii*, *C. pseudoclavata*, *C. pseudoellisii*, *C. pseudointermedia*, *C. pseudoprotuberata*, *C. siddiquii* and *C. tribuli*. Moreover, the new combinations *C. cactivora* and *C. patereae* are proposed, and an epitype for *C. oryzae-sativae* is designated. In addition, illustrations and descriptions are provided for *C. cactivora*, *C. ellisii*, *C. crassiseptata*, *C. neergaardii*, *C. oryzae*, *C. oryzae-sativae*, *C. protuberata* and *C. verruciformis*. The description of *C. pseudobrachyspora* is emended, and its host and distribution records are updated.

**Keywords** *Bipolaris* · *Drechslera* · Dothideomycetes · Helminthosporioid fungi · Human and plant pathogens

## Introduction

*Curvularia* is a genus with a worldwide distribution that includes pathogens or saprobes of a wide range of plant hosts. Species occur mainly on members of the family Poaceae and represent important pathogens of grass and staple crops, including rice, maize, wheat and sorghum. Other hosts are

genera belonging to Actinidiaceae, Aizoaceae, Caricaceae, Convolvulaceae, Fabaceae, Iridaceae, Lamiaceae, Lythraceae, Oleaceae, Polygonaceae and Rubiaceae (Sivanesan 1987; Manamgoda et al. 2015; Marin-Felix et al. 2017a, b; Tan et al. 2018). *Curvularia* also includes emerging opportunistic pathogens of humans that cause respiratory tract, cutaneous, cerebral and corneal infections, mainly in immunocompromised patients, e.g. *C. chlamydospora* and *C. lunata* (Carter and Boudreaux 2004; Madrid et al. 2014). Species such as *C. spicifera*, *C. hawaiiensis*, *C. australiensis* and *C. lunata* were not only isolated from human specimens (da Cunha et al. 2013; Manamgoda et al. 2015), but are also regarded as causal agents of animal and human diseases (de Hoog et al. 2011). Recently, two additional species, *C. hominis* and *C. tuberculata*, have been proven to be causal agents of keratitis (Miqueleiz Zapatero et al. 2018) and a human disseminated phaeohiphomycosis (Vasikasin et al. 2019). *Curvularia* species can also be found in other substrates, i.e. air (*C. aerea* and *C. pallescens*; Manamgoda et al. 2015), aquatic environments (*C. robusta* and *C. senegalensis*; Verma et al. 2013) and soil (*C. soli* and *C. spicifera*; Marin-Felix et al. 2017a; Tan et al. 2018).

*Curvularia* is characterised by the production of brown distoseptate conidia, usually with paler terminal cells and

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inordinately enlarged intermediate cells, which contributes to its characteristic curvature. The curvature of the conidia is the main difference to the similar genus *Bipolaris*, since in the latter the curvature, when present, is throughout the length of the conidium. In *Bipolaris*, conidia are usually also longer than in *Curvularia* (Sivanesan 1987; Marin-Felix et al. 2017a). However, both genera include species that exhibit intermediate conidial characters (Manamgoda et al. 2012), making sequence data essential for proper species delimitation. In this context, several studies based on the internal transcribed spacer regions and intervening 5.8S nrRNA gene (ITS), large subunit of the rDNA (LSU) and partial fragments of the glyceraldehyde-3-phosphate dehydrogenase (*GAPDH*) and the translation elongation factor 1- $\alpha$  (*TEF1*) genes have been performed, resulting in several species being transferred from one genus to another (Manamgoda et al. 2012, 2014; Tan et al. 2014). The *Drechslera* asexual morph of *Pyrenophora*, as well as species of *Exserohilum* and *Johnalcornia*, is also similar to *Bipolaris* and *Curvularia* (Tan et al. 2014; Hernández-Restrepo et al. 2018; Marin-Felix et al. 2019). Some *Exserohilum* species can be easily distinguished from the other three genera by the production of conidia with distinctly protruding hila, but some species of *Curvularia* produce similar structures, leading to wrong identifications (Hernández-Restrepo et al. 2018). *Pyrenophora* differs from the other gramminicolous genera by its muriform septate ascospores, but the asexual morph is similar to *Curvularia*, also leading to incorrect identifications (Marin-Felix et al. 2019). *Johnalcornia* can be distinguished by forming the second conidial septum in the apical cell and producing distinctive conidia-like chlamydospores (Tan et al. 2014). *Cochliobolus*, which is known as the sexual morph of *Curvularia* and *Bipolaris*, is characterised by brown or black, globose ascospores, bitunicate, cylindrical asci and filiform or flagelliform, hyaline ascospores, which are loosely arranged into a helix or parallel (Manamgoda et al. 2012). The only difference is the presence of stromata in some *Curvularia* species, a feature not observed in *Bipolaris* (Manamgoda et al. 2012). Because the sexual morph is rarely found in nature and difficult to induce in culture, it is of limited value to distinguish *Bipolaris* and *Curvularia* (Manamgoda et al. 2014, 2015). Species of both *Curvularia* and *Bipolaris* are therefore mainly differentiated based on their asexual morphs (Marin-Felix et al. 2017a).

*Curvularia* species are difficult to identify based only on morphology since many species share similar characters with overlapping dimensions. In order to get a proper delimitation and identification, several phylogenetic studies using ITS, *GAPDH* and *TEF1* have recently been published (Manamgoda et al. 2012, 2015; Tan et al. 2014, 2018; Marin-Felix et al. 2017a, b). In the revision of the genus carried out by Marin-Felix et al. (2017a), 74 species were accepted based on DNA sequence data. Subsequently, 31 novelties

have been introduced (Hyde et al. 2017; Marin-Felix et al. 2017b; Tan et al. 2018; Dehdari et al. 2018; Heidari et al. 2018; Hernández-Restrepo et al. 2018; Liang et al. 2018; Mehrabi-Koushki et al. 2018; Tibpromma et al. 2018). Hitherto, 105 species are accepted in the genus based on DNA sequence data. Some of these species were described a long time ago, with descriptions and/or illustrations not being readily available. In that context, Manamgoda et al. (2015) revised the genus and provided updated data for ten species. One of the objectives of this study is therefore to further enlarge our knowledge on the diversity and taxonomy of *Curvularia*. Another problem remaining unresolved is the lack of molecular data for those species that have only been described based on morphology, causing many of them to be ignored by the scientific community. A second objective is thus to provide sequence data of the main markers used in molecular studies of *Curvularia* and to determine the taxonomic position of many of these previously described species.

## Materials and methods

### Isolates and morphological analysis

Strains deposited in the Westerdijk Fungal Biodiversity Institute (CBS) collection identified as *Curvularia* or related genera, i.e. *Bipolaris*, *Exserohilum*, *Johnalcornia* and *Pyrenophora*, were examined (Table 1). These strains were cultured on potato dextrose agar (PDA), which is the medium used in the recent revisions of the genus, at 25 °C under an alternating 12-h UV light/dark regime to induce sporulation. When the cultures were mature, the fertile fungal structures were mounted and measured in lactic acid, with at least 30 measurements of each structure. The strains that did not produce reproductive structures on PDA were also cultured on 2% malt extract agar (MEA), oatmeal agar (OA) and synthetic nutrient-poor agar (SNA) (Crous et al. 2019) with pieces of sterile maize leaves in order to induce sporulation. Observations and photomicrographs were obtained with a Nikon SMZ1500 dissecting microscope, and with a Nikon eclipse Ni compound microscope, using a DS-Ri2 digital camera (Nikon, Tokyo, Japan) and NIS-Elements imaging software v. 4.20.

Culture descriptions were done by incubating each isolate on three PDA plates in the dark. After a week, colony diameters were measured, colony morphologies described and the colours rated using the colour chart of Rayner (1970). Taxonomic novelties and typifications were registered in MycoBank ([www.MycoBank.org](http://www.MycoBank.org); Crous et al. 2004).

### DNA isolation and amplification

Genomic DNA was extracted and purified directly from fungal colonies growing on MEA according to the UltraClean™

**Table 1** Details of isolates included in phylogenetic analyses. GenBank accession numbers in bold were newly generated in this study. Novelties are indicated in bold italic

Species	Isolates <sup>a</sup>	Country	Substrate	GenBank accession numbers <sup>b</sup>		
				ITS	<i>GAPDH</i>	<i>TEF1</i>
<i>Bipolaris maydis</i>	CBS 136.29 <sup>PT</sup>	Japan	<i>Zea mays</i>	KJ909769	KM034845	KM093793
<i>B. panici-miliacei</i>	CBS 199.29 <sup>LT</sup>	Japan	<i>Panicum miliaceum</i>	KJ909773	KM042896	KM093788
<i>B. peregrinensis</i>	DAOM 221998	Australia	<i>Cynodon dactylon</i>	KJ922393	KM034849	KM093797
<i>B. sorokiniana</i>	CBS 110.14	USA	<i>Hordeum</i> sp.	KJ922381	KM034822	KM093763
<i>Curvularia aerea</i>	CBS 294.61 <sup>T</sup>	Brazil	Air	HE861850	HF565450	–
<i>C. affinis</i>	CBS 154.34 <sup>SynT</sup>	Indonesia	Unknown	KJ909780	KM230401	KM196566
<i>C. ahvazensis</i>	CBS 144673 <sup>T</sup>	Iran	<i>Zinnia elegans</i> rotten roots	KX139029	MG428693	MG428686
<i>C. akaii</i>	CBS 317.86	Japan	<i>Themada triandra</i>	KJ909782	KM230402	KM196569
<i>C. akaiiensis</i>	BRIP 16080 <sup>IsoT</sup>	India	Unknown	KJ415539	KJ415407	KJ415453
<i>C. alcornii</i>	MFLUCC 10-0703 <sup>T</sup>	Thailand	<i>Zea</i> sp.	JX256420	JX276433	JX266589
<i>C. americana</i>	UTHSC 08-3414 <sup>T</sup>	USA	Human ankle	HE861833	HF565488	–
<b><i>C. arcana</i></b>	CBS 127224 <sup>T</sup>	Unknown	Unknown	<b>MN688801</b>	<b>MN688828</b>	<b>MN688855</b>
<i>C. asiatica</i>	MFLUCC 10-0711 <sup>T</sup>	Thailand	<i>Panicum</i> sp.	JX256424	JX276436	JX266593
<i>C. australiensis</i>	BRIP 12044 <sup>T</sup>	Australia	<i>Oryza sativa</i>	KJ415540	KJ415406	KJ415452
<i>C. australis</i>	BRIP 12521 <sup>T</sup>	Australia	<i>Sporobolus</i> sp.	KJ415541	KJ415405	KJ415451
<b><i>C. austriaca</i></b>	CBS 102694 <sup>T</sup>	Austria	Nasal cavity of patient with sinusitis	<b>MN688802</b>	<b>MN688829</b>	<b>MN688856</b>
	UTHSC 08-2957	USA	Corneal ulcer	HE861846	HF565456	–
	UTHSC 09-3510	USA	Peritoneal dialysis fluid	HE861847	HF565458	–
<i>C. bannonii</i>	BRIP 16732 <sup>IsoT</sup>	USA	<i>Jacquemontia tamnifolia</i>	KJ415542	KJ415404	KJ415450
<i>C. beasleyi</i>	BRIP 10972 <sup>T</sup>	Australia	<i>Chloris gayana</i>	MH414892	MH433638	MH433654
<i>C. beerburumensis</i>	BRIP 12942 <sup>T</sup>	Australia	<i>Eragrostis bahiensis</i>	MH414894	MH433634	MH433657
<i>C. boeremae</i>	IMI 164633 <sup>T</sup>	India	<i>Portulaca oleracea</i>	MH414911	MH433641	–
<i>C. bothriochloae</i>	BRIP 12522 <sup>T</sup>	Australia	<i>Bothriochloa bladhii</i>	KJ415543	KJ415403	KJ415449
<i>C. brachyspora</i>	CBS 186.50	India	Soil	KJ922372	KM061784	KM230405
<i>C. buchloes</i>	CBS 246.49 <sup>T</sup>	USA	<i>Buchloë dactyloides</i>	KJ909765	KM061789	KM196588
<b><i>C. cactivora</i></b>	CBS 580.74 <sup>R</sup>	Republic of Suriname	Member of Cactaceae	<b>MN688803</b>	<b>MN688830</b>	<b>MN688857</b>
	Strain 737	USA	<i>Hylocereus undatus</i>	HM598679	HM598682	–
	Strain 738	USA	<i>Hylocereus undatus</i>	HM598678	HM598681	–
	Strain 739	USA	<i>Hylocereus undatus</i>	HM598677	HM598680	–
	DB13GEN09	Italy	<i>Cereus peruvianus</i> var. <i>monstruosus</i>	KF041822	–	–
<b><i>C. canadensis</i></b>	CBS 109239 <sup>T</sup>	Canada	Overwintered grass	<b>MN688804</b>	<b>MN688831</b>	<b>MN688858</b>
<i>C. caricae-papayae</i>	CBS 135941 <sup>T</sup>	India	<i>Carica papaya</i>	HG779884	HG779146	–
<i>C. Chiangmaiensis</i>	CPC 28829 <sup>T</sup>	Thailand	<i>Zea mays</i>	MF490814	MF490836	MF490857
<i>C. chlamydospora</i>	UTHSC 07-2764 <sup>T</sup>	USA	Toe nail	HG779021	HG779151	–
<i>C. chonburiensis</i>	MFLUCC 16-0375 <sup>T</sup>	Thailand	dead leaf of <i>Pandanus</i> sp.	MH275055	MH41274	–
<i>C. clavata</i>	BRIP 61680b	Australia	<i>Oryza rufipogon</i>	KU552205	KU552167	KU552159
<i>C. coatesiae</i>	BRIP 24261 <sup>T</sup>	Australia	<i>Litchi chinensis</i>	MH414897	MH433636	MH433659
<i>C. coicis</i>	CBS 192.29 <sup>SynT</sup>	Japan	<i>Coix lacryma</i>	JN192373	JN600962	JN601006
<i>C. colbranii</i>	BRIP 13066 <sup>T</sup>	Australia	<i>Crinum zeylanicum</i>	MH414898	MH433642	MH433660
<i>C. crassiseptata</i>	CBS 503.90 <sup>T</sup>	Nigeria	Plant material	LT631310	LT715882	<b>MN688859</b>
<i>C. crustacea</i>	BRIP 13524 <sup>ET</sup>	Indonesia	<i>Sporobolus</i> sp.	KJ415544	KJ415402	KJ415448
<i>C. cymbopogonis</i>	CBS 419.78	The Netherlands	<i>Yucca</i> sp.	HG778985	HG779129	HG779163
<i>C. dactyloctenii</i>	CPC 28810 <sup>T</sup>	Thailand	<i>Dactyloctenium aegyptium</i>	MF490815	MF490837	MF490858
<i>C. dactyloctenii</i>	BRIP 12846 <sup>T</sup>	Australia	<i>Dactyloctenium radulans</i>	KJ415545	KJ415401	KJ415447
<b><i>C. ellisii</i></b>	CBS 193.62 <sup>T</sup>	Pakistan	Air	JN192375	JN600963	JN601007
	CBS 127083	Australia	<i>Dactyloctenium aegyptium</i>	<b>MN688805</b>	<b>MN688832</b>	<b>MN688860</b>
<i>C. eragrostidicola</i>	BRIP 12538 <sup>T</sup>	Australia	<i>Eragrostis pilosa</i>	MH414899	MH433643	MH433661
<i>C. eragrostidis</i>	CBS 189.48	Indonesia	<i>Sorghum</i> sp.	HG778986	HG779154	HG779164
<i>C. geniculata</i>	CBS 187.50	Indonesia	Unknown seed	KJ909781	KM083609	KM230410
<i>C. gladioli</i>	CBS 210.79	Romania	<i>Gladiolus</i> sp.	HG778987	HG779123	–
<i>C. graminicola</i>	BRIP 23186 <sup>T</sup>	Australia	Unknown	JN192376	JN600964	JN601008
<i>C. “gudauskasii”</i>	DAOMC 165085	Tanzania	<i>Triticum aestivum</i>	AF071338	–	–
<i>C. harveyi</i>	BRIP 57412 <sup>IsoT</sup>	Australia	<i>Triticum aestivum</i>	KJ415546	KJ415400	KJ415446
<i>C. hawaiiensis</i>	BRIP 11987 <sup>IsoLT</sup>	USA	<i>Oryza sativa</i>	KJ415547	KJ415399	KJ415445
<i>C. heteropogonicola</i>	BRIP 14579 <sup>IsoT</sup>	India	<i>Heteropogon contortus</i>	KJ415548	KJ415398	KJ415444
<i>C. heteropogonis</i>	CBS 284.91 <sup>T</sup>	Australia	<i>Heteropogon contortus</i>	JN192379	JN600969	JN601013

**Table 1** (continued)

Species	Isolates <sup>a</sup>	Country	Substrate	GenBank accession numbers <sup>b</sup>		
				ITS	<i>GAPDH</i>	<i>TEF1</i>
<i>C. hominis</i>	CBS 136985 <sup>T</sup>	USA	<i>Homo sapiens</i>	HG779011	HG779106	–
<i>C. homomorpha</i>	CBS 156.60 <sup>T</sup>	USA	Air	JN192380	JN600970	JN601014
<i>C. inaequalis</i>	CBS 102.42 <sup>T</sup>	France	Sand dune soil	KJ922375	KM061787	KM196574
<i>C. intermedia</i>	CBS 334.64	USA	<i>Avena versicolor</i>	HG778991	HG779155	HG779169
<i>C. ischaemi</i>	CBS 630.82 <sup>T</sup>	New Zealand	<i>Ischaemum indicum</i>	JX256428	JX276440	–
<i>C. kenpeggii</i>	BRIP 14530 <sup>T</sup>	Australia	<i>Triticum aestivum</i>	MH414900	MH433644	MH433662
<i>C. kusanoi</i>	CBS 137.29	Japan	<i>Eragrostis major</i>	JN192381	–	JN601016
<i>C. lamingtonensis</i>	BRIP 12259 <sup>T</sup>	Australia	<i>Microlaena stipoides</i>	MH414901	MH433645	MH433663
<i>C. lunata</i>	CBS 730.96 <sup>NT</sup>	USA	Lung biopsy	JX256429	JX276441	JX266596
<i>C. malina</i>	CBS 131274 <sup>T</sup>	USA	<i>Zoysia matrella</i>	JF812154	KP153179	KR493095
<i>C. mebaldsii</i>	BRIP 12900 <sup>T</sup>	Australia	<i>Cynodon transvaalensis</i>	MH414902	MH433647	MH433664
<i>C. micropus</i>	CBS 127235 <sup>ET</sup>	USA	<i>Paspalum notatum</i>	HE792934	LT715859	–
<i>C. microspora</i>	GUCC 6272 <sup>T</sup>	China	<i>Hippeastrum striatum</i> leaf spot	MF139088	MF139097	MF139115
<i>C. miyakei</i>	CBS 197.29 <sup>SynT</sup>	Japan	<i>Eragrostis pilosa</i>	KJ909770	KM083611	KM196568
<i>C. mosaddeghii</i>	IRAN 3131C <sup>T</sup>	Iran	<i>Syzygium cumini</i> leaf spot	MG846737	MH392155	MH392152
<i>C. muehlenbeckiae</i>	CBS 144.63 <sup>T</sup>	India	<i>Muehlenbeckia</i> sp.	HG779002	HG779108	–
<i>C. neergaardii</i>	BRIP 12919 <sup>isoT</sup>	Ghana	<i>Oryza sativa</i>	KJ415550	KJ415397	KJ415443
	CBS 276.91	Australia	Unknown	<b>MN688806</b>	<b>MN688833</b>	<b>MN688861</b>
	CBS 277.91	Australia	Unknown	<b>MN688807</b>	<b>MN688834</b>	<b>MN688862</b>
<i>C. neoindica</i>	IMI 129790 <sup>T</sup>	India	<i>Brassica nigra</i>	NR_158450	MH433649	MH433667
<i>C. nicotiae</i>	CBS 655.74 <sup>isoT</sup>	Algeria	Desert soil	KJ415551	KJ415396	KJ415442
<i>C. nodosa</i>	CPC 28800 <sup>T</sup>	Thailand	<i>Digitaria ciliaris</i>	MF490816	MF490838	MF490859
<i>C. nodulosa</i>	CBS 160.58	USA	<i>Eleusine indica</i>	JN601033	JN600975	JN601019
<i>C. oryzae</i>	CBS 169.53 <sup>isoT</sup>	Vietnam	<i>Oryza sativa</i>	KP400650	KP645344	KM196590
<i>C. oryzae-sativae</i>	CBS 127725 <sup>ET</sup>	Argentina	<i>Oryza sativa</i>	<b>MN688808</b>	<b>MN688835</b>	<b>MN688863</b>
<i>C. ovariicola</i>	CBS 470.90 <sup>T</sup>	Australia	<i>Eragrostis interrupta</i>	<b>MN688809</b>	<b>MN688836</b>	–
<i>C. pandanicola</i>	MFLUCC 15-0746 <sup>T</sup>	Thailand	Dead leaf of <i>Pandanus</i> sp.	MH275056	MH412748	MH412763
<i>C. papendorfii</i>	CBS 308.67 <sup>T</sup>	South Africa	<i>Acacia karroo</i>	KJ909774	KM083617	KM196594
<i>C. pallescens</i>	CBS 156.35 <sup>T</sup>	Java	Air	KJ922380	KM083606	KM196570
	CBS 859.73	Chile	Volcanic ash soil	HE861848	HF565455	–
<i>C. palmicola</i>	MFLUCC 14-0404 <sup>T</sup>	Thailand	Dead branches of <i>Acoelorrhaphe wrightii</i>	MF621582	–	–
<i>C. patereae</i>	CBS 198.87 <sup>T</sup>	Argentina	<i>Triticum durum</i> seed	<b>MN688810</b>	<b>MN688837</b>	<b>MN688864</b>
<i>C. penniseti</i>	CBS 528.70	Unknown	<i>Pennisetum</i> sp. seed	<b>MN688811</b>	<b>MN688838</b>	–
<i>C. perotidis</i>	CBS 350.90 <sup>T</sup>	Australia	<i>Perotis rara</i>	JN192385	KJ415394	JN601021
<i>C. petersonii</i>	BRIP 14642 <sup>T</sup>	Australia	<i>Dactyloctenium aegyptium</i>	MH414905	MH433667	MH433668
<i>C. pisi</i>	CBS 190.48 <sup>T</sup>	Canada	<i>Pisum sativum</i>	KY905678	KY905690	KY905697
<i>C. platzii</i>	BRIP 27703b <sup>T</sup>	Australia	<i>Cenchrus clandestinum</i>	MH414906	MH433651	MH433669
<i>C. portulacae</i>	BRIP 14541 <sup>isoT</sup>	USA	<i>Portulaca oleracea</i>	KJ415553	KJ415393	KJ415440
<i>C. prasadii</i>	CBS 143.64 <sup>T</sup>	India	<i>Jasminum sambac</i>	KJ922373	KM061785	KM230408
<i>C. protuberata</i>	CBS 376.65 <sup>T</sup>	Scotland	<i>Deschampsia flexuosa</i> leaf	KJ922376	KM083605	KM196576
<i>C. pseudobrachyspora</i>	CPC 28808 <sup>T</sup>	Thailand	<i>Eleusine indica</i>	MF490819	MF490819	MF490819
	CBS 207.59	Unknown	Unknown	<b>MN688812</b>	<b>MN688839</b>	<b>MN688865</b>
	CBS 533.70	Denmark	<i>Pennisetum</i> sp. seed	<b>MN688813</b>	<b>MN688840</b>	<b>MN688866</b>
	CBS 336.64	USA	<i>Trisetum</i> sp.	<b>MN688814</b>	<b>MN688841</b>	–
	CBS 337.64	USA	<i>Agropyron repens</i>	<b>MN688815</b>	<b>MN688842</b>	<b>MN688867</b>
	CBS 339.64	USA	<i>Pennisetum glaucum</i>	<b>MN688816</b>	<b>MN688843</b>	<b>MN688868</b>
	MFLUCC 10-0739	Thailand	<i>Oryza sativa</i>	JX256443	JX276454	JX266603
	HNWN001	China	<i>Areca catechu</i> leaf	MH516132	MH516133	MH516134
<i>C. pseudoclavata</i>	CBS 539.70 <sup>T</sup>	Denmark	<i>Oryza sativa</i> seeds	<b>MN688817</b>	<b>MN688844</b>	<b>MN688869</b>
<i>C. pseudoellisii</i>	CBS 298.80 <sup>T</sup>	Sudan	<i>Sorghum bicolor</i> seed	<b>MN688818</b>	<b>MN688845</b>	<b>MN688870</b>
<i>C. pseudointermedia</i>	CBS 553.89 <sup>T</sup>	Brazil	Cultivated pasture soil	<b>MN688819</b>	<b>MN688846</b>	<b>MN688871</b>
	CBS 188.61	Guadeloupe	Decaying grass	<b>MN688820</b>	<b>MN688847</b>	<b>MN688872</b>
<i>C. pseudolunata</i>	UTHSC 09-2092 <sup>T</sup>	USA	Nasal sinus	HE861842	HF565459	–
<i>C. pseudoprotuberata</i>	CBS 385.69 <sup>T</sup>	Canada	Soil under <i>Thuja occidentalis</i>	<b>MN688821</b>	<b>MN688848</b>	<b>MN688873</b>
	CBS 550.69	Canada	Soil under <i>Pinus strobus</i>	<b>MN688822</b>	<b>MN688849</b>	<b>MN688874</b>
<i>C. pseudorobusta</i>	UTHSC 08-3458	USA	Nasal sinus	HE861838	HF565476	–
<i>C. ravenelii</i>	BRIP 13165 <sup>T</sup>	Australia	<i>Sporobolus fertilis</i>	JN192386	JN600978	JN601024
<i>C. reesii</i>	BRIP 4358 <sup>T</sup>	Australia	Air	MH414907	MH433637	MH433670
<i>C. richardiae</i>	BRIP 4371 <sup>isoLT</sup>	Australia	<i>Richardia brasiliensis</i>	KJ415555	KJ415391	KJ415438

**Table 1** (continued)

Species	Isolates <sup>a</sup>	Country	Substrate	GenBank accession numbers <sup>b</sup>		
				ITS	GAPDH	TEF1
<i>C. robusta</i>	CBS 624.68 <sup>IsoT</sup>	USA	<i>Dichanthium annulatum</i>	KJ909783	KM083613	KM196577
<i>C. rouhaniai</i>	CBS 144674 <sup>T</sup>	Iran	Blighted leaves of <i>Syngonium vellozianum</i>	KX139030	MG428694	MG428687
<i>C. ryleyi</i>	BRIP 12554 <sup>T</sup>	Australia	<i>Sporobolus creber</i>	KJ415556	KJ415390	KJ415437
<i>C. senegalensis</i>	CBS 149.71	Nigeria	Unknown	HG779001	HG779128	–
<i>C. sesuvi</i>	Bp-Zj 01	Unknown	<i>Sesuvium</i> sp.	EF175940	–	–
<i>C. shahidchamranensis</i>	IRAN 3133C <sup>T</sup>	Iran	Soil	MH550084	MH550083	–
<i>C. sichuanensis</i>	HSAUP II.2650-1 <sup>T</sup>	China	Undetermined plant of Gramineae	AB453881	–	–
<b><i>C. siddiquii</i></b>	CBS 196.62 <sup>T</sup>	Pakistan	Air	<b>MN688823</b>	<b>MN688850</b>	–
	CBS 142.78	Egypt	Unknown	<b>MN688824</b>	<b>MN688851</b>	–
<i>C. soli</i>	CBS 222.96 <sup>T</sup>	Papua New Guinea	Soil	KY905679	KY905691	KY905698
<i>C. sorghina</i>	BRIP 15900 <sup>IsoT</sup>	Australia	<i>Sorghum bicolor</i>	KJ415558	KJ415388	KJ415435
<i>C. spicifera</i>	CBS 274.52	Spain	Soil	JN192387	JN600979	JN601023
<i>C. sporobolcola</i>	BRIP 23040b <sup>T</sup>	Australia	<i>Sporobolus australasicus</i>	MH414908	MH433652	MH433671
<i>C. subpapendorffii</i>	CBS 656.74 <sup>T</sup>	Egypt	Desert soil	KJ909777	KM061791	KM196585
<i>C. thailandica</i>	MFLUCC 15-0747 <sup>T</sup>	Thailand	Dead leaf of <i>Pandanus</i> sp.	MH275057	MH412749	MH412764
<b><i>C. tribuli</i></b>	CBS 126975 <sup>T</sup>	South Africa	<i>Tribulus terrestris</i> leaf	<b>MN688825</b>	<b>MN688852</b>	<b>MN688875</b>
<i>C. trifolii</i>	CBS 173.55	USA	<i>Trifolium repens</i>	HG779023	HG779124	–
<i>C. tripogonis</i>	BRIP 12375 <sup>T</sup>	Australia	Unknown	JN192388	JN600980	JN601025
<i>C. tropicalis</i>	BRIP 14834 <sup>IsoT</sup>	India	<i>Coffea arabica</i>	KJ415559	KJ415387	KJ415434
<i>C. tsudae</i>	ATCC 44764 <sup>PT</sup>	Japan	<i>Chloris gayana</i>	KC424596	KC747745	KC503940
<i>C. tuberculata</i>	CBS 146.63 <sup>IsoT</sup>	India	<i>Zea mays</i>	JX256433	JX276445	JX266599
<i>C. uncinata</i>	CBS 221.52 <sup>T</sup>	Vietnam	<i>Oryza sativa</i>	HG779024	HG779134	–
<i>C. variabilis</i>	CPC 28815 <sup>T</sup>	Thailand	<i>Chloris barbata</i>	MF490822	MF490844	MF490865
<i>C. verruciformis</i>	CBS 537.75	New Zealand	<i>Lobibyx</i> (masked plover) feather	HG779026	HG779133	HG779211
<i>C. verrucosa</i>	CBS 422.93	Cuba	Air	<b>MN688826</b>	<b>MN688853</b>	<b>MN688876</b>
<i>C. verruculosa</i>	CBS 150.63	India	<i>Punica granatum</i>	KP400652	KP645346	KP735695
<i>C. warraberensis</i>	BRIP 14817 <sup>T</sup>	Australia	<i>Dactyloctenium aegyptium</i>	MH414909	MH433653	MH433672
<i>C. xishuangbannaensis</i>	MFLUCC 17-2271 <sup>T</sup>	Thailand	Dead leaf of <i>Pandanus</i> sp.	MH275058	MH412750	MH412765
<i>Exserohilum rostratum</i>	CBS 325.87	USA	<i>Homo sapiens</i>	HE664035	LT715898	HE664082
<i>E. turcicum</i>	CBS 690.71 <sup>ET</sup>	Germany	<i>Zea mays</i>	LT837487	LT882581	LT896618
<i>Johnalcornia aberrans</i>	CBS 510.91 <sup>IsoT</sup>	Australia	<i>Eragrostis parviflora</i>	KJ415522	KJ415424	KJ415473
	CBS 281.91	Australia	Unknown	<b>MN688827</b>	<b>MN688854</b>	<b>MN688877</b>
<i>Pyrenophora phaeocomes</i>	DAOMC 222769	Switzerland	<i>Calamagrostis villosa</i>	JN943649	–	DQ497607
<i>P. poae</i>	BRIP 10953	Australia	Member of Poaceae	KJ415566	KJ415380	KJ415427
<i>P. seminiperda</i>	BRIP 10941	Australia	<i>Triticum aestivum</i>	KJ415564	KJ415382	KJ415429

<sup>a</sup> ATCC, American Type Culture Collection, Virginia, USA; BRIP, Queensland Plant Pathology Herbarium, Brisbane, Australia; Bp-Zj, isolate housed in Biotechnology Institute, Zhejiang University, Hangzhou, China; CBS, Westerdijk Fungal Biodiversity Institute, Utrecht, the Netherlands; CPC, culture collection of Pedro Crous, housed at the Westerdijk Fungal Biodiversity Institute; DAOMC, Plant Research Institute, Department of Agriculture (Mycology), Ottawa, Canada; GUCC, Culture collection at the Department of Plant Pathology, Agriculture College, Guizhou University, China; HSAUP, Herbarium of the Department of Plant Pathology of Shandong Agricultural University, Shandong, China; IMI, International Mycological Institute, CABI-Bioscience, Egham, Bakenham Lane, UK; IRAN, Iranian Fungal Culture Collection, Iranian Research Institute of Plant Protection, Tehran, Iran; MFLUCC, Mae Fah Luang University Culture Collection, Chiang Rai, Thailand; UTHSC, Fungus Testing Laboratory, Department of Pathology at the University of Texas Health Science Center, San Antonio, Texas, USA; DB13GEN09, isolate housed in Italy; HNWN001, isolate housed in China; strains 737, 738, 739: isolates housed in Florida. <sup>ET</sup>, <sup>IsoT</sup>, <sup>IsoLT</sup>, <sup>PT</sup>, <sup>R</sup>, <sup>SynT</sup> and <sup>T</sup> indicate ex-epitype, ex-isotype, ex-isolectotype, ex-paratype, reference, ex-syntype and ex-type strains, respectively

<sup>b</sup> ITS, internal transcribed spacers and intervening 5.8S nrDNA; GAPDH, partial glyceraldehyde-3-phosphate dehydrogenase gene; TEF1, partial translation elongation factor 1-alpha gene

Microbial DNA Isolation kit (MoBio Laboratories, Inc., Solana Beach, CA, USA) and Wizard® Genomic DNA purification kit (Promega, Madison, USA) protocols.

The amplification of the ITS and fragments of the *GAPDH* and *TEF1* genes was performed for the selected strains, according to White et al. (1990) (ITS) and Manamgoda et al. (2012) (*GAPDH* and *TEF1*).

## Phylogenetic study

The phylogenetic analysis based on ITS, *GAPDH* and *TEF1* was carried out, including strains available in the CBS collection and sequences of ex-type and reference strains of *Curvularia* spp. available in GenBank (Table 1). Each locus was aligned separately using MAFFT v. 7 (Kato and Standley 2013) and manually adjusted in MEGA v. 6.06 (Tamura et al. 2013). The maximum likelihood (ML) and Bayesian inference (BI) were performed for the combined dataset using RAxML as was described by Hernández-Restrepo et al. (2016). The sequences generated in this study were deposited in GenBank, and the alignments in TreeBASE ([www.treebase.org](http://www.treebase.org), S23887).

## Results

The lengths of the fragments of the three genes used in the combined dataset were 505 bp (ITS), 477 bp (*GAPDH*) and 892 bp (*TEF1*). The length of the final alignment was 1874 bp. The consensus tree obtained from the RAxML analysis of the combined dataset is shown in Fig. 1, which agreed with the topology of the Bayesian analysis. It includes RAxML bootstrap support (BS) and Bayesian posterior probability at the nodes. In the combined phylogenetic tree (Fig. 1), species of *Curvularia* formed a supported clade (92% bs/1 pp) clearly separated from other gramicolous helminthosporioid genera included in the phylogenetic study, i.e. *Bipolaris*, *Exserohilum*, *Johnalcornia* and *Pyrenophora*.

Seventeen strains included in the phylogenetic study were located in ten independent branches from other species of *Curvularia*. The morphological study of these strains revealed enough differences to propose ten new species, i.e. *C. arcana*, *C. austriaca*, *C. canadensis*, *C. ellisii*, *C. pseudoclavata*, *C. pseudoellisii*, *C. pseudointermedia*, *C. pseudoprotuberata*, *C. siddiquii* and *C. tribuli*.

Interestingly, CBS 198.87, the ex-type strain of *Drechslera patereae*, was located in the main clade representing the genus *Curvularia*. Therefore, a new combination is proposed in the taxonomy section. Moreover, five different isolates identified as *Bipolaris cactivora* were located in a fully supported subclade (100% bs/

1 pp) within the *Curvularia* clade. Based on sequence similarities and morphological data, the new combination *C. cactivora* is also proposed.

The ex-type isolate (CBS 193.62) of the currently invalid *C. ellisii*, which is validly redescribed below, and the isolate CBS 127083 (obtained from a sexual cross) were located in a well-supported clade (86% bs/1 pp).

Finally, seven strains, CBS 207.59, CBS 533.70, CBS 336.64, CBS 337.64, CBS 339.64, MFLUCC 10-0739 and HNWN001, were located in a clade (89% bs/– pp) together with CPC 28808, the ex-type strain of *C. pseudobrachyspora*. Strain CBS 533.70 was found to differ morphologically from the ex-type strain, and thus, the original description is herewith emended, and new host and distribution reports are included.

## Taxonomy

***Curvularia arcana*** Hern.-Restr. & Y. Marín, sp. nov. Fig. 2.

**MB832460**

*Etymology.* Name refers to the mystery of the origin of the ex-type strain.

*Holotype.* Unknown data, CBS H-24098.

*Ex-type strain.* CBS 127224.

**Asexual morph on PDA** *Hyphae* hyaline to pale brown, branched, septate, smooth-walled, 1–3 µm. *Conidiophores* single or in small groups, semi- to macronematous, septate, sometimes reduced to conidiogenous cells, straight to flexuous, geniculate, branched, cell walls thicker than those of vegetative hyphae, mononematous, pale brown to brown, not swollen at the base, 8–93 × 2–4 µm. *Conidiogenous cells* smooth-walled, terminal or intercalary, proliferating sympodially, pale brown to brown, subcylindrical to slightly swollen, 4–15 × 1.5–4 µm. *Conidia* smooth-walled, straight, sometimes curved, ellipsoidal to ovoid, pale brown to brown, (1)3–4-distoseptate, 10.5–28 × 6–9(11.5) µm; *hila* protruding, flat, darkened, thickened, 1–1.5 µm wide. *Chlamydospores*, *microconidiation* and *sexual morph* not observed.

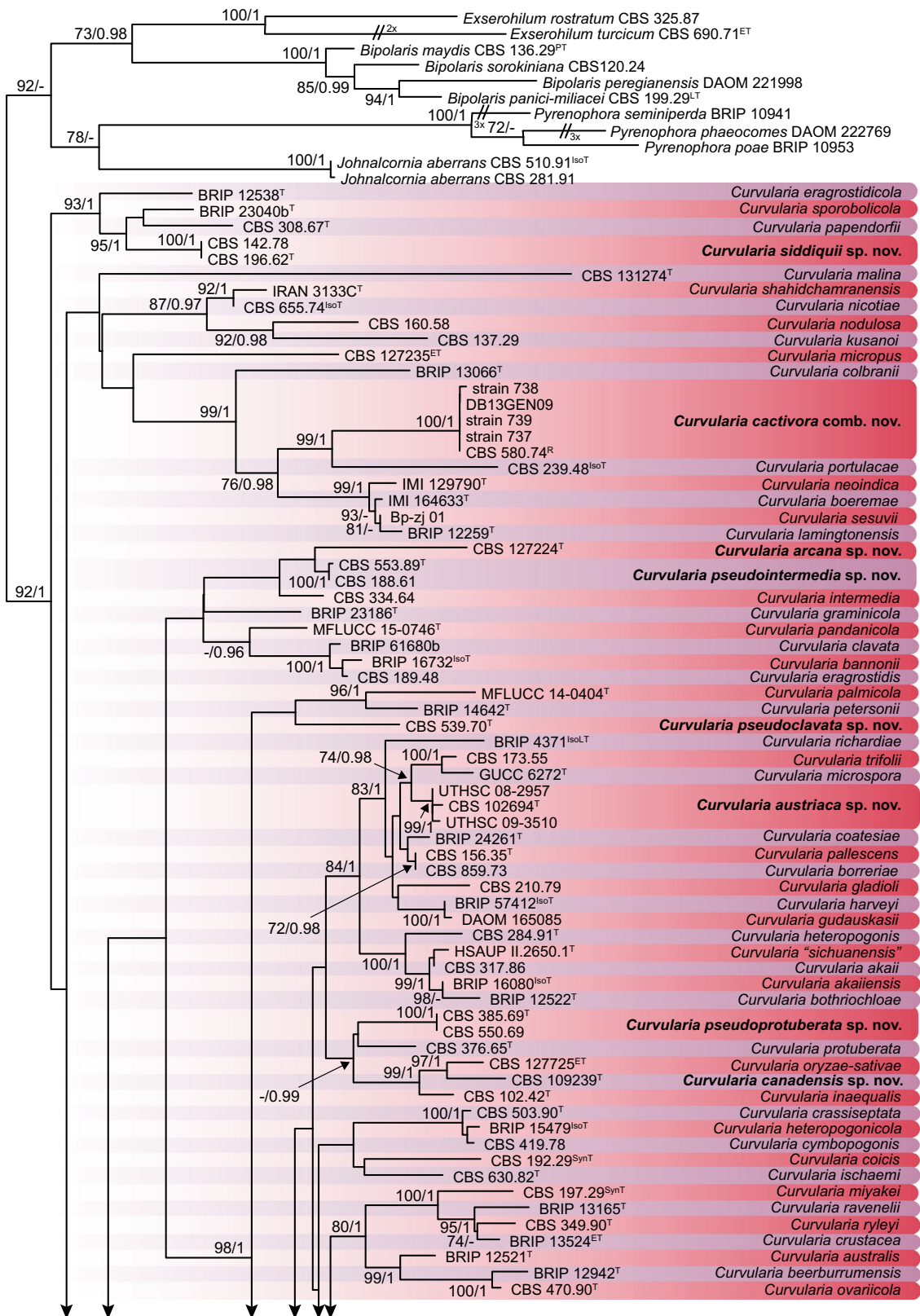
**Culture characteristics** Colonies on PDA reaching 62–70 mm diam in 1 week, smoke grey to olivaceous black, with moderate aerial mycelium giving the colony a cottony appearance, margin fimbriate to lobate; reverse olivaceous black.

**Notes** In our phylogenetic study, *C. arcana* was located on an independent branch representing a new species (Fig. 1). Regrettably, no data about the ex-type strain are available. *Curvularia arcana* is located in a basal clade that includes *C. intermedia* and *C. pseudointermedia* (Fig. 1). For morphological differences, see notes under *C. pseudointermedia*.

***Curvularia austriaca*** Y. Marín & Crous, sp. nov. Fig. 3.

**MB830045**

*Etymology.* Named after the country where the type material was collected, Austria.



**Fig. 1** RAxML phylogram obtained from the combined ITS, *GAPDH* and *TEF1*, sequences of strains belonging to the genus *Curvularia*. The tree was rooted to other members of Pleosporaceae, i.e. *Bipolaris* spp., *Exserohilum* spp., *Pyrenophora* spp. and *Johnalcornia aberrans*. The novelties proposed in this study are shown in bold. RAxML bootstrap

support (BS) values above 70% and Bayesian posterior probability scores above 0.95 are shown at the nodes. <sup>ET</sup>, <sup>ISO</sup>, <sup>ISO</sup>LT, <sup>PT</sup>, <sup>R</sup>, <sup>SYNT</sup> and <sup>T</sup> indicate ex-epitype, ex-isotype, ex-isolectotype, ex-paratype, reference, ex-syntype and ex-type strains, respectively

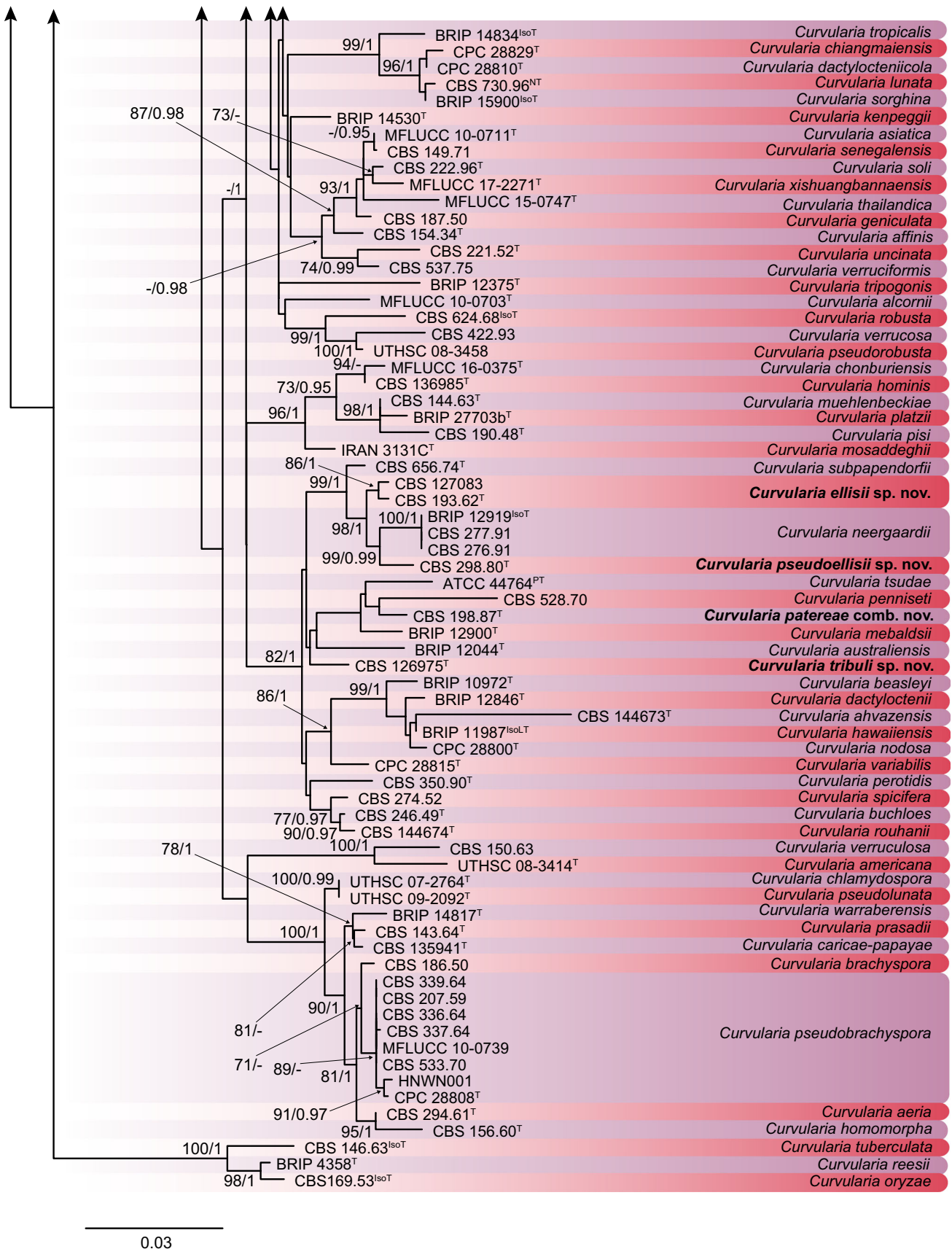


Fig. 1 (continued)





**Fig. 2** *Curvularia arcana* (CBS 127224 ex-type). **a–c** Conidiophores, conidiogenous cells and conidia; **d–g** conidia. Scale bars **a–c** = 10  $\mu\text{m}$ ; **j** = 5  $\mu\text{m}$ , **j** applies to **d–j**

*Holotype*. Austria: Graz, from a nasal cavity of patient with sinusitis, 28 Aug. 1968, W. Buzina, CBS H-24091.

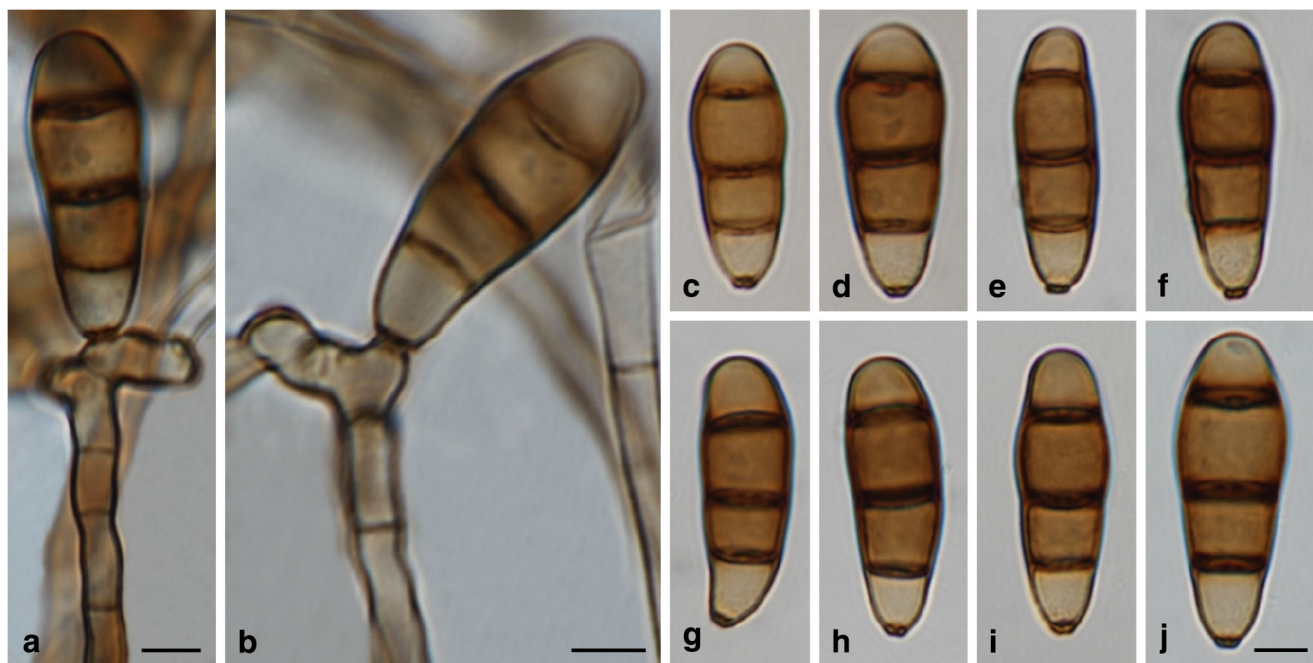
*Ex-type strain*. CBS 102694.

*Additional material examined*. USA: West Virginia, corneal ulcer, D.A. Sutton, UTHSC 08-2957 = FMR 11669. Washington, District of Columbia, peritoneal dialysis fluid, D.A. Sutton, UTHSC 09-3510 = FMR 11507.

**Asexual morph on OA** *Hyphae* subhyaline to pale brown, branched, septate, thick-walled, 2–4.5  $\mu\text{m}$ . *Conidiophores* arising in groups, mononematous, semi- to macronematous, septate, straight to flexuous, mostly geniculate at upper part, not swollen at the base, cell size not decreasing towards apex, rarely branched, cell walls thicker than those of vegetative hyphae, pale brown, rarely brown, not paler towards apex,

60–260  $\times$  2.5–5(6.5)  $\mu\text{m}$ . *Conidiogenous cells* smooth-walled, terminal or intercalary, proliferating sympodially, pale brown, rarely brown, subcylindrical to slightly swollen, 5–13(14)  $\times$  4–6  $\mu\text{m}$ . *Conidia* smooth-walled to finely verruculose, straight or slightly curved, ellipsoidal to ovoid, middle cells slightly enlarged, pale brown to brown, apical and basal cells paler, (2)3-distoseptate, (20.5)23–32  $\times$  7.5–12.5(13.5)  $\mu\text{m}$ ; *hila* protuberant, darkened, thickened, 2–3  $\mu\text{m}$  wide. *Chlamydospores*, *microconidiation* and *sexual morph* not observed.

**Culture characteristics** Colonies on PDA reaching 75–90 mm diam in 1 week, luteous to orange, umber in the centre, with moderate aerial mycelium giving the colony a slightly cottony appearance, lobulate; reverse luteous to orange.



**Fig. 3** *Curvularia austriaca* (CBS 102694 ex-type). **a, b** Conidiogenous cells and conidia; **c–j** conidia. Scale bars 5  $\mu\text{m}$ , **j** applies to **c–j**

**Notes** *Curvularia austriaca* is related to *C. borrieriae*, *C. coatesiae*, *C. microspora*, *C. pallescens* and *C. trifolii*. These species all primarily produce 3-distoseptate conidia. *Curvularia coatesiae* and *C. microspora* differ from *C. austriaca* in producing smaller conidia [(20.5)23–32  $\times$  7.5–12.5(13.5)  $\mu\text{m}$  in *C. austriaca* vs (20)23–26(30)  $\times$  (7)8–9(10)  $\mu\text{m}$  in *C. coatesiae* vs 4.5–11.5  $\times$  2–6  $\mu\text{m}$  in *C. microspora*], while *C. borrieriae* produces thicker conidia (up to 15  $\mu\text{m}$ ). *Curvularia trifolii* differs from *C. austriaca* in producing longer conidiophores (up to 400  $\mu\text{m}$ ) and more protuberant conidial hila, while *C. pallescens* can be distinguished by its pale to somewhat coloured, almost concolorous conidia. The three strains belonging to *C. austriaca* were isolated from human clinical specimens, while the other species are associated with plant hosts, air or soil (Manamgoda et al. 2014; Tan et al. 2018; Farr and Rossman 2019).

***Curvularia cactivora*** (Petr.) Y. Marín & Crous, comb. nov. Fig. 4.

**MB832462**

**Basionym.** *Helminthosporium cactivorum* Petr., Gartenbauwissenschaft 5: 226 (1931).

**Synonyms.** *Drechslera cactivora* (Petr.) M.B. Ellis, Dematiaceous Hyphomycetes (Kew): 432 (1971).

*Bipolaris cactivora* (Petr.) Alcorn, Mycotaxon 17: 67 (1983).

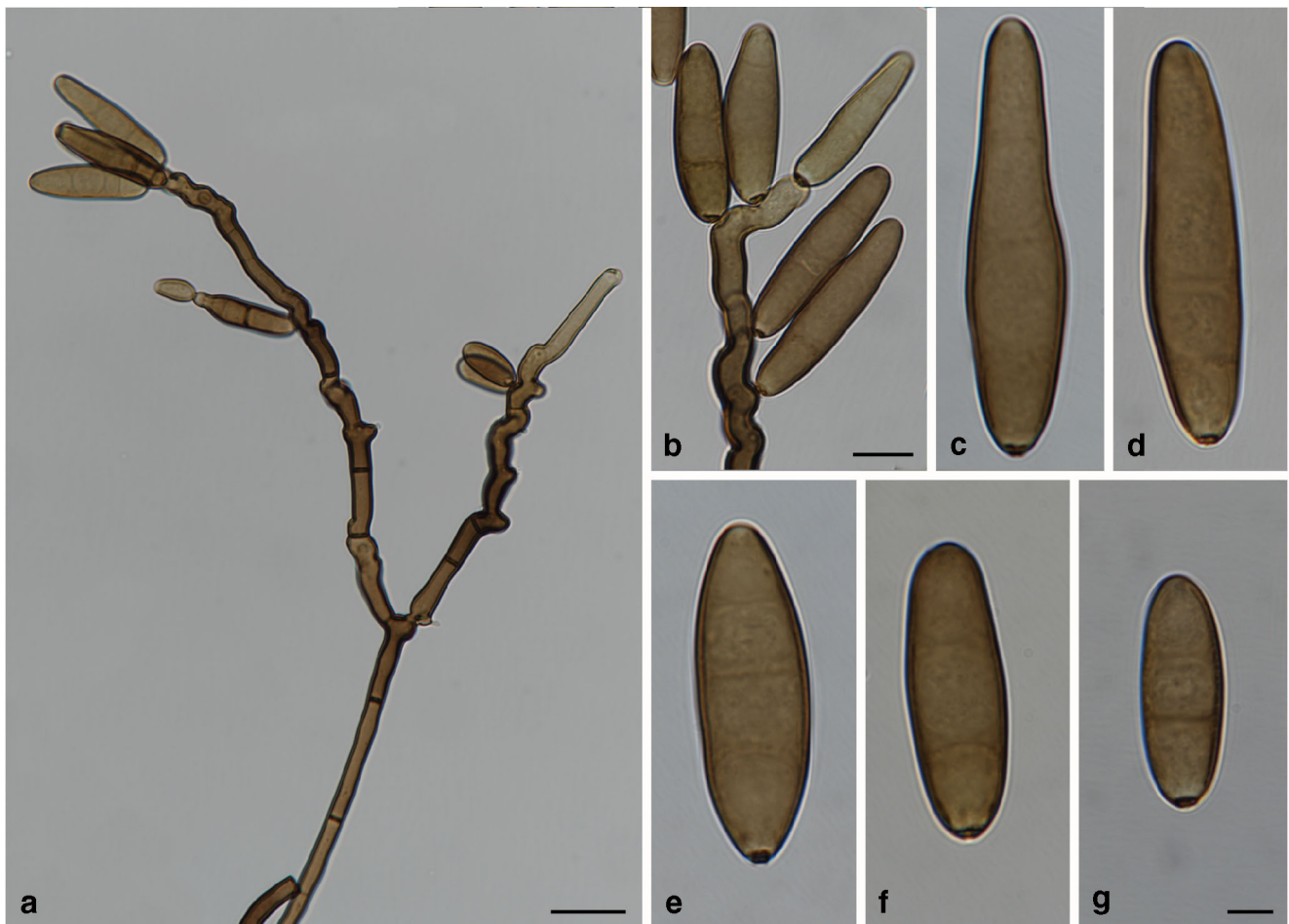
**Reference strain:** Republic of Suriname: on Cactaceae, isol. J.H. van Emden, CBS 580.74 (reference strain designated here).

**Asexual morph on PDA** *Hyphae* hyaline, branched, septate, thin-walled, 2.5–5.5  $\mu\text{m}$ . *Conidiophores* arising in groups,

mononematous, macronematous, rarely semimacronematous, septate, straight or flexuous, geniculate at upper part, cell size decreasing towards apex, irregularly branched, cell walls thicker than those of vegetative hyphae, pale brown to brown, paler towards apex, up to 1000  $\mu\text{m}$  long. *Conidiogenous cells* smooth-walled, terminal or intercalary, proliferating sympodially, pale brown to brown, subcylindrical to slightly swollen, (10)14–50(60)  $\times$  4.5–10(20)  $\mu\text{m}$ . *Conidia* smooth-walled, straight, rarely curved, ellipsoidal to obclavate, rarely irregular, subhyaline, becoming pale brown to brown when mature, 0–3(5)-distoseptate, (18)26–51  $\times$  6.5–14  $\mu\text{m}$ ; *hila* protuberant, darkened, thickened, 2–4  $\mu\text{m}$  wide. *Chlamydospores*, *microconidiation* and *sexual morph* not observed.

**Culture characteristics** Colonies on PDA covering the surface of the Petri dish in 1 week, olivaceous to dark olivaceous, margin hyaline, powdery to granular, abundantly sporulating; reverse grey olivaceous to olivaceous black, margin hyaline.

**Notes** *Curvularia cactivora* was originally described in *Helminthosporium* (Petrak 1931). Later, it was transferred to *Drechslera* (Ellis 1971), and then to *Bipolaris* (Alcorn 1983a). In the most recent revision of the genus *Bipolaris*, Manamgoda et al. (2014) considered the placement of this species as doubtful since it is morphologically similar to *C. hawaiiensis*. However, they did not include sequence data of this species at the time, and its placement in *Curvularia* could not be demonstrated. The type specimen of this species could not be located. It was isolated from a member of the Cactaceae in



**Fig. 4** *Curvularia cactivora* (CBS 580.74 reference strain). **a** Conidiophore, conidiogenous cells and conidia; **b** conidiogenous cells and conidia; **c–g** conidia. Scale bars **a** 20  $\mu\text{m}$ ; **b** 10  $\mu\text{m}$ ; **g** 5  $\mu\text{m}$ , **g** applies to **c–g**

Moravia, Czech Republic (Petrak 1931). In the present study, CBS 580.74 is considered as a reference strain since it was also isolated from a member of the Cactaceae, and its morphology fits with the original description. The only difference found with the original description (Petrak 1931) and the description available in Ellis (1971) is the conidiophore size (up to 1000  $\mu\text{m}$  in our study vs 280  $\mu\text{m}$  in Petrak 1931 vs 280  $\mu\text{m}$  in Ellis 1971). Our phylogenetic study (Fig. 1) places this species in *Curvularia*. It grouped with other strains identified as *C. cactivora*, i.e. DB13GEN09, 737, 738 and 739, whose morphology fits with the original description of this species, three of them (737, 738, 739) causing fruit rot on *Hylocereus undatus* (Cactaceae) in South Florida (Tarnowski et al. 2010), and the other (DB13GEN09) causing stem rot on *Cereus peruvianus* var. *monstruosus* (Cactaceae) in Italy (Garibaldi et al. 2014). In all these strains, the conidiophore size is similar to that mentioned in the original description, being up to 313  $\mu\text{m}$  long in the strains from South Florida, and up to

176  $\mu\text{m}$  long in the strain from Italy (Tarnowski et al. 2010; Garibaldi et al. 2014).

***Curvularia canadensis*** Y. Marín & Crous, sp. nov. Fig. 5. MB830047

*Etymology.* Named after the country where the material was collected, Canada.

*Holotype.* Canada: Vancouver, Acadia park (the campus of UBC), from overwintered grass, Sep. 2000, G. Zhang, CBS H-24092.

*Ex-type strain.* CBS 109239.

**Asexual morph on PDA** *Hyphae* hyaline to subhyaline, branched, septate, thin-walled, 1.5–5  $\mu\text{m}$ . *Conidiophores* arising in groups, mononematous, macronematous, septate, flexuous, rarely straight, geniculate at upper part, cell size not decreasing towards apex, frequently 2–3-branched, cell walls thicker than those of vegetative hyphae, pale brown to brown, paler towards apex, not swollen at the base, 65–220  $\times$  3–6  $\mu\text{m}$ . *Conidiogenous cells* smooth-walled, terminal or intercalary, proliferating sympodially, pale brown to brown, subcylindrical



**Fig. 5** *Curvularia canadensis* (CBS 109239 ex-type). **a–c** Conidiophores, conidiogenous cells and conidia; **d** conidiogenous cells and conidia; **e–i** conidia. Scale bars **a, b** = 10  $\mu\text{m}$ ; **c–i** = 5  $\mu\text{m}$

to swollen,  $5.5\text{--}16 \times 4.5\text{--}9 \mu\text{m}$ . *Conidia* finely verruculose, straight to curved, middle cells disproportionately enlarged, ellipsoidal to broadly ellipsoidal or ovoid, brown, apical cells paler than middle cells being subhyaline to pale brown, (1)3–4-distoseptate,  $12\text{--}36 \times 8\text{--}16.5(19) \mu\text{m}$ ; *hila* protuberant, darkened, thickened,  $1.5\text{--}3 \mu\text{m}$  wide. *Chlamydozoospores*, *microconidiation* and *sexual morph* not observed.

**Culture characteristics** Colonies on PDA reaching 58–60 mm diam in 1 week, powdery, greenish black, margin fimbriate; reverse olivaceous black.

**Notes** *Curvularia canadensis* formed a clade separate from the other *Curvularia* spp., with *C. oryzae-sativae* being its closest relative. Both species were found on grass, which is the common host of *Curvularia* spp., but *C. canadensis* was collected in Canada, while *C. oryzae-sativae* was reported only in Argentina. Morphologically, *C. oryzae-sativae* can be easily distinguished by its mostly straight conidia with the middle cells not as enlarged as in *C. canadensis*, and with

more distosepta [3–8 (mostly 6–7) in *C. oryzae-sativae* vs (1)3–4 in *C. canadensis*].

***Curvularia crassiseptata*** Meng Zhang & T.Y. Zhang, Mycosystema 23: 177 (2004) (as ‘crassiseptum’). Fig. 6.

*Replaced synonym.* *Exserohilum inaequale* Sivan., Trans. Brit. Mycol. Soc. 83: 325 (1984), non *Curvularia inaequalis* (Shear) Boedijn (1907).

*Holotype.* Nigeria: from plant material, D.B. Olufolagi, IMI 280438.

*Ex-type strain.* CBS 503.90 = IMI 280438.

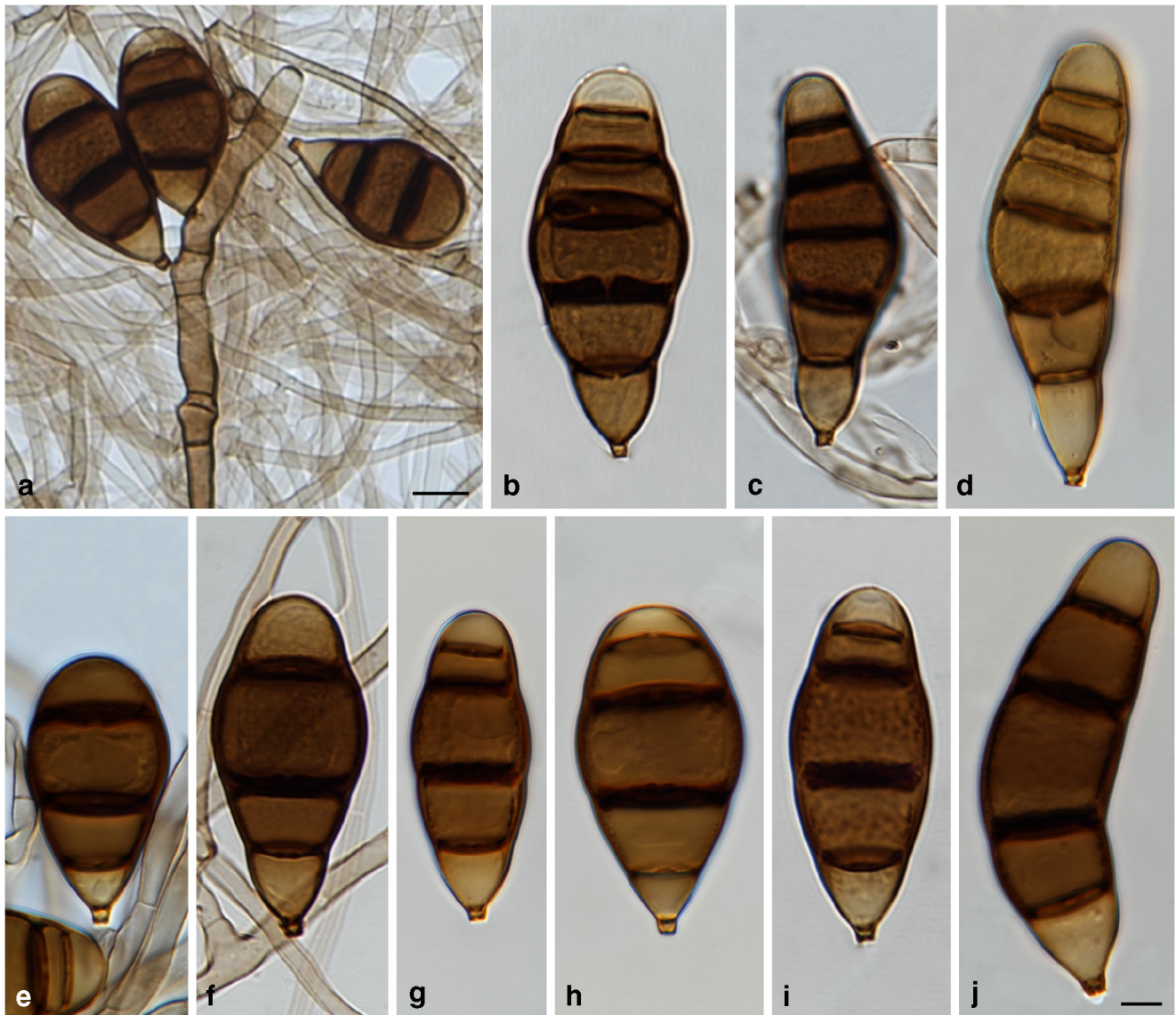
**Asexual morph on PDA** *Hyphae* subhyaline to pale brown, branched, septate, thin to thick-walled,  $(1.5)2\text{--}4(5) \mu\text{m}$ . *Conidiophores* arising single or in small groups, mononematous, semi- to macronematous, septate, straight or flexuous, sometimes geniculate at upper part, cell size not decreasing towards apex, unbranched, cell walls thicker than those of vegetative hyphae, pale brown to brown, paler

towards apex, up to 500  $\mu\text{m}$ . *Conidiogenous cells* smooth-walled to slightly verruculose, terminal or intercalary, sometimes proliferating sympodially, pale brown to brown, subcylindrical to slightly swollen, 7–26(28.5)  $\times$  5–8  $\mu\text{m}$ . *Conidia* smooth-walled to finely verruculose, straight or curved, ellipsoidal, broadly ellipsoidal or ovoid, middle cells enlarged, pale brown to brown, apical and basal cells usually paler, (2)3–5(6)-distoseptate, (25)33.5–50(60)  $\times$  (14)16–23.5  $\mu\text{m}$ ; *hila* protuberant, rarely darkened, thickened, 2–3.5(4)  $\mu\text{m}$  wide, 1.5–3  $\mu\text{m}$  long. *Chlamydozoospores*, *microconidiation* and *sexual morph* not observed.

**Culture characteristics** Colonies on PDA covering the surface of the Petri dish in 1 week, smoke grey to grey olivaceous, abundant aerial mycelium giving the colony a cottony appearance; reverse dark slate blue.

**Notes** This species was initially described as *Exserohilum inaequale*, due to the production of conidia with protuberant hila similar to those found in this genus (Sivanesan 1984). Subsequently, it was transferred to *Curvularia* changing the epithet to *C. crassiseptata* since *inaequale* was pre-occupied by another species (Zhang et al. 2004). Recently, the position of this species in *Curvularia* was confirmed by Hernández-Restrepo et al. (2018). In the present study, we provide a morphological description and illustrations of the type material.

*Curvularia crassiseptata* is located in a clade together with *C. cymbopogonis* and *C. heteropogonicola* (Fig. 1), all of which produce conidia with protuberant hila (Sivanesan 1984; Manamgoda et al. 2014). *Curvularia crassiseptata*



**Fig. 6** *Curvularia crassiseptata* (CBS 503.90 ex-type). **a** Conidiogenous cells and conidia; **b–j** conidia. Scale bars **a** 10  $\mu\text{m}$ ; **j** 5  $\mu\text{m}$ , **j** applies to **b–j**

differs from *C. heteropogoncola* by the size and septation of its conidia [(25)33.5–50(60) × (14)16–23.5 μm and (2)3–5(6)-distoseptate in *C. crassiseptata* vs 41–80 × 16–21 μm and 3–10-distoseptate in *C. heteropogoncola* (Sivanesan 1984)]. It can be distinguished from *C. cymbopogonis* by having (2)3–5(6)-distoseptate conidia, while those of *C. cymbopogonis* are 4-distoseptate (Manamgoda et al. 2014).

***Curvularia ellisii*** Y. Marín & Crous, sp. nov. Fig. 7.

**MB830048**

**Synonyms:** *Curvularia ellisii* S.I. Ahmad & Quraishi [as ‘ellisii’], Pakistan J. Sci. Industr. Res. 3: 177 (1960), nom. inval., Art. 39.1 (Melbourne).

*Drechslera ellisii* Danquah, Trans. Brit. Mycol. Soc. 64: 545 (1975).

*Bipolaris ellisii* (Danquah) Alcorn, Trans. Brit. Mycol. Soc. 81: 174 (1983).

*Cochliobolus ellisii* Alcorn, Trans. Brit. Mycol. Soc. 81: 172 (1983).

**Holotype.** Pakistan: Karachi, isolated from air, 1956, M.S. Quraishi, CBS 193.62 (specimen preserved as metabolically inactive strain).

**Ex-type strain.** CBS 193.62 = ATCC 14848 = IMI 75862 = QM 8355 = DAOM 155097.

**Additional material examined.** Australia: on *Dactyloctenium aegyptium* (Poaceae), 24 Dec. 1981, J.L. Alcorn, CBS 127083 = BRIP 13509a (derived from sexual morph, BRIP 13515).

**Asexual morph on PDA** *Hyphae* subhyaline to pale brown, branched, septate, 2–4 μm. *Conidiophores* arising in groups,

mononematous, semi- to macronematous, septate, straight or flexuous, geniculate at upper part, cell size not decreasing towards apex, branched, cell walls thicker than those of vegetative hyphae, pale brown to brown, paler towards apex, not swollen at the base, 45–700 × (2.5)4–7.5 μm. *Conidiogenous cells* verruculose, terminal or intercalary, proliferating sympodially, pale brown to brown, subcylindrical to swollen, 7.5–16.5 × 5–7.5(9) μm. *Conidia* verruculose, straight or curved, ovoid, pale brown to brown, paler towards hilum, (2)3–4(5)-distoseptate, (11.5)14–23.5(26) × (8)9.5–13(14.5) μm; *hila* flat to slightly protuberant, darkened, thickened, 2–4 μm wide. *Chlamydozoospores*, *microconidiation* and *sexual morph* not observed.

**Culture characteristics** Colonies on PDA reaching 57–61 mm diam in 1 week, fuscous olivaceous, fasciculate, margin fimbriate; reverse olivaceous black.

**Notes** *Curvularia ellisii* (Pakistan, isolated from air, ex-type CBS 193.62) was introduced by Ahmad and Quraishi (1960), but due to the lack of a Latin description, the name was invalid. Danquah (1975) again used this epithet for a species he described in *Drechslera* (Ghana, from *Capsicum* sp.), as *D. ellisii*. Alcorn (1983b) described *Cochliobolus ellisii* (Australia, on the leaves of *Zea mays*, BRIP 13633), which he considered the sexual morph of *D. ellisii* (as *Bipolaris ellisii* comb. nov.). Based on DNA sequence data, Manamgoda et al. (2012) used the name *Curvularia ellisii*, which is, however, invalid. Here we validate the original name, *C. ellisii*, based on the ex-type culture deposited by M.S. Quraishi, CBS 193.62.



**Fig. 7** *Curvularia ellisii* (CBS 127083). **a** Conidiophores, conidiogenous cells and conidia; **b** conidiogenous cells and conidia; **c–h** conidia. Scale bars **a**, **b** 10 μm; **h** 5 μm, **h** applies to **c–h**

*Curvularia ellisii* is related to *C. neergaardii* and *C. pseudoellisii*, another new species proposed in the present study (Fig. 1). See notes of the latter species for morphological differences among these taxa.

***Curvularia neergaardii*** (Danquah) Y.P. Tan & R.G. Shivas, Australas. Pl. Pathol. 43: 600 (2014). Fig. 8.

**Basionym.** *Drechslera neergaardii* Danquah, Trans. Brit. Mycol. Soc. 64: 545 (1975).

**Synonyms.** *Bipolaris neergaardii* (Danquah) Alcorn, Mycotaxon 17: 68 (1983).

*Cochliobolus neergaardii* Alcorn, Mycotaxon 39: 385 (1990).

**Holotype.** Ghana: from seeds of *Oryza sativa* (Poaceae), 1973, O.A. Danquah, IMI 174949.

**Ex-isotype strain.** BRIP 12919.

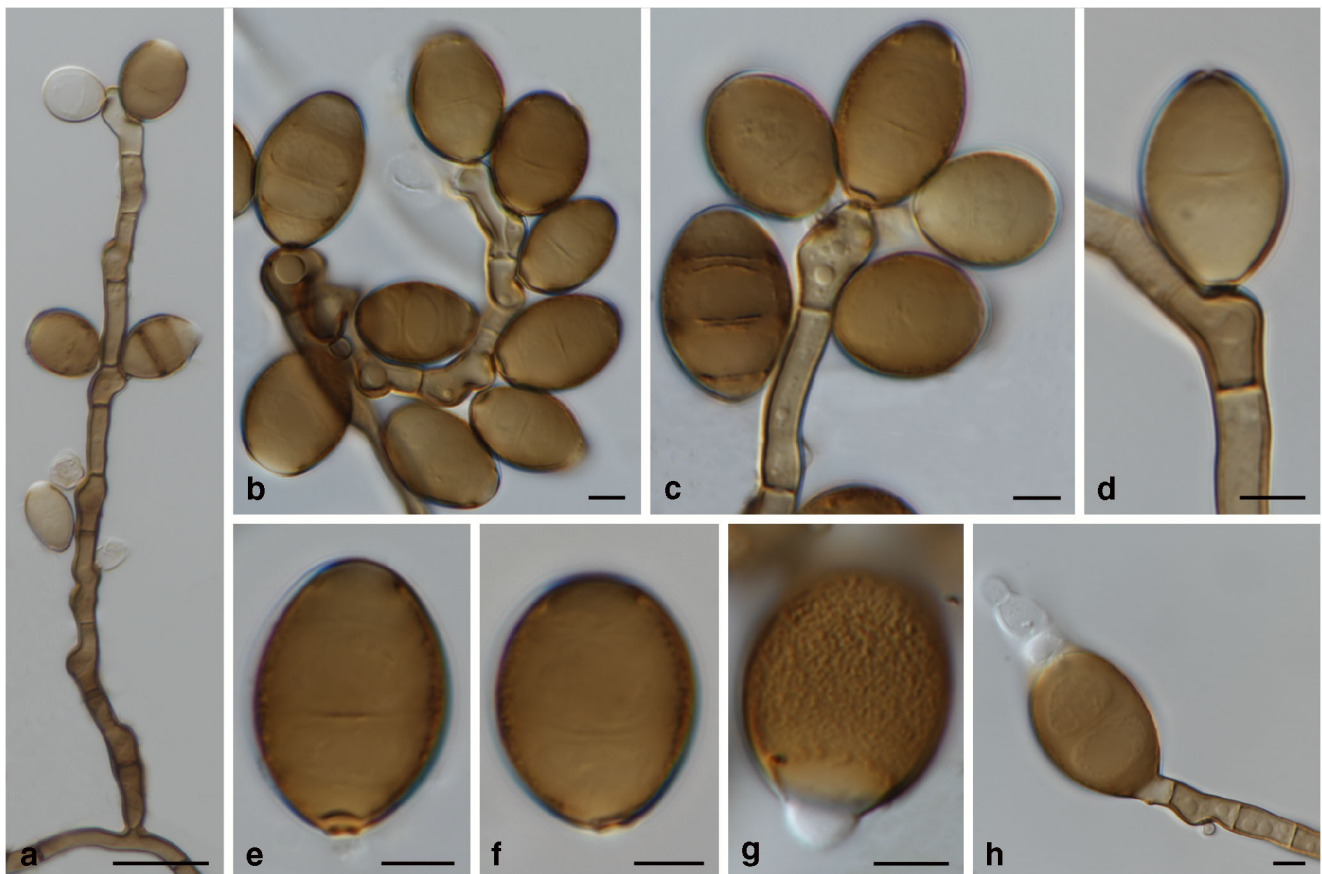
**Additional material examined.** Australia: Queensland, May 1985, J.L. Alcorn, CBS 276.91 = Alcorn 8509-2; CBS 277.91 = Alcorn 8509-3.

**Asexual morph on PDA** *Hyphae* hyaline to pale brown, branched, septate, thin-walled, 2–5.5  $\mu\text{m}$ . *Conidiophores* arising in groups, septate, mononematous, macronematous, straight or flexuous, geniculate at upper part, verruculose, cell

size not decreasing towards apex, sometimes branched, cell walls thicker than those of vegetative hyphae, pale brown to brown, paler towards apex, rarely slightly swollen at the base, 50–275(370)  $\times$  (1.8)2.5–5  $\mu\text{m}$ . *Conidiogenous cells* verruculose, terminal or intercalary, proliferating sympodially, pale brown to brown, subcylindrical to swollen, 5.5–17.5(19.5)  $\times$  4.5–7  $\mu\text{m}$ . *Conidia* verruculose, subglobose to broadly ellipsoidal, pale brown to brown, paler at both apices, 1–3-distoseptate, 14.5–24  $\times$  9.5–16  $\mu\text{m}$ ; *hila* sometimes inconspicuous, flat to slightly protuberant, darkened, thickened, 1–3  $\mu\text{m}$  wide. *Chlamydospores*, *microconidiation* and *sexual morph* not observed.

**Culture characteristics** Colonies on PDA reaching 53–59 mm diam in 1 week, olivaceous black with white to olivaceous grey zones, with sparse aerial mycelium, margin fimbriate; reverse olivaceous black to dark slate blue.

**Notes** *Curvularia neergaardii* was originally described in *Drechslera* by Danquah (1975), and subsequently transferred to *Bipolaris* (Alcorn 1983a). Finally, Tan et al. (2014) placed this taxon in *Curvularia* based on sequence data obtained from the ex-type strain. Alcorn (1990) described the sexual morph as *Cochliobolus neergaardii*, which is now a synonym of *C. neergaardii* based on the new fungal nomenclature (Tan



**Fig. 8** *Curvularia neergaardii* (CBS 277.91). **a** Conidiophore, conidiogenous cells and conidia; **b–d** conidiogenous cells and conidia; **e–g** conidia; **h** germinating conidium. Scale bars **a** 20  $\mu\text{m}$ , all others 5  $\mu\text{m}$ . Pictures **a** and **h** taken from Marin-Felix et al. (2017a)

et al. 2014). In the present study, we provide a description and illustrations of the asexual morph of this species (Fig. 8).

*Curvularia neergaardii* is related to the new species *C. pseudoellisii* and *C. ellisii*, both proposed in the present study (Fig. 1). For a morphological comparison, see notes of *C. pseudoellisii*.

***Curvularia oryzae*** Bugnic., Rev. Gén. Bot. 57: 69 (1950). Fig. 9.

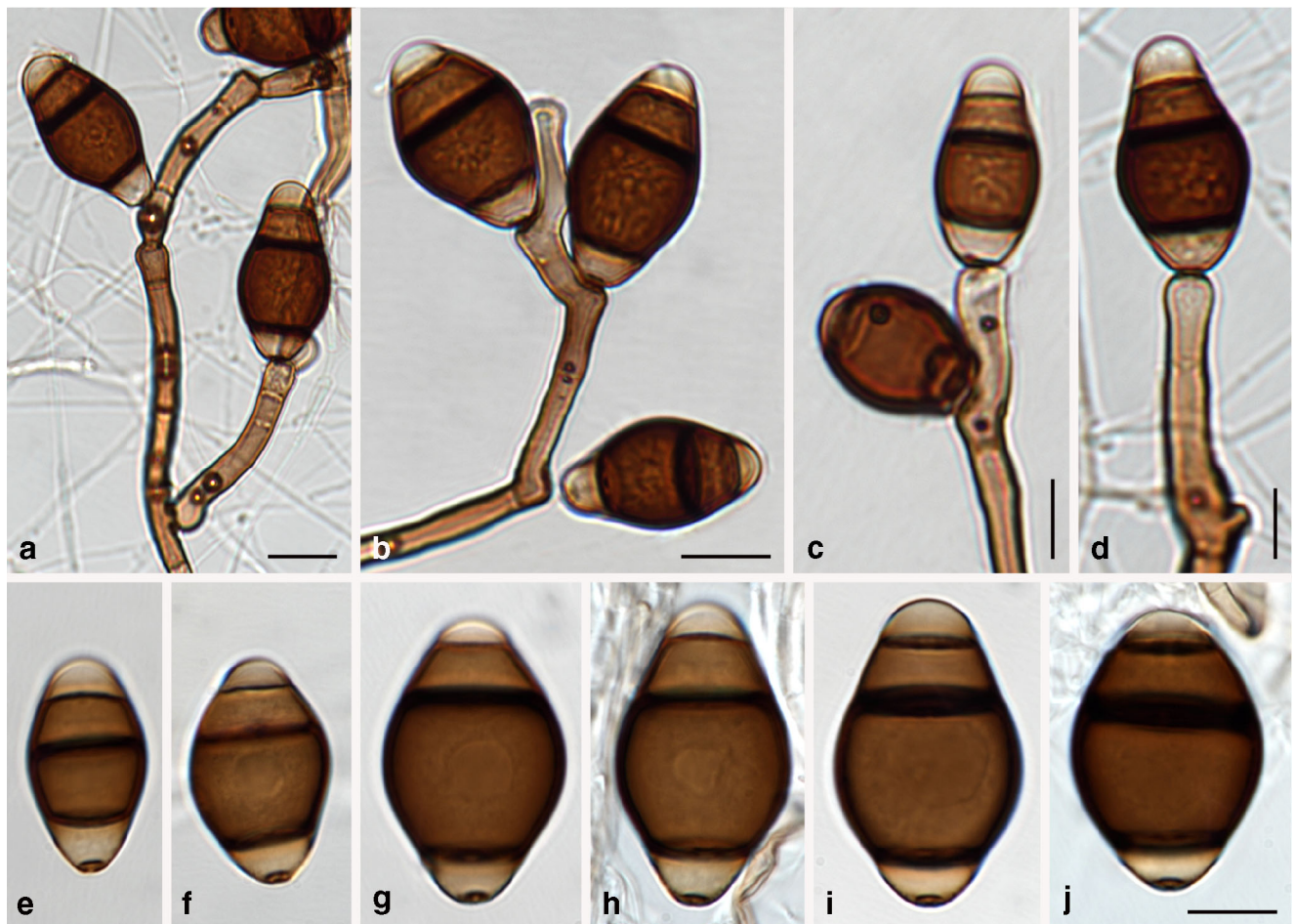
*Ex-isotype strain*. Vietnam: from *Oryza sativa* seed (Poaceae), 1949, coll. J. Nicot, isol. F. Bugnicourt, CBS 169.53.

**Asexual morph on PDA** *Hyphae* hyaline to pale brown, branched, septate, thin-walled, 1–4  $\mu\text{m}$ . *Conidiophores* arising in groups, mononematous, semi- to macronematous, septate, straight or flexuous, sometimes geniculate at upper part, rarely branched, cell walls thicker than those of vegetative hyphae, pale brown to brown, paler towards apex, 40–400  $\times$  3–8  $\mu\text{m}$ . *Conidiogenous cells* smooth-walled to finely verruculose, terminal or intercalary, sometimes proliferating sympodially, pale brown to brown, subcylindrical to slightly

swollen, 6.5–20(29)  $\times$  5–8.5  $\mu\text{m}$ . *Conidia* smooth-walled to finely verruculose, straight to slightly curved, rarely curved, middle cells enlarged, ellipsoidal to broadly ellipsoidal or obovoid, pale brown to brown, apical cells paler, (2)3-distoseptate, 20–37.5  $\times$  11–21.5  $\mu\text{m}$ ; *hila* flat to slightly protuberant, darkened, thickened, 2–4.7  $\mu\text{m}$  wide. *Chlamydospores*, *microconidiation* and *sexual morph* not observed.

**Culture characteristics** Colonies on PDA covering the surface of the Petri dish in 1 week, saffron to apricot, abundant aerial mycelium giving the colony a cottony appearance; reverse saffron to apricot or umber.

**Notes** This species is related to *C. reesii* and *C. tuberculata* (Fig. 1). *Curvularia oryzae* and *C. tuberculata* are mainly found in Asia (Farr and Rossman 2019) while *C. reesii* occurs in Australia (Tan et al. 2018). *Curvularia tuberculata* can be distinguished by having verrucose or rough, longer (up to 51  $\mu\text{m}$  long) conidia. *Curvularia reesii* produces shorter conidiophores (up to 200  $\mu\text{m}$  long) and conidia (up to 14  $\mu\text{m}$  long) than *C. oryzae* (up to 400 and 21.5  $\mu\text{m}$  long, respectively). A morphological description and illustrations are provided of the ex-type strain (Fig. 9).



**Fig. 9** *Curvularia oryzae* (CBS 169.53 ex-isotype). Conidiogenous cells and conidia; **a–d** e–j conidia. Scale bars **a, b** 15  $\mu\text{m}$ ; **c, d, j** 10  $\mu\text{m}$ , **j** applies to **e–j**



*Curvularia oryzae-sativae* Sivan., Mycol. Pap. 158: 140 (1987). Fig. 10.

*Holotype*. Argentina: Buenos Aires, from *Oryza sativa* seed (Poaceae), 8 Oct. 1984, IMI 289758.

*Epitype designated here*. Argentina: from *Oryza sativa* seed (Poaceae), 28 Jul. 1986, M.N. Sisterna, CBS H-24093.

*Ex-epitype strain*. CBS 127725 = BRIP 15350a.

**Asexual morph on PDA** *Hyphae* hyaline to pale brown, branched, septate, thick-walled, 1.5–3.5  $\mu\text{m}$ . *Conidiophores* arising in groups, mononematous, semi- to macronematous, septate, straight or flexuous, geniculate at upper part, branched, cell walls thicker than those of vegetative hyphae, pale brown to brown, paler towards apex, not swollen at the base, 80–440  $\times$  (2.5)3–6  $\mu\text{m}$ . *Conidiogenous cells* smooth-walled to verruculose, terminal or intercalary, proliferating sympodially, pale brown to brown, subcylindrical to swollen, 7.5–16  $\times$  4.5–8.5  $\mu\text{m}$ . *Conidia* smooth-walled to finely verruculose, straight or curved, usually middle cells enlarged, ellipsoidal to ovoid, brown, basal cells and sometimes apical cells paler, 3–7(8)-distoseptate, 20.5–50(61)  $\times$  (8.5)10–12.5  $\mu\text{m}$ ; *hila* protuberant, darkened, thickened, (2.5)3–4  $\mu\text{m}$  wide. *Chlamydozoospores*, *microconidiation* and *sexual morph* not observed.

**Culture characteristics** Colonies on PDA reaching 50–60 mm diam in 1 week, grey olivaceous, sparse aerial mycelium, margin lobate; reverse dark slate blue.

**Notes** As no living culture was associated with the original material, we designate an epitype with an ex-epitype culture to phylogenetically fix the application of this name. The epitype was found on the same host in the same location as the holotype. A description and illustrations are provided in the present study (Fig. 10). Hitherto, this species has neither been reported from another host nor from another region.

*Curvularia oryzae-sativae* is related to *C. canadensis* (Fig. 1), but this can be easily distinguished based on morphology (for morphological differences, see notes under *C. canadensis*).

***Curvularia patereae*** (M.R. Carranza) Y. Marín, Hern.-Restr. & Crous, comb. nov.

**MB830049**

*Basionym*. *Drechslera patereae* M.R. Carranza, Revista Fac. Agron. Univ. Nac. La Plata 59: 66 (1983).

*Synonym*. *Bipolaris patereae* (M.R. Carranza) B.A. Khasanov, Opredelitel' Gribov-Vozbuditelei 'Gel'mintosporiozov' Rasteniĭ iz Rodov Bipolaris, Drechslera i Exserohilum (Tashkent): 78 (1992).

*Ex-type strain*. Argentina: on *Triticum durum* seed (Poaceae), M.R. Carranza, CBS 198.87.

**Description adapted from Carranza (1983)** *Conidiophores* arising single or in groups, mononematous, macronematous, septate, straight, sometimes geniculate at upper part, unbranched, 37.5–130  $\times$  3.5–7.5  $\mu\text{m}$ . *Conidiogenous cells*

terminal or intercalary, proliferating sympodially, subcylindrical to swollen. *Conidia* straight or curved, ellipsoidal to ovoid, sometimes middle cells slightly enlarged, 2–6-distoseptate, 16.5–30  $\times$  7.5–9  $\mu\text{m}$ ; *hila* protuberant, darkened, thickened. *Chlamydozoospores*, *microconidiation* and *sexual morph* not observed.

**Notes** This species was introduced by Carranza (1983) as *Drechslera patereae*, a fungus causing a seedborne disease in *Triticum durum*. Subsequently, it was transferred to *Bipolaris* by Khasanov (1992). In our phylogenetic study, the ex-type strain clustered in *Curvularia* (Fig. 1). Therefore, the new combination *C. patereae* is herewith proposed.

*Curvularia patereae* is related to *C. mebaldsii*, *C. tsudae* and *C. penniseti* (Fig. 1). These species all produce 3-distoseptate conidia, except for *C. patereae*, which is characterised by 2–6-distoseptate conidia. *Curvularia penniseti* can be easily distinguished by its larger conidia (29–42  $\mu\text{m}$  vs up to 30  $\mu\text{m}$  in the other three species) with an enlarged middle cell, which is not or slightly enlarged in the other species. The four species of this clade are mainly reported on members of the Poaceae (Farr and Rossman 2019).

***Curvularia protuberata*** R.R. Nelson & Hodges, Mycologia 57: 823 (1965). Fig. 11.

*Holotype*. Scotland: Edinburgh, from *Deschampsia flexuosa* leaf (Poaceae), 24 Aug. 1964, R.R. Nelson, BPI 442848.

*Ex-type strain*. CBS 376.65 = ATCC 16397 = IMI 115840.

**Asexual morph on PDA** *Hyphae* hyaline to pale brown, branched, septate, 1.5–5.5  $\mu\text{m}$ . *Conidiophores* arising single or in groups, mononematous, semi- to macronematous, septate, straight or flexuous, geniculate at upper part, sometimes branched, cell walls thicker than those of vegetative hyphae, pale brown, rarely paler towards apex, cell size not decreasing towards apex, rarely swollen at the base, 55–300  $\times$  2.5–5  $\mu\text{m}$ . *Conidiogenous cells* smooth-walled to slightly verruculose, terminal or intercalary, proliferating sympodially, pale brown, subcylindrical to swollen, 4.5–14  $\times$  4–7(8.5)  $\mu\text{m}$ . *Conidia* smooth-walled, straight or curved, ellipsoidal to ovoid, middle cells enlarged, pale brown to brown, apical and basal cells paler, 3(4)-distoseptate, 16.5–27.5  $\times$  8–12.5  $\mu\text{m}$ ; *hila* protuberant, darkened, thickened, 2–3(4)  $\mu\text{m}$  wide. *Chlamydozoospores*, *microconidiation* and *sexual morph* not observed.

**Culture characteristics** Colonies on PDA covering the dish in 1 week, smoke grey to olivaceous black, abundant aerial mycelium giving the colony a cottony appearance, margin lobate; reverse olivaceous black.

**Notes** *Curvularia protuberata* was introduced for a specimen with protruding hila (Nelson 1965). In the present study, a morphological description and illustrations are



**Fig. 10** *Curvularia oryzae-sativae* (CBS 127725 ex-epitype). **a** Conidiophore, conidiogenous cells and conidia; **b, c** conidiogenous cells and conidia; **d–j** conidia. Scale bars **a–c** 10  $\mu\text{m}$ ; **j** 5  $\mu\text{m}$ . **j** applies to **d–j**

provided for the ex-type (Fig. 11). The species is similar and phylogenetically related to *C. pseudoprotuberata*, a new species introduced below. For a morphological comparison, see notes under *C. pseudoprotuberata*.

*Curvularia protuberata* has been reported on a wide host range including the families Fabaceae (*Aeschynomene falcata*, *Glycine max*), Juncaceae (*Juncus roemerianus*) and Poaceae (*Aristida oligantha*, *Avena sativa*, *Deschampsia* spp., *Eragrostis* spp., *Panicum texanum*, *Paspalum dilatatum*, *Phleum* spp., *Sorghum* sp., *Sporobolus vaginiflorus*, *Tridens flavus*, *Tripsacum dactyloides*, *Triticum durum*, *Zea mays*), from Africa, America and Europe (Farr and Rossman 2019).

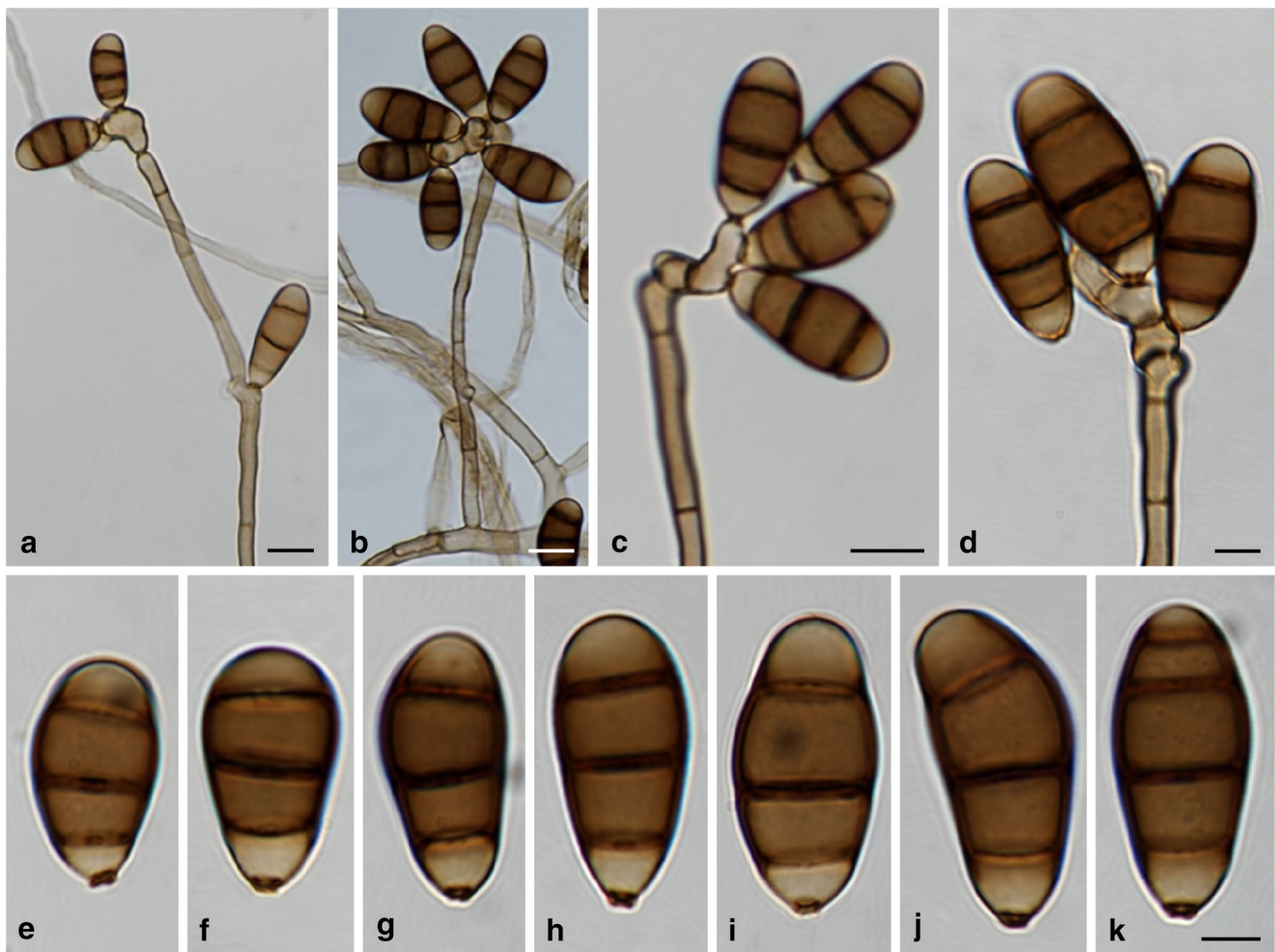
***Curvularia pseudobrachyspora*** Y. Marín, Cheew. & Crous, Mycosphere 8: 1569 (2017). Fig. 12.

*Holotype*. Thailand: Chiang Mai, Jom Thong, on *Eleusine indica* (Poaceae), 23 May 2010, R. Cheewangkoon, CBS H-23195.

*Ex-type strain*. CPC 28808.

*Additional material examined*. China: Hainan Province, Wanning, on *Areca catechu* leaf (*Areaceae*), Jul. 2017, HNWN001. Denmark: on *Pennisetum* sp. seed (Poaceae), 16 Apr. 1970, S.B. Mathur, CBS 533.70 = IMI 148192. Thailand: on *Oryza sativa* (Poaceae), D.S. Manamgoda, MFLUCC 10-0739. Unknown location, substrate, date and collector, CBS 207.59 = ATCC 13633 = NRRL 2434. USA: on *Trisetum* sp. (Poaceae), R.R. Nelson, CBS 336.64 = MUCL 38848; *ibid.*, on *Agropyron repens* (Poaceae), CBS 337.69 = MUCL 38849; *ibid.*, on *Pennisetum glaucum* (Poaceae), CBS 339.69.

**Asexual morph on PDA** *Hyphae* subhyaline to pale brown, branched, septate, thin-walled, (1)1.5–5  $\mu\text{m}$ . *Conidiophores* arising single or in groups, mononematous, semi- to macronematous, septate, straight or flexuous, geniculate at upper part, sometimes swollen at the base, cell size rarely decreasing towards apex, sometimes branched, cell walls thicker than those of vegetative hyphae, pale brown to brown, sometimes paler towards apex, 30–420  $\times$  (2.5)3–6(7)  $\mu\text{m}$ . *Conidiogenous cells* smooth-walled to verruculose, terminal or intercalary, proliferating sympodially,



**Fig. 11** *Curvularia protuberata* (CBS 376.65 ex-isotype). **a, b** Conidiophores, conidiogenous cells and conidia; **c, d** conidiogenous cells and conidia; **e–k** conidia. Scale bars **a–d** 10  $\mu\text{m}$ ; **k** 5  $\mu\text{m}$ , **k** applies to **e–k**

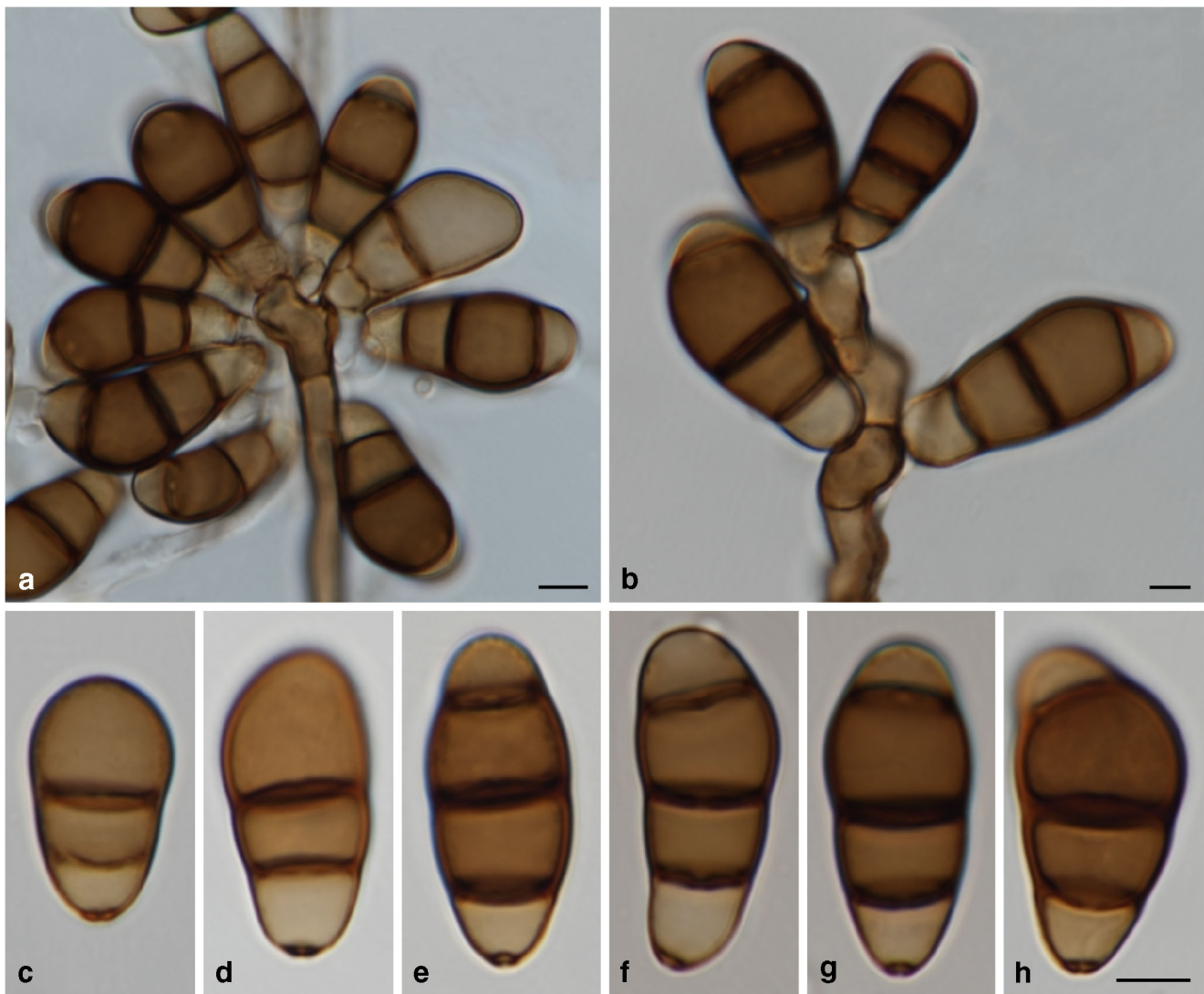
pale brown to brown, subcylindrical to swollen,  $(5)7\text{--}27 \times 4\text{--}15.5(18) \mu\text{m}$ . *Conidia* smooth-walled to verruculose, straight or curved, ellipsoidal to ovoid, middle cells enlarged, pale brown to brown, apical cell paler, basal cells sometimes paler, (1)2–3-distoseptate,  $13\text{--}27(28.5) \times 6\text{--}14 \mu\text{m}$ ; *hila* inconspicuous to slightly conspicuous, flat to slightly protruding, darkened, slightly thickened,  $1.5\text{--}3(4) \mu\text{m}$  wide. *Chlamydozoospores*, *microconidiation* and *sexual morph* not observed.

**Culture characteristics** Colonies on PDA reaching 64–90 mm diam in 1 week, smoke grey to grey olivaceous, or with zones of pale mouse grey, and alternate zones grey olivaceous to olivaceous, with sparse aerial mycelium, margin fimbriate; reverse brown to dark brown, with margin pale yellow, or dark olivaceous with margin hyaline.

**Notes** *Curvularia pseudobrachyspora*, recently introduced in Marin-Felix et al. (2017b), causes leaf spots on *Eleusine indica* in Thailand. In our phylogenetic study, seven additional strains, collected in China, Denmark, the USA and Thailand, clustered in the same clade representing *C. pseudobrachyspora* (Fig. 1).

These strains were isolated from different hosts, i.e. *Agropyron repens*, *Areca catechu*, *Oryza sativa*, *Pennisetum glaucum*, *Pennisetum* sp. and *Trisetum* sp., all of them, except *Areca catechu*, belong to the Poaceae, as well as *Eleusine indica*, which is the host of the ex-type strain. The strain isolated from *Areca catechu* (Arecaceae) causes leaf spots. Although this disease has rarely been observed in China to date, it causes serious symptoms in areca palm (Wang et al. 2019). Apart from the reports on new hosts and distribution, the description of *C. pseudobrachyspora* is emended here to incorporate the morphology observed in the strain CBS 533.70. Basically, the main difference was in the size of the conidiophores, being  $110\text{--}420 \times (2.5)3.5\text{--}6(7) \mu\text{m}$  in the ex-type strain, while these measure  $30\text{--}100(178) \times 3\text{--}5(5.5) \mu\text{m}$  in CBS 533.70.

*Curvularia pseudobrachyspora* is related to *C. brachyspora* (Fig. 1). However, *C. pseudobrachyspora* is easily distinguishable by producing shorter conidiophores (up to  $420 \mu\text{m}$  long in *C. pseudobrachyspora* vs up to  $700 \mu\text{m}$  in *C. brachyspora*; Sivanesan 1987).



**Fig. 12** *Curvularia pseudobrachyspora* (CBS 533.70). **a, b** Conidiogenous cells and conidia; **c–h** conidia. Scale bars 5  $\mu\text{m}$ , **h** applies to **c–h**

***Curvularia pseudoclavata*** Y. Marín & Crous, sp. nov.  
Fig. 13.

**MB830051**

**Etymology.** Name refers to the similarity with *Curvularia clavata*.

**Holotype.** Denmark: Copenhagen, on *Oryza sativa* seeds (Poaceae), Apr. 1970, S.B. Mathur, preserved in a metabolically inactive state, CBS 539.70.

**Ex-type strain.** CBS 539.70 = ATCC 34596 = IMI 148186.

**Asexual morph on PDA** *Hyphae* subhyaline to pale brown, branched, septate, thick-walled, 1.5–3.5  $\mu\text{m}$ . *Conidiophores* arising single or in groups, mononematous, semi- to macronematous, septate, straight or flexuous, sometimes geniculate at upper part, branched, cell walls thicker than those of vegetative hyphae, pale brown to brown, usually paler towards apex, not swollen at the base, 34–102.5(137)  $\times$  2.5–5.5  $\mu\text{m}$ . *Conidiogenous cells* smooth-walled, terminal or intercalary, proliferating sympodially, pale brown to brown,

subcylindrical to swollen, 5.5–12(17)  $\times$  4–6  $\mu\text{m}$ . *Conidia* verruculose, straight or curved, ovoid to clavate, middle cells disproportionately enlarged, pale brown to brown, apical cells and sometimes basal cells paler, (2)3(4)-distoseptate, (16.5)19–27(29)  $\times$  7–13.5  $\mu\text{m}$ ; *hila* protuberant, darkened, thickened, 2–3  $\mu\text{m}$  wide. *Chlamydospores*, *microconidiation* and *sexual morph* not observed.

**Culture characteristics** Colonies on PDA reaching 52–57 mm diam in 1 week, saffron to luteous, abundant aerial mycelium giving the colony a cottony appearance, margin luteous to umber and fimbriate; reverse pale luteous to luteous.

**Notes** In our phylogenetic study, this species was located on an independent branch. The most related species are *C. palmicola* and *C. petersonii*. All of them produce mostly 3-distoseptate conidia; however, these differ in size [23.9–34.7  $\times$  9.3–15.7  $\mu\text{m}$  in *C. palmicola* vs (15)17–19(21)  $\times$  (5)5.5–6(7)  $\mu\text{m}$  in *C. petersonii* vs (16.5)19–27(29)  $\times$  7–13.5  $\mu\text{m}$  in *C. pseudoclavata*]. Moreover, these

species have been found on different hosts, i.e. *C. palmicola* on *Acoelorrhaphes wrightii*, *C. petersonii* on *Dactyloctenium aegyptium* and *C. pseudoclavata* on *Oryza sativa* (Hyde et al. 2017; Tan et al. 2018).

*Curvularia pseudoclavata* is similar to *C. clavata*, both species producing ovoid to clavate, mostly 3-distoseptate conidia. The size of their asexual structures is also similar. The only difference observed is in the ornamentation of their conidia, being smooth-walled in *C. clavata* (Sivanesan 1987) and verruculose in *C. pseudoclavata*. However, both species are phylogenetically distant. *Curvularia pseudoclavata* was found in Denmark, while *C. clavata* has never been reported in Europe (Farr and Rossman 2019). *Curvularia clavata* has been reported on a wide host range, including *Oryza sativa*, from which *C. pseudoclavata* was isolated.

***Curvularia pseudoellisii*** Y. Marín & Crous, sp. nov. Fig. 14.

**MB830061**

**Etymology.** Named after its morphological similarity with *Curvularia ellisii*.

**Holotype.** Sudan: on *Sorghum bicolor* seed (Poaceae), A.E. Elshafie, CBS H-24096.

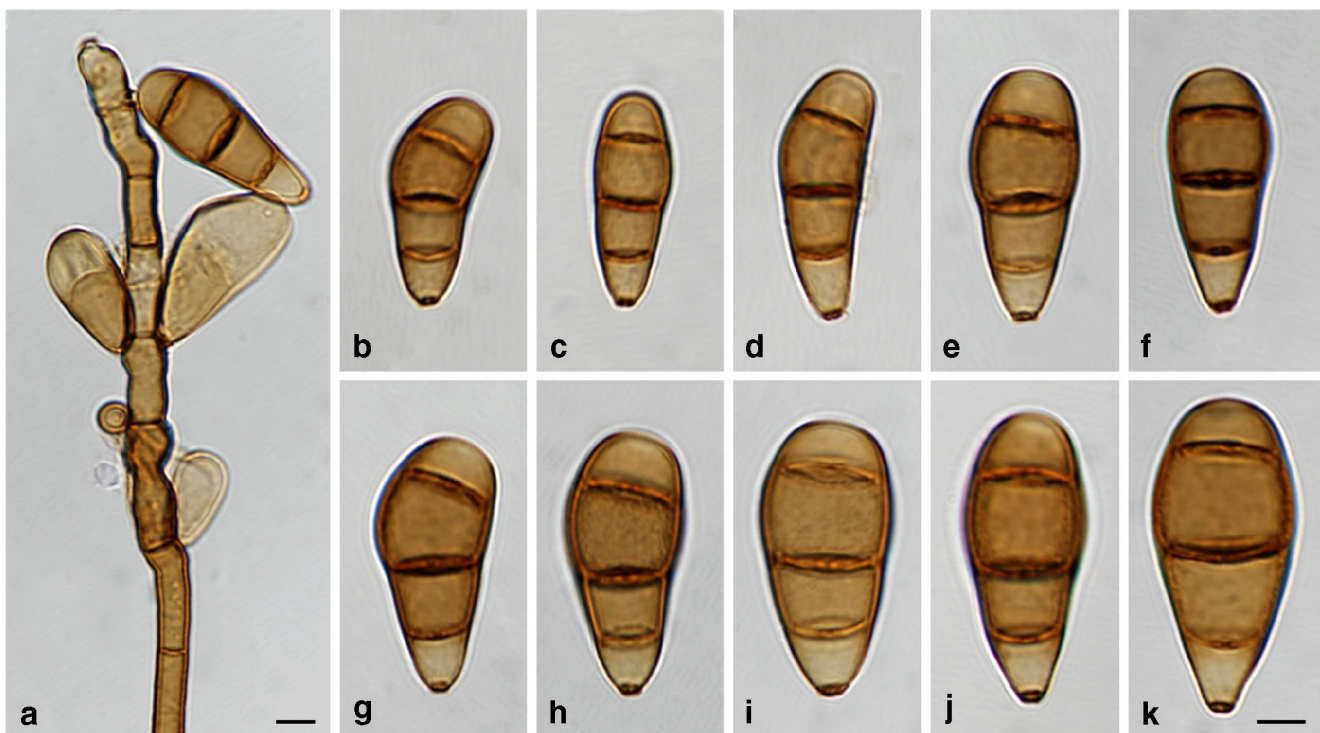
**Ex-type strain.** CBS 298.80.

**Asexual morph on PDA** *Hyphae* hyaline to pale brown, branched, septate, thin-walled, 1.5–4 µm. *Conidiophores* arising in groups, mononematous, semi- to macronematous, septate, straight to flexuous, geniculate at upper part, finely

verruculose, cell size not decreasing towards apex, branched, cell walls thicker than those of vegetative hyphae, pale brown to brown, paler towards apex, not swollen at the base, 55–200 × 3–5(7) µm. *Conidiogenous cells* finely verruculose, terminal or intercalary, proliferating sympodially, pale brown to brown, subcylindrical to swollen, 6.5–18(22) × 3–6 µm. *Conidia* finely verruculose, mostly curved, ovoid to navicular, pale brown to brown, paler towards hilum, 0–3(4)-distoseptate, 17–30 × 8.5–13 µm; *hila* inconspicuous to slightly conspicuous, flat to slightly protuberant, darkened, thickened, 1–3.5 µm wide. *Chlamydospores*, *microconidiation* and *sexual morph* not observed.

**Culture characteristics** Colonies on PDA reaching 49–54 mm diam in 1 week, olivaceous grey to olivaceous black, with sparse aerial mycelium, lobulate, margin fimbriate; reverse olivaceous black to dark slate blue.

**Notes** *Curvularia pseudoellisii* is phylogenetically related to *C. ellisii* and *C. neergaardii* (Fig. 1). In *C. pseudoellisii*, the sexual morph was not observed, while the other two species produce both sexual and asexual morphs (Alcorn 1983b; Manamgoda et al. 2014). *Curvularia neergaardii* differs from this new species in producing subglobose to broadly ellipsoidal conidia (Fig. 8). *Curvularia pseudoellisii* and *C. ellisii* are similar in producing ovoid conidia, but can be easily distinguished by the size of the conidiophores (up to 700 µm in *C. ellisii* vs up to 200 µm in *C. pseudoellisii*) and the navicular conidia only present in *C. pseudoellisii* (Fig. 14). The three



**Fig. 13** *Curvularia pseudoclavata* (CBS 539.70 ex-type). **a** Conidiophore, conidiogenous cells and conidia; **b–k** conidia. Scale bars 5 µm, **k** applies to **b–k**

species have been reported from Africa, but only *C. neergaardii* has been reported on *Sorghum*, the host from which the new species *C. pseudoellisii* was isolated.

***Curvularia pseudointermedia*** Y. Marín & Crous, sp. nov.  
Fig. 15.

**MB830052**

*Etymology.* Name based on its morphological similarity with *Curvularia intermedia*.

*Holotype.* Brazil: Pará, 200 km SE from Belém, Capitão Poço, from cultivated pasture soil, L. Pfenning, CBS H-24094.

*Ex-type strain.* CBS 553.89.

*Additional material examined.* Guadeloupe: decaying grass, unknown collector, unknown date, Plantziektkundige Dienst, CBS 188.61.

**Asexual morph on PDA** *Hyphae* hyaline to pale brown, branched, septate, 2–4.5  $\mu\text{m}$ . *Conidiophores* arising in groups, mononematous, semimacronematous, septate, straight or flexuous, rarely geniculate at upper part, sometimes cell size decreasing towards apex, branched, pale brown, paler towards apex being hyaline to subhyaline, sometimes swollen at the base, up to 520  $\mu\text{m}$ . *Conidiogenous cells* smooth-walled to finely verruculose, terminal or intercalary, subhyaline to pale brown, subcylindrical to swollen, 6–25  $\times$  4–7  $\mu\text{m}$ . *Conidia* smooth-walled to finely verruculose, straight or curved, middle cells disproportionately enlarged, ellipsoidal to ovoid, pale brown, apical cells paler than middle cells, (2)3-distoseptate, with a truly medium septum cutting the conidium transversely at its widest point, 20.5–28.5  $\times$  10–16  $\mu\text{m}$ ; *hila*



**Fig. 14** *Curvularia pseudoellisii* (CBS 298.80 ex-type). **a, b** Conidiophores, conidiogenous cells and conidia; **c** conidiogenous cells and conidia; **d–g** conidia. Scale bars **a** 20  $\mu\text{m}$ , **all others** 5  $\mu\text{m}$

inconspicuous, flat to slightly protuberant, darkened, slightly thickened, 1.5–3  $\mu\text{m}$  wide. *Chlamydoconidia*, *microconidiation* and *sexual morph* not observed.

**Culture characteristics** Colonies on PDA covering the surface of the Petri dish in 1 week, olivaceous grey to greenish black, with abundant aerial mycelium, margin fimbriate; reverse dark slate blue.

**Notes** *Curvularia pseudointermedia* is closely related to *C. arcana* and *C. intermedia* (Fig. 1). The morphology of the asexual morph of *C. intermedia* and *C. pseudointermedia* is similar, producing conidia with a truly medium septum at its widest point (Sivanesan 1987). However, conidiophores and conidia are larger in *C. intermedia*, up to 1  $\mu\text{m}$ , and 40  $\mu\text{m}$ , respectively (up to 520 and 28.5  $\mu\text{m}$  in *C. pseudointermedia*). *Curvularia arcana* can be easily distinguished from the other two species by the lack of a medium septum and disproportionally enlarged middle cells.

*Curvularia pseudoprotuberata* Y. Marín & Crous, sp. nov. Fig. 16.

**MB830054**

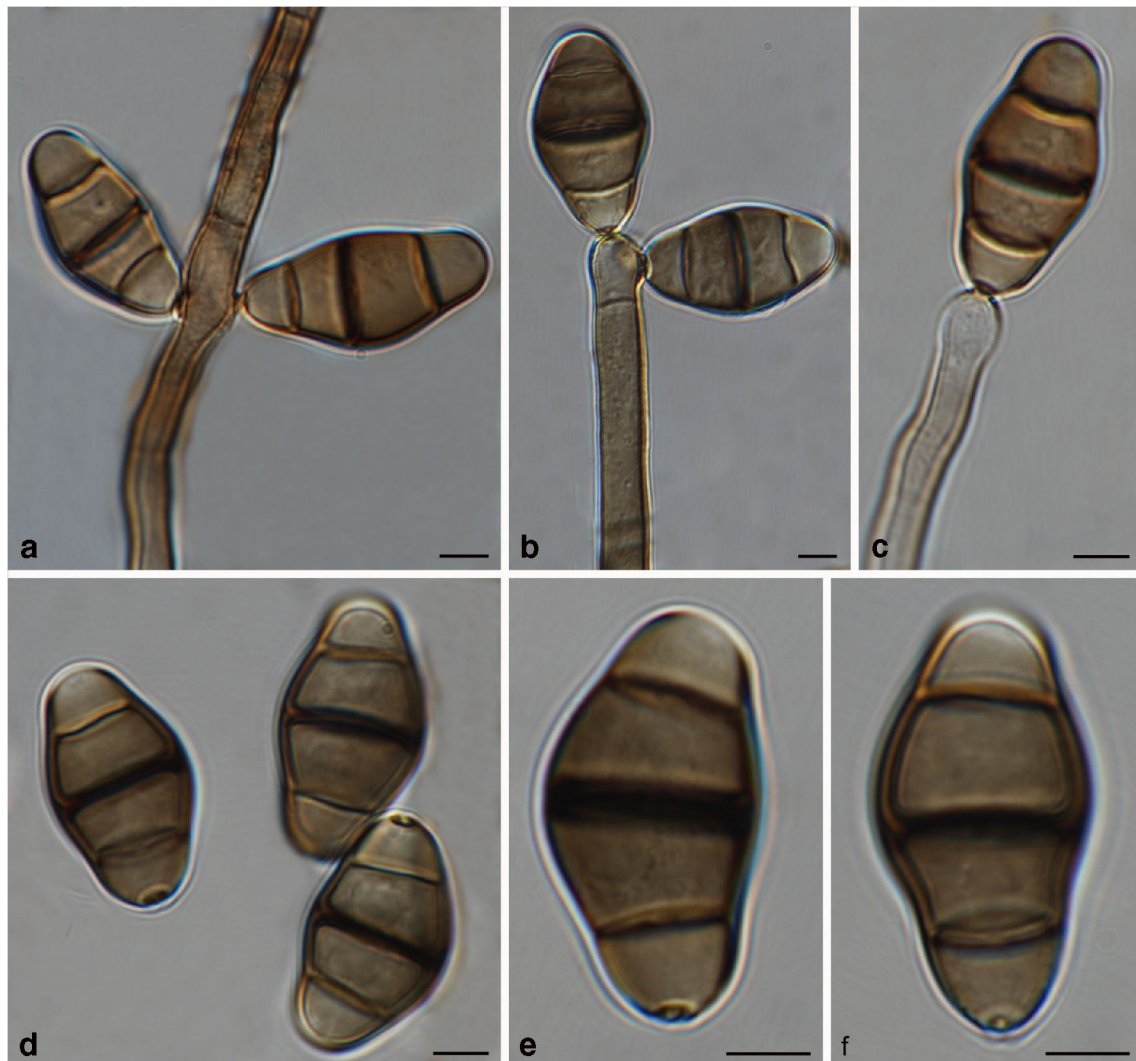
**Etymology.** Named after its resemblance with *Curvularia protuberata*.

**Holotype.** Canada: Ontario, Puslinch, soil under *Thuja occidentalis* (Cupressaceae), 28 Aug. 1968, G.C. Bhatt, CBS H-24095.

**Ex-type strain.** CBS 385.69.

**Additional material examined.** Canada: Ontario, St. Williams, soil under *Pinus strobus* (Pinaceae), Jul. 1966, G.C. Bhatt, CBS 550.69.

**Asexual morph on PDA** *Hyphae* subhyaline to pale brown, branched, septate, thin-walled, 2–4.5  $\mu\text{m}$ . *Conidiophores* arising in groups, mononematous, semi- to macronematous, septate, mostly flexuous, mostly geniculate at upper part, cell size



**Fig. 15** *Curvularia pseudointermedia* (CBS 553.89 ex-type). **a–c** Conidiogenous cells and conidia; **d–f** conidia. Scale bars 5  $\mu\text{m}$

not decreasing towards apex, unbranched, cell walls thicker than those of vegetative hyphae, pale brown to brown, sometimes paler towards apex,  $19\text{--}135(330) \times (1.5)2\text{--}5(6) \mu\text{m}$ . *Conidiogenous cells* smooth-walled to slightly verruculose, terminal or intercalary, proliferating sympodially, pale brown to brown, subcylindrical to slightly swollen,  $5\text{--}13(14.5) \times 4\text{--}6 \mu\text{m}$ . *Conidia* smooth-walled to finely verruculose, straight or curved, ellipsoidal to ovoid, middle cells enlarged, pale brown to brown, apical cell paler, basal cells mostly paler,  $3\text{--}4(5)$ -distoseptate,  $19\text{--}33(35.5) \times 8\text{--}12 \mu\text{m}$ ; *hila* protuberant, darkened, thickened,  $1.5\text{--}3 \mu\text{m}$  wide. *Chlamydospores*, *microconidiation* and *sexual morph* not observed.

**Culture characteristics** Colonies on PDA covering the surface of the Petri dish in 1 week, grey olivaceous with centre smoke grey and abundant aerial mycelium giving the colony a cottony appearance, margin fimbriate; reverse dark slate blue with margin greenish grey.

**Notes** *Curvularia pseudoprotuberata* is similar and phylogenetically closely related to *C. protuberata* (Fig. 1). However, *C. pseudoprotuberata* produces longer conidia [ $19\text{--}33(35.5) \mu\text{m}$ ;  $16.5\text{--}27 \mu\text{m}$  in *C. protuberata*].

*Curvularia pseudoprotuberata* is represented by CBS 385.69 and CBS 550.69 (Fig. 1), both strains isolated from soil from the same location in Canada, Ontario. *Curvularia protuberata* has also been reported in Canada, apart from other locations in North America, South America, Africa and Europe, on a wide range of host plants included in different families (see notes under *C. protuberata*).

***Curvularia siddiquii*** Y. Marín & Crous, sp. nov. Fig. 17.  
**MB830060**

**Synonym.** *Curvularia siddiquii* S.I. Ahmed & M. Quraishi [as ‘*siddiqui*’], Pakistan J. Sci. Industr. Res. 3(3): 177 (1960), nom. inval., Art. 39.1 (Melbourne).

**Etymology.** Named after Dr. Salimuzzaman Siddiqui, who assisted Ahmad and Quraishi (1960) in the preparation of their original publication.

**Holotype.** Pakistan: Karachi, isolated from air, 1958, M.S. Quraishi, CBS H-12240.

**Ex-type strain.** CBS 196.62 = ATCC 14861 = IMI 075861 = QM 8356.

**Additional material examined:** Egypt: H.M. Abdel-Fattah, CBS 142.78.



**Fig. 16** *Curvularia pseudoprotuberata* (CBS 385.69 ex-type). **a** Conidiophore, conidiogenous cells and conidia; **b–i** Conidia. Scale bars  $5 \mu\text{m}$ , **i** applies to **b–i**





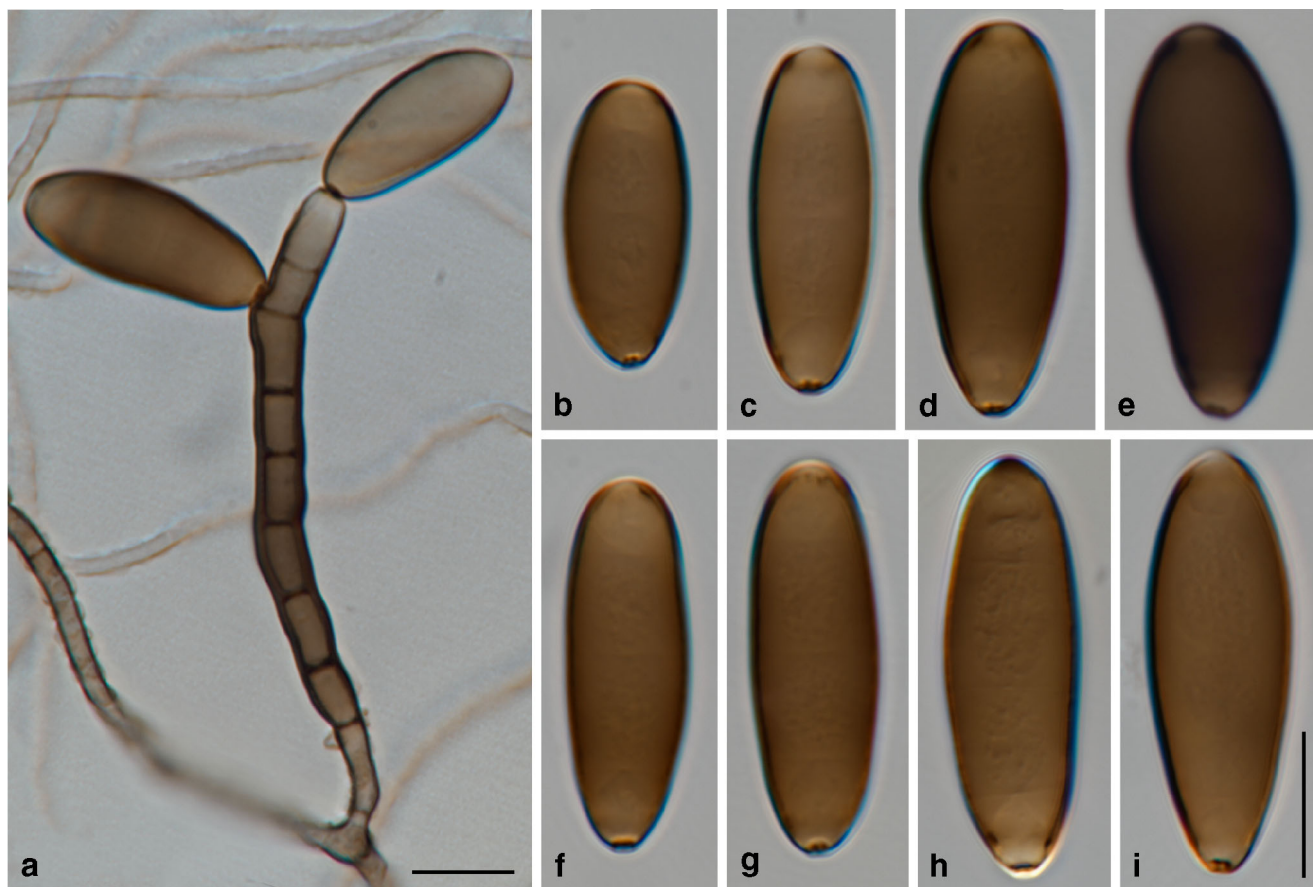
**Fig. 17** *Curvularia siddiquii* (CBS 196.62 ex-type). **a–c** Conidiogenous cells and conidia; **d–g** conidia; **h** chlamydospores. Scale bars **a–c, h** = 10  $\mu$ m; **g** 5  $\mu$ m, **g** applies to **d–g**

**Asexual morph on PDA** *Hyphae* hyaline to subhyaline, branched, septate, anastomosing, thin-walled, 2–4  $\mu$ m. *Conidiophores* arising in groups, mononematous, macronematous, septate, straight or flexuous, geniculate at upper part, cell size decreasing towards apex, unbranched, sometimes branched, cell walls thicker than those of vegetative hyphae, pale brown, rarely paler towards apex, not swollen at the base, up to 600  $\mu$ m. *Conidiogenous cells* smooth-walled, terminal or intercalary, proliferating sympodially, pale brown, subcylindrical to swollen, 5–16(21)  $\times$  6.5–8.5  $\mu$ m. *Conidia* smooth-walled, curved, rarely straight, middle cells disproportionately enlarged, navicular, rarely ellipsoidal, pale brown to brown, sometimes apical cells paler than middle cells being subhyaline, (1)2–3(4)-distoseptate, (21.5)24–40  $\times$  (15)17–23  $\mu$ m; *hila* inconspicuous to slightly conspicuous, flat to slightly protuberant, darkened, slightly thickened, 2–4  $\mu$ m wide. *Chlamydospores* globose to subglobose or cylindrical, brown, thick-walled, terminally and intercalary, 8.5–22.5  $\mu$ m diam. *Microconidiation* and *sexual morph* not observed.

**Culture characteristics** Ex-type strain CBS 196.62: Colonies on PDA reaching 64–71 mm diam in 1 week, apricot to chestnut, fasciculate, irregular form, margin fimbriate; reverse

umber to chestnut. Strain CBS 142.78: Colonies on PDA attaining 52–62 mm diam in 1 week, olivaceous, mouse grey and white in the centre, cottony, raised, margin fimbriate; reverse olivaceous to fuscus olivaceous, margin buff.

**Notes** *Curvularia siddiquii* was introduced by Ahmad and Quraishi (1960) to accommodate a fungus isolated from air in Pakistan. However, this species is invalid due to the lack of a Latin description. Subsequently, Ellis (1971) synonymised *C. siddiquii* with *Drechslera papendorfii*, which clusters in *Curvularia* (Marin-Felix et al. 2017a) where it was initially described (van der Aa 1967). This synonymy was not molecularly corroborated since no sequence data were available at that moment. In the phylogenetic tree generated here (Fig. 1), the ex-type strains of *C. siddiquii* (CBS 196.62) and *C. papendorfii* (CBS 308.67) formed two separate lineages, representing two distinct species from other *Curvularia* spp. Therefore, we resurrected the former taxon as a new species. Morphologically, *C. siddiquii* can be distinguished from *C. papendorfii* by the length of its conidiophores (up to 200  $\mu$ m in *C. papendorfii* vs up to 600  $\mu$ m in *C. siddiquii*) and the production of chlamydospores, which have not been observed in *C. papendorfii*.



**Fig. 18** *Curvularia tribuli* (CBS 126975 ex-type). **a** Conidiophore, conidiogenous cells and conidia; **b–i** Conidia. Scale bars 10  $\mu\text{m}$ , **i** applies to **b–i**

*Curvularia papendorffii* has been reported from soil and on various genera of Poaceae, causing leaf spots (Farr and Rossman 2019), while the type material of *C. siddiquii* was isolated from air, and the substrate of the second strain belonging to this species is unknown. Both species have been reported only in Asia and Africa, respectively.

***Curvularia tribuli*** Hern.-Restr. & Y. Marín, sp. nov. Fig. 18.

**MB830062**

**Etymology.** Name refers to *Tribulus*, the host genus from which this fungus was collected.

**Holotype.** South Africa: Cape Province, on *Tribulus terrestris* leaf (Zygophyllaceae), Aug. 1971, coll. W.F.O. Marasas, CBS H-24097.

**Ex-type strain.** CBS 126975 = CCFC000890 = DAOMC 137386.

**Asexual morph on PDA** *Hyphae* pale brown to brown, branched, septate, smooth-walled to verrucose, thick-walled, 1.5–3(4.5)  $\mu\text{m}$ . *Conidiophores* arising in groups, mononematous, semi- to macronematous, septate, straight to flexuous, rarely geniculate at upper part, cell size not decreasing towards apex, unbranched, cell walls thicker than those of vegetative hyphae, brown to dark brown, paler towards the apex, not

swollen at the base, 15.5–104  $\times$  4–6.5  $\mu\text{m}$ . *Conidiogenous cells* smooth-walled, terminal or intercalary, proliferating sympodially, pale brown to brown, subcylindrical to slightly swollen, 6.5–14  $\times$  4–5(7)  $\mu\text{m}$ . *Conidia* smooth-walled, straight, rarely curved, ellipsoidal to ovoid, pale brown to brown, mostly paler at base, sometimes paler at apex, 1–4(6)-distoseptate, 17–30  $\times$  8.5–13  $\mu\text{m}$ ; *hila* flat, darkened, slightly thickened, 1–2  $\mu\text{m}$  wide. *Chlamydospores*, *microconidiation* and *sexual morph* not observed.

**Culture characteristics** Colonies on PDA reaching 41–53 mm diam in 1 week, olivaceous grey to olivaceous black, with abundant aerial mycelium giving the colony a cottony appearance, convex, margin fimbriate; reverse olivaceous black.

**Notes** In our phylogenetic study, *C. tribuli* was located on an independent branch far from other species of the genus (Fig. 1). This is the first species of *Curvularia* reported on *Tribulus terrestris* (Zygophyllaceae).

***Curvularia verruciformis*** G.P. Agarwal & V.P. Sahni, Curr. Sci. 32: 277 (1963). Fig. 19.

**Holotype.** India: Jabalpur, from *Triticum*, 20 Mar. 1962, G.P. Agarwal, IMI 92671.



**Fig. 19** *Curvularia verruciformis* (CBS 537.75). **a–c** Conidiophores, conidiogenous cells and conidia; **d** conidiogenous cells and conidia; **e–j** conidia. Scale bars **a** 20  $\mu\text{m}$ ; **b, c** 10  $\mu\text{m}$ ; **d, j** 5  $\mu\text{m}$ , **j** applies to **e–j**

**Material examined.** New Zealand: Mitchell River, from *Lobibyx* (masked plover) feather, 17 Apr. 1965, J.L. Alcorn, CBS 537.75.

**Asexual morph on PDA** *Hyphae* subhyaline to pale brown, branched, septate, thick-walled, 2–4.5  $\mu\text{m}$ . *Conidiophores* arising single or in groups, mononematous, semi- to macronematous, septate, straight or flexuous, geniculate at upper part, branched, cell walls thicker than those of vegetative hyphae, pale brown, paler towards apex, mostly swollen at the base, 40–500  $\times$  3.5–6(7.5)  $\mu\text{m}$ . *Conidiogenous cells* smooth-walled, terminal or intercalary, proliferating sympodially, pale brown, subcylindrical to swollen, 6–17.5  $\times$  3–6  $\mu\text{m}$ . *Conidia* verrucose, mostly curved, sometimes geniculate, ellipsoidal to ovoid or clavate, middle cells disproportionately enlarged, pale brown to brown, apical and basal cells paler, (3)4-distoseptate, 20–27.5  $\times$  8–12  $\mu\text{m}$ ; *hila* protuberant, darkened, slightly thickened, 1.8–3.2  $\mu\text{m}$  wide. *Chlamydozoospores*, *microconidiation* and *sexual morph* not observed.

**Notes** *Curvularia verruciformis* is morphologically similar to *C. verrucosa* and *C. verruculosa* since all three species produce verrucose conidia. However, they differ in the number of conidial septa being mostly 3-distoseptate in *C. verruculosa* and 4-distoseptate in *C. verruciformis* and *C. verrucosa* (Ellis 1966; Sivanesan 1992). The conidia of *C. verrucosa* and *C. verruculosa* are wider (14–18 and 12–17  $\mu\text{m}$ , respectively) than in *C. verruciformis* due to the middle cell being more enlarged. Conidia in *C. verruciformis* tend to be more geniculate which makes the longitude of the conidia shorter than in *C. verruculosa* (20–27.5  $\mu\text{m}$  in *C. verruciformis* vs 20–35  $\mu\text{m}$  in *C. verruculosa*). *Curvularia verrucosa* also produces more geniculate conidia than *C. verruculosa*, but these are longer than in the other two species (27–40  $\mu\text{m}$ ). Phylogenetically, these species are very distant (Fig. 1).

The closest relative of *C. verruciformis* is *C. uncinata* (Fig. 1), but both species can be easily distinguished by the ornamentation of the conidia, being smooth-walled in *C. uncinata* and verrucose in *C. verruciformis* (Sivanesan 1987).

*Curvularia verruciformis* causes root rot of wheat in India (Agarwal and Sahni 1963). *Curvularia uncinata* and *C. verruculosa* have also been reported from this host and location, while *C. verrucosa* has been reported in India, but never from wheat (Farr and Rossman 2019). However, the strain included in the molecular study was isolated from *Lobibyx* in New Zealand, a substrate and location not reported for the other three species.

## Discussion

*Curvularia* is morphologically similar to the helminthosporioid genus *Bipolaris*, the main difference being the conidial curvature and length. Species in both genera present intermediate morphology, making sequence data necessary to properly delineate both genera. Recent phylogenetic studies based on ITS, *GAPDH* and *TEF1* demonstrated that some species placed in *Bipolaris* belonged to *Curvularia*, and vice versa (Manamgoda et al. 2014, 2015; Tan et al. 2014). In the present study, an additional new combination is proposed in *Curvularia* to accommodate *B. cactivora*.

The genus *Pyrenophora* also produces an asexual morph similar to that of *Bipolaris* and *Curvularia*. The asexual morph was known as *Drechslera*, but its synonymy was recently discussed (Rossman et al. 2015). Although some species have already been transferred to *Pyrenophora* (Ariyawansa et al. 2014; Marin-Felix et al. 2019), there are still a large number of species which await treatment. The main problem encountered is the lack of type or reference material of *Drechslera* spp. While the sexual morph of *Pyrenophora* can be easily distinguished from that of *Curvularia* by its muriformly septate ascospores, the asexual morphs are similar. DNA sequence data therefore remain essential to properly delineate both genera. In the present study, *D. patereae* is newly combined in *Curvularia* since this genus accommodated the ex-type strain of this species.

*Exserohilum* is another gramincolous genus related to *Curvularia*. Historically, *Exserohilum* was delimited based on its conidia having protuberant hila (Alcorn 1983a; Sivanesan 1987). However, in some *Curvularia* species, the hilum is also protruding, differing from that of *Exserohilum* in being separated from the conidial body by a septum (Hernández-Restrepo et al. 2018). This resemblance led to the wrong allocation of some species to *Exserohilum*, which were subsequently transferred to *Curvularia*, as in the case of *C. micropus*, *C. sorgnicola* (Hernández-Restrepo et al. 2018) and *C. heteropogonicola* (Alcorn 1991). Another example is *C. crassiseptata*, which was originally introduced as *E. inaequale* (Zhang et al. 2004). Recently, the placement of this species in *Curvularia* was molecularly demonstrated by Hernández-Restrepo et al. (2018). In the present study, the

morphological study of the ex-type strain was conducted, providing a description and illustrations of the type material. This species produces conidia with protuberant hila similar to those found in *Exserohilum* spp., and therefore, DNA sequence data are necessary to properly delineate these two genera.

Species delimitation in *Curvularia* remains problematic due to the overlapping morphological characters among many species (Manamgoda et al. 2015; Marin-Felix et al. 2017b). Therefore, sequence data are essential for an accurate identification of species, with ITS, *GAPDH* and *TEF1* being the loci selected for this purpose (Marin-Felix et al. 2017a), although the ITS and *GAPDH* alone can also resolve the majority of taxa in *Curvularia* (Manamgoda et al. 2015). Sequences of *RPB2* are also available for some *Curvularia* species and were used in previous phylogenetic studies (Madrid et al. 2014; Hernández-Restrepo et al. 2018), but it has not been included as barcode for delimiting species of *Curvularia* due to the general lack of *RPB2* data for most taxa (Marin-Felix et al. 2017a). Our phylogenetic study based on ITS, *GAPDH* and *TEF1* sequences demonstrated that 15 strains housed in the Westerdijk Fungal Biodiversity Institute collection represent 10 different species, i.e. *C. austriaca*, *C. canadensis*, *C. ellisii*, *C. pseudoclavata*, *C. pseudoellisii*, *C. pseudointermedia*, *C. pseudoprotuberata*, *C. siddiquii* and *C. tribuli*. *Curvularia canadensis*, *C. ellisii*, *C. pseudoclavata*, *C. pseudoellisii* and *C. tribuli* were isolated from plant hosts, all of them being members of the Poaceae, which is the common host family of *Curvularia* spp., except for *C. tribuli*, which was isolated from *Tribulus terrestris* (Zygophyllaceae). *Curvularia austriaca* has been exclusively isolated from human clinical specimens, i.e. nasal cavity, corneal ulcer and peritoneal dialysis fluid. Other *Curvularia* spp. were previously associated with clinical samples, e.g. *C. australiensis*, *C. hawaiiensis*, *C. lunata* and *C. spicifera* (da Cunha et al. 2013). These taxa are considered potential opportunistic pathogens, causing respiratory tract, cutaneous, cerebral and corneal infections, mainly in immunocompromised patients (McGinnis et al. 1986; Carter and Boudreaux 2004; Madrid et al. 2014). *Curvularia pseudointermedia* and *C. pseudoprotuberata* were isolated from soil. Several species were previously isolated from this substrate (Watanabe 2002; Manamgoda et al. 2011, 2015; Marin-Felix et al. 2017a), demonstrating that soil is a reservoir for *Curvularia* species. Finally, *C. ellisii* and *C. siddiquii*, both validated in this study, were isolated from air.

*Curvularia sichuanensis* (Zhang et al. 2007) was not included in previous phylogenetic studies (Manamgoda et al. 2014; Marin-Felix et al. 2017a, b), although the ITS sequence of the ex-type strain was available. In our phylogenetic study, it clustered close to *C. akaii* and *C. akaiiensis*. The ITS sequence showed only one nucleotide difference with respect to *C. akaiiensis* and three compared to *C. akaii*. Although the

ITS regions alone can resolve the majority of taxa in *Curvularia* (Manamgoda et al. 2015), sequences of *GAPDH* and *TEF1* are needed to clarify if it is a different species. Therefore, the synonymy of *C. sichuanensis* with *C. akaii* remains unconfirmed.

*Curvularia chlamydospora* and *C. pseudolunata*, both clinical species associated with nasal sinus and *C. chlamydospora* also found in a toenail (Madrid et al. 2014), clustered together in the same well-supported clade (100% bs/0.99 pp) without phylogenetic distance. Although ITS and *GAPDH* sequences of the ex-type strains showed 100% nucleotide similarity, these species can be distinguished based on *RPB2* sequences, which had only 94.91% nucleotide similarity. Another two species located in the same well-supported clade (100% bs/1 pp) without phylogenetic distance are *C. harveyi* and *C. gudauskasii*. However, DAOMC 165085, which is the strain identified as *C. gudauskasii* in previous phylogenetic studies (Berbee et al. 1999; Marin-Felix et al. 2017a, b), was not morphologically studied in any previous study, and it was deposited in DAOMC collection as *C. trifolii*. Therefore, the status of this species remains uncertain. *Curvularia borrieriae* and *C. pallescens* were also located in the same clade (72% bs/0.98 pp). According to the descriptions provided by Sivanesan (1987), these species are similar, differing mainly in the colour of the conidia, being almost concolorous in *C. pallescens* and brown or dark brown in *C. borrieriae*. However, the strain CBS 859.73, identified as *C. borrieriae* in previous phylogenetic studies (da Cunha et al. 2013; Marin-Felix et al. 2017a, b; Hernández-Restrepo et al. 2018), is not ex-type and proved to be sterile, making morphological comparisons impossible. Therefore, the potential synonymy of these species remains unresolved.

*Curvularia ahvazensis* was isolated from rotten roots of *Zinnia elegans* in Iran (Mehrabi-Koushki et al. 2018). The ex-type strain of this species clustered in an independent branch with a long distance (Fig. 1). Surprisingly, the *GAPDH* and *TEF1* sequences showed a nucleotide similarity higher than 99% with different *Curvularia* spp., but the ITS sequence presented only 95% nucleotide similarity with the closest species, i.e. *C. hawaiiensis* and *C. sorokiniana*. Considering that the ITS has more constant characters (Manamgoda et al. 2015) and tends to show less nucleotide variability between different species than *GAPDH* (Tan et al. 2018), this sequence needs to be redone to verify if it is correct, and confirm if *C. ahvazensis* is a distinct species. According to our phylogenetic and morphological studies, and the new species and combinations proposed, as well as the synonymy performed, the genus *Curvularia* presently comprises 118 accepted species. However, there are still numerous species that lack molecular data and in a high number of cases due to the lack of type material. Therefore, it is of utmost importance to recollect material of these taxa, and designate epi- or neotypes to secure the application of these

names. In this context, an epitype and ex-epitype culture for *C. oryzae-sativae* is designated here from a strain that morphologically fits with the original description and was isolated from the same host in the same location to that of the holotype.

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