



Multi-locus phylogeny and taxonomy of *Exserohilum*

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Key words

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Abstract *Exserohilum* includes a number of plant pathogenic, saprobic and clinically relevant fungi. Some of these species are of great importance in human activities, but the genus has never been revised in a phylogenetic framework. In this study, we revise *Exserohilum* based on available ex-type cultures from worldwide collections, observation of the holotypes and/or protologues, and additional isolates from diverse substrates and geographical origins. Based on nine nuclear loci, i.e., ITS, LSU, *act*, *tub2*, *cam*, *gapdh*, *his*, *tef1* and *rpb2*, as well as phenotypic data, the genus and species boundaries are assessed for *Exserohilum*. Three species, i.e., *E. novae-zelandiae*, *E. paspali* and *E. sorghicola*, are excluded from the genus and reallocated in *Sporidesmiella* and *Curvularia*, respectively, whereas *E. heteropogoncola* and *E. inaequale* are confirmed as members of *Curvularia*. *Exserohilum rostratum* is revealed as conspecific with species previously described in *Exserohilum* such as *E. antillanum*, *E. gedarefense*, *E. leptochloae*, *E. longirostratum*, *E. macginnisii* and *E. prolatum*. Additionally, *E. curvatum* is revealed as synonym of *E. holmii*, and *E. fusiforme* of *E. oryzicola*. A total of 11 *Exserohilum* phylogenetic species are described, illustrated and discussed, including one novel taxon, *E. corniculatum*. The placements of 15 other doubtful species are discussed, and *E. elongatum* is validated.

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INTRODUCTION

The genus *Helminthosporium* was erected by Link (1809). The type species, *H. velutinum*, is a saprobic dematiaceous fungus occurring on dead stems of *Alnus*, *Cornus*, *Salix* and numerous other plants (Voglmayr & Jaklitsch 2017). It has macronematous, rather straight conidiophores arising from stromata. Conidia are elongate, distoseptate, brown and are produced laterally from small, inconspicuous pores while the conidiophore is elongating. The production of terminal conidia usually determines the end of conidiophore growth (Luttrell 1963b, Hughes 1978, Alcorn 1988a). Originally, *Helminthosporium* was defined very vaguely and over the years it became a repository for numerous taxa of which only a few were congeneric with the type species. MycoBank (<http://www.mycobank.org/>, consulted in September 2017) lists over 760 names in *Helminthosporium*, but currently less than 50 are considered to represent true *Helminthosporium* species (Seifert et al. 2011, Tanaka et al. 2015, Voglmayr & Jaklitsch 2017). Refinements in the taxonomy of this genus resulted in the reallocation of many of its members to genera such as *Alternaria*, *Corynespora*, *Dendryphon*, *Septonema* and others (Bolle 1924, Wei

1950, Subramanian & Jain 1966, Ellis 1971, 1976, Simmons 1971, 2007, Sivanesan 1984, Seifert et al. 2011, Voglmayr & Jaklitsch 2017). Several grass parasites originally described in *Helminthosporium* differed from the type species in producing conidia from sympodial, often strongly geniculate conidiophores (Drechsler 1923). The conidiogenous cells of these fungi had pores which were surrounded by dark scars, in contrast to the inconspicuous small pores of *H. velutinum* (Alcorn 1988a). Nisikado (1928) classified the graminicolous *Helminthosporium* species into two subgenera, *Cylindro-Helminthosporium* and *Eu-Helminthosporium*. *Cylindro-Helminthosporium* included species with straight, cylindrical conidia that germinate from any cell, which later were accommodated in the segregate genus *Drechslera* by Ito (1930) and were often associated with the dictyosporous sexual morph *Pyrenophora* (Shoemaker 1961, Paul & Parbery 1968, Paul 1972). *Eu-Helminthosporium* grouped species with fusiform, often curved conidia which germinate from end cells. Later, Shoemaker (1959) erected *Bipolaris* for taxa previously accommodated in *Eu-Helminthosporium*. *Bipolaris* was a heterogeneous entity which included two subgroups based on differences of the hilum morphology and associated with two different sexual morphs. The group that has conidia with non- or slightly protruding hila was often associated with the sexual morph *Cochliobolus*, characterised by filiform ascospores that often appear more or less coiled in a helix within the ascus (Drechsler 1934, Nelson 1964, Alcorn 1983, 1996, Manamgoda et al. 2011). On the other hand, the group that has conidia with a protruding hilum had sexual morphs with fusoid ascospores enveloped in gelatinous sheaths, which was originally described in *Trichometasphaeria* (Luttrell 1958, 1963a, Nelson 1965). Later Leonard & Suggs (1974) erected *Exserohilum* to accommodate those *Bipolaris* s.lat. species with a distinctly protruding hilum, and *Setosphaeria* for the sexual morph. *Setosphaeria* differs from *Trichometasphaeria* by the production of non-clypeate ascomata which can be erumpent or superficial and produce larger ascospores (Leonard & Suggs

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1974). Recently, Rossman et al. (2015) recommend to use the name *Exserohilum* over *Setosphaeria* according to Article 57.2 of the International Code of Nomenclature for algae, fungi and plants (McNeill et al. 2012). MycoBank currently lists 38 taxa in *Exserohilum*, most of which are associated with diseases of grasses (Sivanesan 1984, 1987), although a few have been described from other substrates such as river sediments (Sivanesan et al. 1993), soil (Guiraud et al. 1997, Steiman et al. 2000), grains (El Shafie 1980), the palm tree *Borassus flabellifer* (Subramanian 1956), plant debris (Castañeda-Ruiz et al. 1995), and humans (McGinnis et al. 1986, Padhye et al. 1986). Members of this genus are distinguished mainly on the basis of morphological features such as conidial shape and size, number of distosepta and the presence or absence of thick, dark distosepta (McGinnis et al. 1986, Sivanesan 1987). So far, eight *Setosphaeria* species have been described, most of which were obtained by mating of compatible isolates (Luttrell 1958, 1963a, Leonard & Suggs 1974, Leonard 1976, Alcorn 1978). However, homothallism has also been described in this genus (El Shafie & Webster 1981, Alcorn 1986). Successful mating is achieved by inoculating compatible strains onto culture media with sterilized fragments of natural substrates such as barley grains, maize leaf or wheat straw (Leonard & Suggs 1974, Alcorn 1978). A pre-incubation step near 5 °C, for a few months may be required before performing the mating tests in some species (Leonard 1976). Some *Exserohilum* s.lat. species show an atypical morphology and have been excluded from the genus by some authors. For instance, *E. heteropogonicola* and *E. inaequale* were reallocated to *Curvularia* as *C. heteropogonicola* and *C. crassiseptum*, respectively (Alcorn 1991, Zhang et al. 2004), and *E. paspali* was considered a synonym of *Bipolaris micropus* (Alcorn 1991). Although species of other genera might belong to *Exserohilum*, as previously noticed by other authors, like in the case of *Helminthosporium leptochloae*, which was considered similar to *E. rostratum* by Alcorn (1991), no synonymy or new combination in *Exserohilum* was proposed.

The type species of *Exserohilum*, *E. turcicum*, was originally described from Italy as *Helminthosporium turcicum* (Passerini 1876). This fungus causes northern leaf blight of corn, a widespread foliar disease characterised by oblong, straw-coloured to greyish necrotic lesions which can coalesce and cause significant death of foliar tissue. The reduction of photosynthetic leaf area can lead, in severe cases, to grain yield losses of 20–25 % (Smith et al. 1988). *Exserohilum turcicum* is also an important blight agent in *Sorghum* spp. (Bunker & Mathur 2006). Other *Exserohilum* species attacking economically relevant crops include *E. pedicellatum* (causing root rot of maize and brown lesions on wheat roots), *E. prolatum* (producing leaf spots on maize), and *E. rostratum* (associated with leaf spot and foot rot of wheat, damping off of sugarcane seedlings, leaf spot of banana, and blackening and seed germination failure in many cereals) (Sivanesan 1987, Lin et al. 2011). Many *Exserohilum* species attack weeds and some of them have been proposed as potential biocontrol agents, e.g., *E. monoceras* against *Echinochloa* spp. (Zhang & Watson 1997, Tosiah et al. 2011) and *E. prolatum* against *Rottboellia cochinchinensis* (Alloub et al. 2009). Presently, *Exserohilum* species have been reported from over 30 plant genera (Sivanesan 1987, 1992, Pachkhede 1989, Wu 1990, Sun et al. 1997, Chen et al. 2002, Lin et al. 2011, Sakoda & Tsukiboshi 2011).

Exserohilum spp. are emerging agents of opportunistic, sometimes life-threatening infections in humans. The most commonly reported species is *E. rostratum*, but some cases are attributed to *E. longirostratum* and *E. macginnisii* (McGinnis et al. 1986, De Hoog et al. 2000, Al-Attar et al. 2006). They have a broad clinical spectrum that includes skin infections (Hsu & Lee 1993, Lin et al. 2009), keratitis (Bouchon et al. 1994, Mathews &

Maharajan 1999, Joseph et al. 2012), non-invasive allergies (Friedman et al. 1991, Torres et al. 1996) and invasive sinusitis (Lasala et al. 2005, Togitani et al. 2007, Derber et al. 2010) and disseminated infections (Bhigjee et al. 1993, Aquino et al. 1995, Levy et al. 2003). Predisposing factors include traumatism, especially with plant material for keratitis, atopy for non-invasive sinusitis and immunosuppression for skin infections, invasive sinusitis and disseminated disease (Adler et al. 2006, Joseph et al. 2012). Recently, *E. rostratum* was reported as the main etiological agent in a dramatic outbreak of infections associated with contaminated glucocorticoid injections in the USA. The outbreak involved several states and there were over 749 reported cases of infection of which 31 % presented meningitis. Six percent of the infections were fatal (Kainer et al. 2012, Smith et al. 2013). A case of dermal granulomas caused by *Exserohilum* sp. in a bovine was reported by Whitford et al. (1989). Some authors have suggested that the three mentioned clinically-relevant *Exserohilum* species are conspecific based on analyses of sequences of the internal transcribed spacer region (ITS), the large subunit ribosomal rDNA (LSU), the actin (*act*) and the translation elongation factor 1-alpha (*tef1*) genes (Lin et al. 2011, Da Cunha et al. 2012).

Phylogenetic studies based on different loci indicated that *Exserohilum* belongs to the *Pleosporaceae*, *Pleosporales* (Berbee et al. 1999, Olivier et al. 2000, Zhang & Berbee 2001, Rossman et al. 2002, Kodsueb et al. 2006, Zhang et al. 2009, 2012, Amardasa et al. 2014). However, none of these studies included more than four species of the genus, and so a reassessment of the genus is necessary to determine the evolutionary relationships of the remaining species. A revision of these fungi is also necessary to clarify the phylogenetic placement of species with atypical morphology, and to assess whether previously suggested synonymies (Alcorn 1991, Zhang et al. 2004) are correct. In this paper we present a monograph of the genus *Exserohilum* based on the analysis of multi-locus sequence data and the morphological study of numerous isolates and herbarium collections. A robust phylogenetic tree based on seven loci is provided, representing the main plant-pathogens and clinically-relevant species.

MATERIAL AND METHODS

Fungal isolates

The *Exserohilum/Setosphaeria* isolates included in this study were obtained from various substrates and countries and acquired from public culture collections, including the Westerdijk Fungal Biodiversity Institute (CBS; Utrecht, The Netherlands), the Faculty of Medicine of the Universitat Rovira i Virgili (FMR; Reus, Spain) and the Queensland Plant Pathology Herbarium (BRIP; Brisbane, Australia) as listed in Table 1. Herbarium specimens were loaned from the US National Fungus Collections (BPI; Maryland, USA), BRIP, Canadian National Mycological Herbarium (DAOM; Ottawa, Canada) and the Kew Royal Botanical Gardens (IMI; Kew, England).

Phenotypic study and species descriptions

Colony morphology was studied mainly on synthetic nutrient-poor agar (SNA, Nirenberg 1976) supplemented with fragments of sterilized maize or banana leaves, after 7 d of incubation at 24 °C in the dark. Microscopic features were studied in clear lactic acid from colonies growing on the culture media mentioned above after 7–14 d of incubation at 24 °C under near UV light with a 12 h photoperiod. Fungal structures from herbarium material were also mounted in lactic acid, but these were gently heated with the flame of a Bunsen burner before observation if they appeared dehydrated. Size ranges of each structure in the species descriptions are derived from at least 30 measurements.

Table 1 Details of isolates included in phylogenetic analyses. GenBank accession numbers in **bold** were newly generated in this study. New species and new combinations are indicated in **bold italic**.

Taxon	Old name/identified as ¹	Strain no. ²	Other collections ²	Status of the strain ^{1,3}	Geographical origin (country, province, locality)	Substrate	ITS	LSU	act	cam	tef1	gapdh	his	tub2	rpb2	
<i>Bipolaris chloridis</i>	CBS 242.77B	ATCC 34706; IMI 208338			Australia	<i>Chloris gayana</i>	HF934928	HF934869	-	-	-	HG779083	-	-	HF934830	
	CBS 285.51				Kenya	<i>Cynodon transvaalensis</i>	HF934929	HF934874	-	-	-	HG779081	-	-	HF934831	
<i>B. cynodontis</i>	CBS 305.64				USA	<i>Cynodon dactylon</i>	HF934930	HF934883	-	-	-	HG779082	-	-	HF934832	
	CBS 130.26	ATCC 22246			Unknown	Unknown	HF934923	HF934873	-	-	-	HG779084	-	-	HF934825	
	CBS 136.29			PT	Japan	Unknown	HF934926	HF934879	-	-	-	HG779086	-	-	HF934828	
<i>B. microlaenae</i>	CBS 280.91	BRIP 15613; IT: IMI 335218		T	Australia	<i>Microlaena stipoides</i>	HF934933	HF934877	-	-	-	HG779092	-	-	HF934835	
	CBS 157.50				Indonesia	<i>Oryza sativa</i>	HF934931	HF934870	-	-	-	HG779090	-	-	HF934833	
<i>B. oryzae</i>	CBS 199.54	MUCL 9689			New Guinea	<i>Oryza sativa</i>	HF934932	HF934884	-	-	-	HG779091	-	-	HF934834	
	CBS 249.49			T	Unknown	<i>Sorghum vulgare</i> var. <i>sudanense</i>	HF934927	HF934868	-	-	-	HG779087	-	-	HF934829	
	CBS 294.61				Brazil	Air	HF934910	HF934902	-	-	-	HF565450	-	-	HF934812	
<i>C. akaii</i>	CBS 318.86				Japan	Unknown	HF934921	HF934897	-	-	-	HG779118	-	-	HF934823	
	CBS 127728	IMI 309517			Japan	<i>Themeda triandra</i>	HF934920	HF934898	-	-	-	HG779119	-	-	HF934822	
	CBS 127726			T	India	Unknown	KJ415539	KJ415494	-	-	-	KJ415407	-	-	HF934822	
<i>C. andropogonis</i>	CBS 186.49				Indonesia	<i>Andropogon nardus</i>	LT631354	LT715570	-	-	-	LT715835	-	-	LT652470	
	CBS 859.73				Chile	Volcanic ash soil	HE861848	LT715573	-	-	-	HF565455	-	-	LT652471	
<i>C. carica-papayae</i>	CBS 135941			T	India	<i>Carica papaya</i>	HG778984	HG779031	-	-	-	HG779146	-	-	HG779162	
	CBS 110673				Unknown	Unknown	LT631357	LT715576	-	-	-	LT715841	-	-	LT652472	
	CBS 503.90			T	Nigeria	Plant material	LT631310	LT715613	-	-	-	LT715882	-	-	LT652473	
<i>C. cymbopogonis</i>	CBS 419.78	IT: BRIP 14583			Netherlands	<i>Yucca</i> sp.	HG778985	HG779032	-	-	-	HG779129	-	-	HG779163	
	CBS 537.70				Denmark	<i>Sorghum vulgare</i>	LT631356	LT715574	-	-	-	LT715839	-	-	LT652474	
	CBS 210.79				Romania	<i>Gladolius</i> sp.	HG778987	HG779034	-	-	-	HG779123	-	-	HG779165	
<i>C. hawaiiensis</i>	CBS 173.57	BRIP 14579		T	Hawaii	<i>Oryza sativa</i>	HG778988	HG779035	-	-	-	HG779140	-	-	HG779166	
	CBS 128052			T	India	<i>Heteropogon contortus</i>	KJ415548	KJ415503	-	-	-	KJ415398	-	-	LT175769	
	CBS 284.91			T	Australia	<i>Heteropogon contortus</i>	HF934919	HF934893	-	-	-	HF934919	-	-	HF934821	
<i>C. kusanol</i>	CBS 511.91			ET	Australia	<i>Heteropogon contortus</i>	HF934918	HF934894	-	-	-	HF934918	-	-	HF934820	
	CBS 137.29			T	Japan	<i>Eragrostis major</i>	JN192381	JN600993	-	-	-	LT175862	-	-	LT175733	
	CBS 730.96			T	USA	<i>Homo sapiens</i>	HF934911	HF934900	-	-	-	JX256429	-	-	HF934813	
<i>C. lunata</i>	BRIP 6516	CBS 127234; IMI 312021			USA	<i>Paspalum notatum</i>	HE792933	LT715598	-	-	-	LT715858	-	-	LT1715730	
	CBS 127235	BRIP 6520; IMI 312022		ET	USA	<i>Paspalum notatum</i>	HE792934	LT715599	-	-	-	LT715859	-	-	LT1715731	
	BRIP 15689a	CBS 127236			USA	<i>Paspalum notatum</i>	HE792935	LT715600	-	-	-	LT715860	-	-	LT1715732	
<i>C. nicotlae</i>	BRIP 16070	CBS 128057		IT	Brazil	<i>Paspalum conjugatum</i>	LT837854	LT715597	-	-	-	LT715857	-	-	LT1715729	
	CBS 655.74			A	Algeria	Desert soil	KJ909772	KM243291	-	-	-	KM083614	-	-	LT1715729	
	CBS 161.58				Unknown	<i>Eleusine indica</i>	-	LT715603	-	-	-	LT715863	-	-	LT1715734	
<i>C. nodulosa</i>	CBS 239.48			IT	USA	<i>Portulaca oleracea</i>	KJ909775	LT715594	-	-	-	LT715855	-	-	-	
	CBS 127241				Unknown	Unknown	LT715593	-	-	-	LT715855	-	-	LT715855	-	-
	CBS 143.64			T	India	<i>Jasminum sambac</i>	HG778996	HG779043	-	-	-	HG779147	-	-	HG779174	
<i>C. prasadii</i>	CBS 198.31				Cyprus	<i>Capsicum annuum</i>	HF934916	HF934905	-	-	-	HG779136	-	-	HF934818	
	CBS 199.31				Cyprus	<i>Cucurbita maxima</i>	HF934915	HF934903	-	-	-	HG779137	-	-	HF934817	
	CBS 173.55				USA	<i>Trifolium repens</i>	HG779023	HG779077	-	-	-	HG779124	-	-	HG779208	
<i>Exserohilum corniculatum</i>	BRIP 11426	IT: IMI 167611		T	Australia	<i>Oryza sativa</i>	LT837453	LT883391	LT837589	LT838283	LT883558	LT883533	LT860104	LT896678	LT852480	
	BRIP 12679				Australia	<i>Dactyloctenium aegyptium</i>	LT837846	LT883453	LT837678	LT852460	LT896667	LT862542	LT860190	LT899370	LT882525	
	CBS 318.64	ATCC 58199			Unknown	<i>Dactyloctenium aegyptium</i>	LT837457	LT883395	LT837596	LT838290	LT883565	LT883537	LT860111	LT896686	LT852487	
<i>H. holmii</i>	CBS 319.64				Unknown	<i>Dactyloctenium aegyptium</i>	LT837458	LT715622	LT837597	LT838291	LT883566	LT715891	LT860112	LT896685	LT852488	
	CBS 413.65	ATCC 15226		IST of <i>H. holmii</i>	USA	<i>Dactyloctenium aegyptium</i>	LT837459	LT715621	LT837598	LT838292	LT883567	LT715890	LT860113	LT896687	LT852489	
	CBS 414.65	IT: IMI 281326; CBS 132712		A of <i>T. holmii</i>	USA	<i>Dactyloctenium aegyptium</i>	LT837460	LT883396	LT837599	LT838293	LT883568	LT883538	-	-	-	
<i>E. curvatum</i>	CBS 505.90	IT: IMI 281326; CBS 132712		T of <i>E. curvatum</i>	Venezuela	<i>Sorghum vulgare</i>	KT265252	LT715620	LT837591	LT838285	LT883560	LT715889	LT860106	LT896680	LT852482	
	CBS 128053	BRIP 12792		T of <i>E. curvatum</i>	Thailand	<i>Dactyloctenium aegyptium</i>	KT265253	LT883441	LT837663	LT852447	LT896652	LT882555	LT715884	LT899383	LT882513	
	IMI 249194	CBS 132708		IT	Sudan	<i>Sorghum bicolor</i> var. <i>meyo</i>	LT837461	LT715619	LT837600	LT838294	LT883569	LT715888	LT862489	LT896688	LT852490	
<i>E. kharfourmensis</i>	BRIP 14612			T of <i>E. curvatum</i>	Australia	Ascoarops formed by BRIP 13597	LT837467	LT715616	LT837609	LT838303	LT883577	LT715884	LT860121	LT896696	LT852491	
	BRIP 14614				Australia	<i>Dactyloctenium aegyptium</i>	LT837468	LT715616	LT837610	LT838304	LT883578	LT715885	LT860122	LT896697	LT852500	
	BRIP 14615	IT: IMI 294530b, DAR 51591, ATCC 62323		T of <i>S. minor</i>	Australia	<i>Dactyloctenium aegyptium</i>	LT837469	LT883402	LT837611	LT838305	LT883579	LT883544	LT860123	LT896698	LT852501	
<i>E. minor</i>	BRIP 14616	IT: IMI 294530a, DAR 51590		T of <i>E. minor</i>	Australia	<i>Dactyloctenium aegyptium</i>	LT837470	LT883403	LT837612	LT838306	LT883580	LT883545	LT860124	LT896699	LT852502	
	BRIP 1542				Australia	<i>Setaria italica</i>	LT837473	LT883404	LT837615	LT838309	LT896604	LT883546	LT860127	LT896702	LT852505	
	BRIP 12236				Australia	<i>Echinochloa colona</i>	LT837472	LT715637	LT837614	LT838308	LT896603	LT715876	LT860126	LT896701	LT852504	

Table 1 (cont.)

Taxon	Old name/ identified as ¹	Strain no. ²	Other collections ²	Status of the strain ^{1,3}	Geographical origin (country, province, locality)	Substrate	ITS	LSU	act	cam	tef1	gadh	his	tub2	rbp2	
<i>E. rostratum</i> (cont.)	<i>E. antillarum</i>	CBS 412-93	FMR 4465, IMI 358615	IT of <i>E. antillarum</i>	Cuba	Plant debris from forest soil	KT265246	LT1715625	LT837587	LT838281	LT883556	LT1715894	LT860102	LT896676	LT852478	
	<i>S. rostrata</i>	CBS 467-75	ATCC 32198, IMI 197580, SFA3		Unknown	Unknown	LT837880	HE664026	LT837682	LT852464	HE664081	LT882538	LT860194	LT899386	LT882529	
	<i>S. proleta</i>	CBS 571-73	ATCC 24775, IMI 175436	A of <i>S. proleta</i>	USA	<i>Zea mays</i>	LT837831	LT1715623	LT837657	-	LT896646	LT1715892	LT860169	LT899389	LT1715760	
		CBS 572-73	ATCC 24774, IMI 175435	A of <i>S. proleta</i>	Guatemala	<i>Zea mays</i>	LT837832	LT1715624	LT837658	-	LT896647	LT1715893	LT860170	LT899388	LT1715759	
		CBS 504-90	IMI 276558		Sudan	<i>Sorghum bicolor</i>	KT265243	LT883394	LT837595	LT838289	LT883564	LT838289	LT883536	LT860107	LT896684	LT852486
	<i>B. australiensis</i> ;	CBS 705-71			India	Soil	LT837841	LT883448	LT837673	LT852455	LT896662	LT882547	LT860185	LT899351	LT882520	
	<i>D. australiensis</i>															
	<i>E. rostratum</i>	CBS 706-71			India	Soil	LT837842	LT883449	LT837674	LT852456	LT896663	LT882546	LT860186	LT899350	LT882521	
	<i>S. rostrata</i>	CBS 732-96	AMMRL 106-9, PPCC 19686		Unknown	<i>Zea mays</i>	KT265240	LT1715631	LT837669	LT852452	LT896658	LT1715900	LT860181	LT899353	LT1715752	
	<i>E. macginnisii</i>	CBS 120308			Unknown	<i>Homo sapiens</i>	KT265236	LT883435	LT837653	LT852442	LT896642	LT882561	LT860165	LT899392	LT882507	
	<i>D. microspus</i>	CBS 127233	DAOM 71176		USA	<i>Leptochloa filliformis</i>	LT837454	LT883392	LT837590	LT838284	LT883559	LT883534	LT860105	LT896679	LT852481	
<i>E. longirostratum</i>	CBS 128054	BRIP 21343 R,11,1,OB40		Namibia	<i>Acacia mellifera</i> subsp. <i>definis</i>	LT837451	LT1715628	LT837586	LT838280	LT883555	LT1715897	LT860101	LT896675	LT852477		
<i>E. longirostratum</i>	CBS 128055	BRIP 21347		Namibia	<i>Acacia mellifera</i> subsp. <i>definis</i>	LT837478	LT883407	LT837620	LT838314	LT896609	LT883549	LT860132	LT898519	LT852509		
<i>S. rostrata</i> ,	CBS 128060	BRIP 12214, Lutt. 8686		USA	<i>Zea mays</i>	KT265245	LT883397	LT837604	LT838298	LT883572	LT883539	LT860116	LT896691	LT852494		
mating type A																
<i>S. rostrata</i> ,	CBS 128061	BRIP 12218, Lutt. 8868		USA	<i>Zea mays</i>	KT265240	LT1715631	LT837669	LT852452	LT896658	LT1715900	LT860181	LT899353	LT1715752		
mating type A																
<i>S. rostrata</i>	CBS 128062	BRIP 12224		Australia	On Barley seed on Sach's agar	KT265247	LT883457	LT837683	LT852465	LT896671	LT882537	LT860195	LT899385	LT882530		
<i>S. rostrata</i>	CBS 128063	BRIP 12223, SFA10		USA	Ascospore isolate from Hay 3 x IMI 76563	KT265239	LT883398	LT837605	LT838299	LT883573	LT883540	LT860117	LT896692	LT852495		
	FMR 11028	UTHSC 08-655		USA	<i>Homo sapiens</i>	LT837837	LT883444	LT837668	-	LT896657	LT882551	LT860180	-	LT882495		
	FMR 11271	UTHSC 05-3456		USA	<i>Homo sapiens</i>	LT837496	LT883423	LT837638	LT838321	LT896627	LT882573	LT860150	-	LT882492		
	FMR 11278	UTHSC 06-2113		USA	<i>Homo sapiens</i>	LT837493	LT883420	LT837635	LT838318	LT896624	LT882576	LT860147	-	LT882493		
	FMR 11280	UTHSC 06-3237		USA	<i>Homo sapiens</i>	LT837494	LT883421	LT837636	LT838319	LT896625	LT882575	LT860148	-	LT882493		
	FMR 11286	UTHSC 07-1292		USA	<i>Homo sapiens</i>	LT837848	LT883455	LT837680	LT852462	LT896669	LT882540	LT860192	LT899368	LT882527		
	FMR 11372	UTHSC 07-1310		USA	<i>Homo sapiens</i>	LT837497	LT883424	LT837639	LT838322	LT896628	LT882572	LT860151	-	LT882496		
	FMR 11390	UTHSC 08-2940		USA	<i>Homo sapiens</i>	LT837495	LT883422	LT837637	LT838320	LT896626	LT882574	LT860149	-	LT882494		
	FMR 11392	UTHSC 08-3638		USA	<i>Homo sapiens</i>	LT837489	LT883416	LT837631	-	LT896620	LT882580	LT860143	-	LT882518		
	FMR 11399	UTHSC 09-131		USA	<i>Homo sapiens</i>	LT837838	LT883445	LT837670	-	LT896622	LT882578	LT860182	-	LT882517		
	FMR 11399	UTHSC 09-1259		USA	<i>Homo sapiens</i>	LT837833	LT883445	LT837670	-	LT896659	LT882550	LT860182	-	LT882514		
	FMR 11773	IP 1229-80		Martinique	<i>Homo sapiens</i>	LT837834	HE664025	LT837665	LT852449	LT896654	LT882554	LT860177	LT899357	LT882514		
<i>D. longirostrata</i>	BRIP 12267			Australia	<i>Sorghum bicolor</i>	LT837482	LT883411	LT837624	-	LT896613	LT883553	LT860136	LT899337	LT882513		
<i>S. turcica</i>	BRIP 13326			Australia	<i>Sorghum sudanense</i>	LT837480	LT883409	LT837622	-	LT896611	LT883551	LT860134	LT898521	LT852511		
<i>S. turcica</i>	CBS 195-26			Indonesia	<i>Zea mays</i>	LT837485	LT883413	LT837627	-	LT896616	LT882583	LT860139	LT899340	-		
<i>S. turcica</i>	CBS 384-58			USA	Single ascospore isolate from holotype of <i>S. turcica</i>	LT837481	LT883410	LT837623	-	LT896612	LT883552	LT860135	LT899336	LT852512		
	CBS 330-64			USA	<i>Zea mays</i>	LT837484	LT1715639	LT837626	-	LT896615	LT1715874	LT860138	LT899339	LT852515		
	CBS 385-58			USA	Single ascospore isolate from holotype of <i>S. turcica</i>	LT837488	LT1715640	LT837630	-	LT896619	LT1715873	LT860142	-	LT852516		
	CBS 386-58	ATCC 13068, NRRL 5239		USA	<i>Sorghum halepense</i>	LT837486	LT883414	LT837628	-	LT896617	LT882582	LT860140	LT899341	-		
	CBS 387-58	NRRL 5240		USA	<i>Zea mays</i>	LT837483	LT883412	LT837625	-	LT896614	LT883554	LT860137	LT899338	LT852514		
	CBS 690-71			Germany	<i>Zea mays</i>	LT837487	LT883415	LT837629	-	LT896618	LT882581	LT860141	LT899342	-		
<i>Porococcospora seminalis</i>	CBS 134906	CPC 21305		USA	<i>Bouteloua dactyloides</i>	HF934942	HF934865	-	-	-	-	-	-	HF934847		
	CPC 21330			USA	<i>Bouteloua dactyloides</i>	HF934948	HF934863	-	-	-	-	-	-	HF934849		
	CPC 21333			USA	<i>Bouteloua dactyloides</i>	HF934946	HF934859	-	-	-	-	-	-	HF934850		
	CBS 280-31			USA	<i>Hordeum vulgare</i>	HF934954	HF934857	-	-	LT1715872	-	-	-	HF934856		

¹ *B. Bipolaris*; *C. Curvularia*; *D. Drechslera*; *E. Exserohilum*; *H. Helminthosporium*; *S. Setosphaeria*; *T. Trichometasphaeria*.
² ATCC: American Type Culture Collection, Bethesda, Maryland, USA; BRIP: Queensland Plant Pathology Herbarium, Brisbane, Australia; CBS: Westerdijk Fungal Biodiversity Institute, Utrecht, The Netherlands; FMR: Faculty of Medicine collection, Reus, Spain; DAOM: Canadian National Mycological Herbarium, Ottawa, Canada; IMI: Kew Royal Botanical Gardens, Kew, England; MUCL: Mycopathologie de L'Université Catholique de Louvain, Louvain-la-Neuve, Belgium; UTHSC: Fungus Testing Laboratory, University of Texas Health Science Center, San Antonio Texas, USA.
³ ET: ex-epitype; IT: ex-isoepitype; IST: ex-isosyntype; PI: ex-paratype; ST: ex-syntype; T: ex-holotype; A: Authentic strain.
⁴ ITS: internal transcribed spacer region; LSU: large subunit ribosomal RNA gene; act: partial actin gene; tub.2: partial β -tubulin gene; cam: partial calmodulin gene; gadpr: partial glyceraldehyde-3-phosphate dehydrogenase gene; his: partial histone H3 gene; tef1: partial translation elongation factor-1 alpha gene; rbp2: RNA polymerase II second largest subunit gene.

Molecular study

DNA extraction was carried out from colonies growing on MEA with the UltraClean® Microbial DNA Isolation Kit (Mo Bio Laboratories, Inc., Solana Beach, CA, USA). Amplification and sequencing of nine nuclear loci, i.e., the internal transcribed spacer (ITS) region, large subunit ribosomal RNA gene (LSU), actin (*act*), β -tubulin (*tub2*), calmodulin (*cam*), glyceraldehyde-3-phosphate dehydrogenase (*gapdh*), histone H3 (*his*), translation elongation factor-1 alpha (*tef1*) and RNA polymerase II second largest subunit (*rpb2*) were performed with primers V9G (De Hoog & Gerrits van den Ende 1998) + ITS4 (White et al. 1990), LROR + LR5 (Vilgalys & Hester 1990), Act1 + Act4 (Voigt & Wöstemeyer 2000), T1 (O'Donnell & Cigelnik 1997) + Bt2b (Glass & Donaldson 1995), CAL228F + CAL737R (Carbone & Kohn 1999), gpd1 + gpd2 (Berbee et al. 1999), CYLH3F + CYLH3R (Crous et al. 2004), 983F + 2218R (Rehner & Buckley 2005) and 5F2 + 7cR (O'Donnell et al. 2007), respectively. Sequencing was performed with the BigDye terminator sequencing kit v. 3.1 (Applied Biosystems) and an ABI Prism™ 3100 DNA sequencer (Applied Biosystems). The program SeqMan Pro (Lasergene, Madison, Wisconsin) was used to obtain consensus sequences from the complementary sequences of each isolate. BLAST queries (Altschul et al. 1990) were performed to compare sequences of the studied isolates with those of other fungi deposited in GenBank. Alignments were produced with MAFFT v. 7 (Kato & Standley 2013), checked and refined using MEGA v. 6 (Tamura et al. 2013) and SequenceMatrix (Vaidya et al. 2011).

Two multi-locus phylogenies were analysed in order to evaluate the generic placement of the strains and to establish the phylogenetic relationship among species of *Exserohilum* s.str. The generic placement is based on a concatenated ITS, LSU, *gapdh* and *rpb2* dataset including species of *Exserohilum* s.lat. and representatives of other helminthosporoid genera (i.e., *Bipolaris*, *Curvularia*, *Johalcornia* and *Porocercospora*), and *Pyrenophora* used as outgroup. This phylogeny was constructed to assess if *Exserohilum* is a well-delimited genus, and to corroborate if the previous reallocation of *E. heteropogonicola* and *E. inaequalis* to *Curvularia*, and the synonymy of *E. paspali* with *Bipolaris micropus* are correct.

The second multi-locus phylogeny was based on a concatenated alignment of ITS, *act*, *tub2*, *gapdh*, *his*, *tef1* and *rpb2* and included 98 isolates of *Exserohilum/Setosphaeria*, excluding *E. paspali*. This analysis was performed to evaluate species boundaries and species groupings within *Exserohilum*. Individual alignments of each locus and the concatenated four- and seven-locus datasets were analysed by maximum likelihood (ML) with gamma model of rate heterogeneity using the RAxML HPC BlackBox v. 8.2.8 (Stamatakis 2014) online server of the Cipres Science gateway portal (Miller et al. 2010). The maximum likelihood search option was used to search for the best-scoring tree after bootstrapping. By default, the RAxML BlackBox calculates statistical support for branches by rapid bootstrap analyses of 1000 replicates (Stamatakis 2014). Bootstrap support (bs) values $\geq 70\%$ were considered significant. Incongruence among datasets was tested by a visual inspection of all groups with $\geq 70\%$ bs in partial trees of each locus to search for potentially conflicting groups. A Markov Chain Monte Carlo (MCMC) algorithm was used to generate phylogenetic trees with Bayesian probabilities from the concatenated four-locus and seven-locus datasets using MrBayes v. 3.2.6 (Ronquist et al. 2012). The best models of nucleotide substitution for each locus were determined using MrModeltest v. 2.3 (Nylander 2004) and the critical value for the topological convergence diagnostic set to 0.01. Two analyses of four MCMC chains were run from random trees, trees were sampled

every 100 generations and 25 % of them were discarded as the burn-in phase. Posterior probabilities (pp) were determined from the remaining trees. The sequences generated during this study and the alignments used in the phylogenetic analyses were deposited in GenBank (Table 1) and TreeBASE (Submission 21627), respectively.

RESULTS

Molecular and phylogenetic analysis

In *Exserohilum*, amplification success rate varied among the different loci tested, i.e., 100 % for ITS, LSU, *act*, *gapdh* and *tef1*, 99 % for *his*, 94 % for *rpb2*, 87 % for *tub2* and 82 % for *cam*. BLAST searches with the ITS sequences revealed that *E. heteropogonicola* and *E. inaequale* are in fact members of *Curvularia* as suggested by Sivanesan (1984) and Zhang et al. (2004). The closest hit for the ITS sequence of CBS 128057, the authentic isolate of *E. paspali*, were three sequences of *B. micropus*, i.e., GenBank accession numbers HE792933, HE792934 and HE792935 (corresponding to CBS 127234, CBS 127235, CBS 127236, respectively), all of them 99 % identical. No close hits were found for the ITS sequence of *E. novae-zelandiae* CBS 135842 (not type strain), but its LSU was 91 % identical to *Conlarium duplumascospora* (GenBank accession numbers JN936991, JN936992, JN936993), a member of *Annulatascaceae*, *Sordariomycetes* (Liu et al. 2012). This clearly indicates that *E. novae-zelandiae* is not a member of *Exserohilum* and should be excluded from this genus, thus a new combination is proposed in *Sporidesmiella*.

The first concatenated matrix contains 3192 nucleotide characters, i.e., 616 from *gapdh*, 834 from ITS, 882 from LSU and 860 from *rpb2*. The second concatenated alignment contains 4736 nucleotide characters, i.e., 653 from *act*, 597 from *gapdh*, 387 from *his*, 794 from ITS, 860 from *rpb2*, 896 from *tef1* and 549 from *tub2*. For Bayesian analysis, MrModeltest proposed a GTR + I + G model for ITS, SYM + G for *act*, *gapdh* and *rpb2*, HKY + G for *tub2*, HKY + I + G for *his* and GTR + I + G for *tef1*. These models were incorporated in the analysis. During the generation of the Bayesian seven-locus tree, a total of 49666 trees were sampled out of the 66222 trees generated (75 %). The consensus tree obtained from the Bayesian analysis agreed with the topology of the best-scoring ML tree for the concatenated four-locus dataset (Fig. 1). Species of *Exserohilum* formed a well-supported clade (100 % bs / 1 pp) clearly separated from other graminicolous helminthosporoid genera, such as *Bipolaris*, *Curvularia*, *Johalcornia*, *Porocercospora* and *Pyrenophora*. Interestingly, the authentic isolate of *Exserohilum paspali* CBS 128057 formed a clade with three isolates of *Bipolaris micropus* (CBS 127234, CBS 127235 and CBS 127236), which appeared more closely related to the genus *Curvularia* than to *Exserohilum* or *Bipolaris*. These results are in partial concordance with a previous proposal of *E. paspali* as a synonym of *B. micropus* by Sivanesan (1987) based on morphology. Nevertheless, they are phylogenetically closely related to *Curvularia* (Fig. 1) and a new combination is proposed in the taxonomy section.

The combined phylogenetic tree inferred based on seven loci (Fig. 2) revealed the existence of 11 phylogenetic species in *Exserohilum*, including one novel taxon, *E. corniculatum*, which is described in the taxonomy section. Species in *Exserohilum* (Fig. 2) were distributed into two major fully supported subclades. The first clade includes isolates identified as *E. corniculatum*, *E. holmii*, *E. khartoumensis*, *E. minor*, *E. neoregeliae* and *E. rostratum*, whereas the second clade included isolates of *E. monoceras*, *E. oryzicola*, *E. pedicellatum*, *E. protrudens* and *E. turcicum*. Most species in the first subclade show one

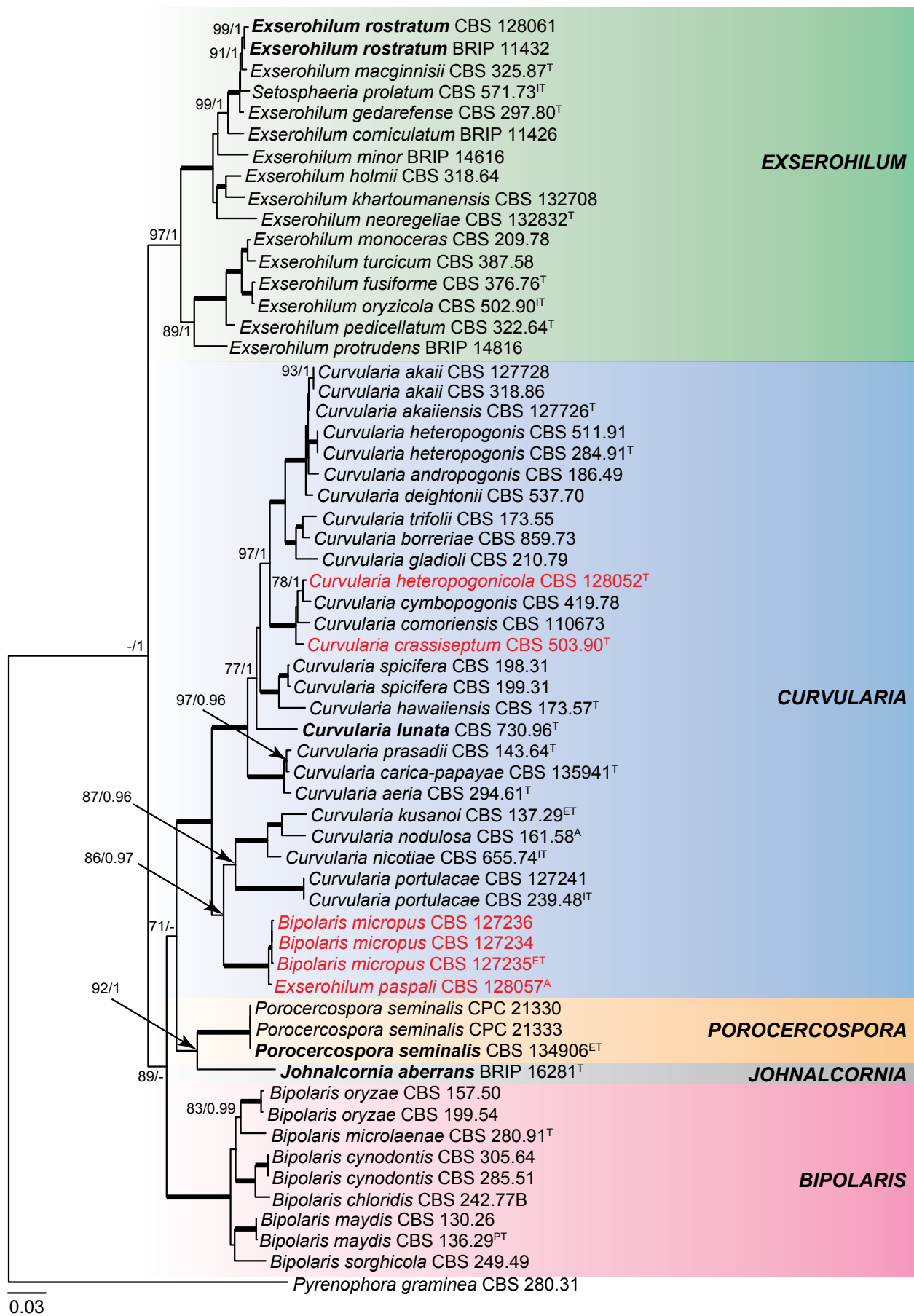


Fig. 1 Phylogenetic tree inferred from a RAxML analysis based on a concatenated alignment of ITS, LSU, *gapdh* and *rpb2* sequences of *Exserohilum* and related genera in *Pleosporaceae*. The bootstrap support values and Bayesian posterior probabilities are given at the nodes (MLBS/BPP). Clades with 100 % MLBS and 1 BPP are indicated by thick lines. In red font are indicated taxa previously known as *Exserohilum*. Ex-type, ex-isotype, ex-epitype and ex-paratype and authentic strains are indicated as T, IT, ET, PT, A, respectively. Generic types are indicated in bold. The tree was rooted to *Pyrenophora graminea* CBS 280.31.

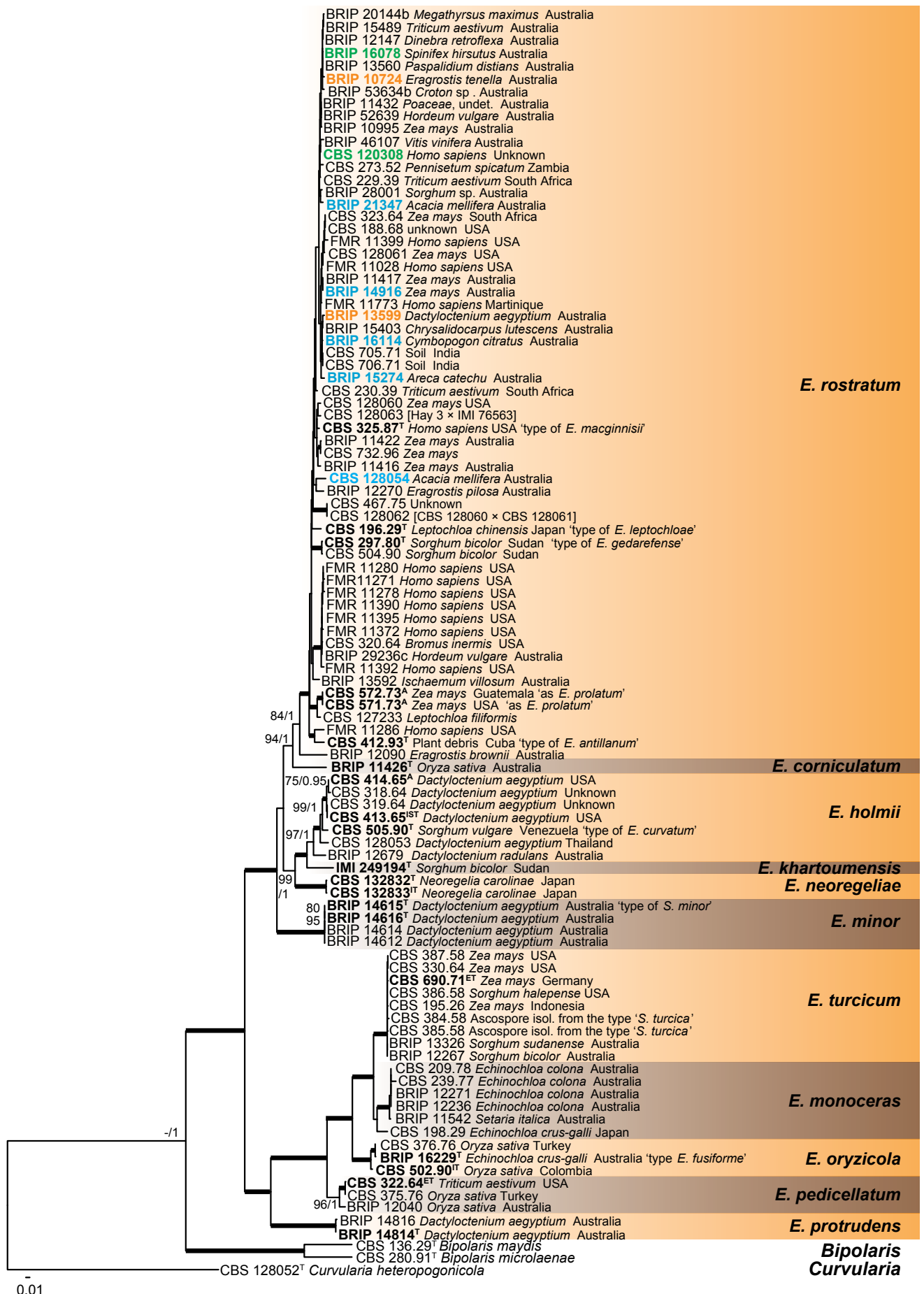


Fig. 2 Phylogenetic tree inferred from a RAXML analysis based on a concatenated alignment of ITS, *act*, *gapdh*, *his*, *rpb2*, *tef1* and *tub2* sequences of *Exserohilum* s.str. The bootstrap support values and Bayesian posterior probabilities are given at the nodes (MLBS/BPP). Clades with 100 % MLBS and 1 BPP are indicated by thickened lines. In the *E. rostratum* clade in green font are indicated taxa previously identified as *E. macginnisii*, in blue identified as *E. longirostratum*, in orange as *E. holmii*. Ex-type, ex-isotype, ex-neotype and ex-epitype strains are indicated in bold. The tree was rooted to *Bipolaris maydis* CBS 136.29, *B. microlaenae* CBS 280.91 and *Curvularia heteropogonicola* CBS 128052.

or more accentuated septa (dark and thick), especially in polar cells. The subclade comprising most isolates includes *E. rostratum* and *E. corniculatum*. Besides the numerous isolates of *E. rostratum*, it also includes several isolates identified as *E. longirostratum* and the ex-type strains of *E. antillanum*, *E. gedarefense*, *E. macginnisii*, *E. prolatum* and *Helminthosporium leptochloae*. Morphological and molecular analyses suggest that those species are conspecific with *E. rostratum* and are treated here as synonyms in the taxonomy section. All clinical isolates included in our study belong to *E. rostratum*. The second subclade includes isolates of *E. curvatum*, *E. holmii*, *E. khartoumensis* and *E. neoregeliae*. Morphological and molecular analyses suggest that *E. curvatum* is conspecific with *E. holmii* and is treated here as synonym in the taxonomy section. A clade formed by four isolates of *E. minor* revealed mostly fusiform conidia which lack accentuated septa, and they have a homothallic sexual behaviour.

Another subclade included *E. fusiforme*, *E. monoceras*, *E. oryzicola* and *E. turcicum*. Morphological and molecular analyses suggest that *E. fusiforme* is conspecific with *E. oryzicola* and is treated here as synonym in the taxonomy section. All isolates in this subclade are characterised by mostly fusiform conidia which lack accentuated septa and show heterothallic sexuality. Two subclades grouped species showing conidia with a prominent subcylindrical basal extension in their conidia, at the base of which the hilum appears. One of these subclades includes two isolates of *E. protrudens* and the other one includes isolates of *E. pedicellatum*. In the former subclade, the basal extension is pale, while in the latter subclade it is strongly pigmented.

TAXONOMY

Dothideomycetes, Pleosporales, Pleosporaceae

Exserohilum K.J. Leonard & Suggs, Mycologia 66: 290. 1974

Synonyms. *Setosphaeria* K.J. Leonard & Suggs, Mycologia 66: 294. 1974.

Luttrellia Khokhr. & Gornostaï (as '*Luttrellia*'; non *Luttrellia* Shearer), Vodorosli, Griby i Mkhi Dal'nego Vostoka [Algae, Fungi and Mosses of the Soviet Far-East] (Vladivostok): 80. 1978.

Type species. *Exserohilum turcicum* (Pass.) K.J. Leonard & Suggs.

Adapted from Sivanesan (1987). *Vegetative hyphae* septate, branched, pale brown to dark brown, smooth to finely verruculose. *Asexual morph.* *Conidiophores* macronematous, mononematous, septate, cylindrical, olivaceous brown to brown, smooth to verruculose, often geniculate above. *Conidiogenous cells* integrated, terminal and intercalary, sympodial, mono- to polytretic, cicatrized; conidiogenous nodes smooth to rough. *Conidia* fusiform, cylindrical or obclavate, straight to curved, multi-distoseptate, with a protruding hilum. *Sexual morph.* *Ascomata* superficial, immersed or erumpent, globose to ellipsoid, unilocular, dark brown to black, with or without a beak, ostiolate, with simple rigid setae over the ostiolar apex and on the upper half of the ascoma where they are often mixed with hyaline, filiform, septate hyphae; peridium composed of pseudoparenchymatous cells, dark brown and thick-walled on the outside, but with more or less hyaline cells towards the inside forming a *textura angularis*. *Pseudoparaphyses* filiform, hyaline, septate, branched, anastomosing. *Asci* arising from a basal cushion of thin-walled pseudoparenchymatous cells, bitunicate, 1–8-spored, cylindrical to cylindrical-clavate, short or moderately long-stalked, thick-walled, with an apical nasse and fissitunicate dehiscence. *Ascospores* fusoid, hyaline to pale brown, smooth, 2–6 or rarely more transversely septate, constricted at the septa, surrounded by a hyaline mucilaginous sheath which often extends some distance beyond the ends of the spore.

Exserohilum corniculatum Madrid, Hern.-Restr., Y.P. Tan & Crous, *sp. nov.* — MycoBank MB821483; Fig. 3

Etymology. From the Latin *corniculatum* - horn-like, referring to the narrow apical extensions observed in rostrate conidia of this fungus, which resemble a horn.

Type material. AUSTRALIA, Queensland, Home Hill, on leaf spot of *Oryza sativa*, 4 May 1972, W. Pont (BRIP 11426 holotype; BRIP 11426 culture ex-type; CBS H-21815, IMI 167611 isotypes).

On SNA + maize leaves. *Vegetative hyphae* septate, branched, pale olivaceous brown to dark olivaceous brown, smooth to finely verruculose, 2–7 µm wide. *Conidiophores* macronematous, mononematous, straight to flexuous, sometimes geniculate towards the apex, septate, unbranched, subcylindrical, brown, smooth-walled, but sometimes becoming finely verruculose near the conidiogenous loci, with cell walls usually thicker than those of the vegetative hyphae, 158–458 × 5–8 µm, with occasional subnodulose to nodulose swellings up to 9.5 µm wide. *Conidiogenous cells* integrated, terminal and intercalary, mostly subcylindrical, mono- to polytretic, proliferating sympodially, 11–56.5 µm long, with scars up to 5.5 µm wide. *Conidia* mostly subcylindrical to fusiform, straight to slightly curved, pale olivaceous brown to dark olivaceous brown, smooth to irregularly verruculose, 4–10(–12)-septate, sometimes with accentuated septa delimiting the basal cell or both the basal and apical cells, often becoming rostrate by means of a narrow apical extension, 41–94.5(–104.5) × (11.5–)15–24 µm, with a strongly protruding hilum. *Sexual morph* not observed.

Culture characteristics — Colonies on SNA + sterilized maize leaves at 24 °C reaching 11 mm diam after 7 d, hairy, olivaceous black towards the periphery, greenish black on maize leaves, with a fimbriate margin; reverse concolorous with obverse.

Notes — *Exserohilum corniculatum* is unique in producing very narrow apical conidial extensions. The rostrate conidia of *E. rostratum* are usually much broader and do not resemble horns as in *E. corniculatum*.

Exserohilum holmii (Luttr.) K.J. Leonard & Suggs, Mycologia 66: 291. 1974 — Fig. 4

Basionym. *Trichometasphaeria holmii* Luttr., Phytopathology 53: 285. 1963.

Synonyms. *Helminthosporium holmii* Luttr., Phytopathology 53: 285. 1963. *Drechslera holmii* (Luttr.) Subram. & B.L. Jain, Curr. Sci. 35: 354. 1966. *Keissleriella holmii* (Luttr.) Arx, Gen. Fungi Sporul. Cult. (Lehr): 126. 1970. *Setosphaeria holmii* (Luttr.) K.J. Leonard & Suggs, Mycologia 66: 295. 1974.

Exserohilum curvatum Sivan. & Muthaiyan, Trans. Brit. Mycol. Soc. 83: 319. 1984.

Type material. USA, Georgia, Griffin, on *Hordeum vulgare*, 15 Aug. 1961, E.S. Luttrell No. 7607 (BPI 623928 lectotype designated here (of *Trichometasphaeria holmii*, MBT379820)); on *Dactyloctenium aegyptium*, 15 Aug. 1961, E.S. Luttrell No. 1607-7 (CBS H-7027 isosyntype (of *Helminthosporium holmii*); CBS 413.65 culture ex-isosyntype); on *Dactyloctenium aegyptium*, 15 Aug. 1961, E.S. Luttrell No. 1607-5 (CBS 414.65 culture ex-isosyntype).

On SNA + maize leaves. *Vegetative hyphae* septate, branched, pale olivaceous to pale olivaceous brown, smooth-walled, 1–6.5 µm wide. *Asexual morph.* *Conidiophores* macronematous, mononematous, straight, curved or more or less flexuous, sometimes geniculate towards the apex, septate, unbranched, subcylindrical, pale to dark olivaceous brown, becoming paler at the apex, smooth-walled, but sometimes very finely verruculose around the conidiogenous loci, with cell walls usually thicker than those of the vegetative hyphae, 57–857.5 × 5–9 µm, occasionally with subnodulose to nodulose swellings up to 9.5 µm wide. *Conidiogenous cells* integrated, terminal and intercalary, mostly subcylindrical, mono- to polytretic, proliferating sympodially, 11–36 µm long, with scars up to 4.5 µm wide. *Conidia*

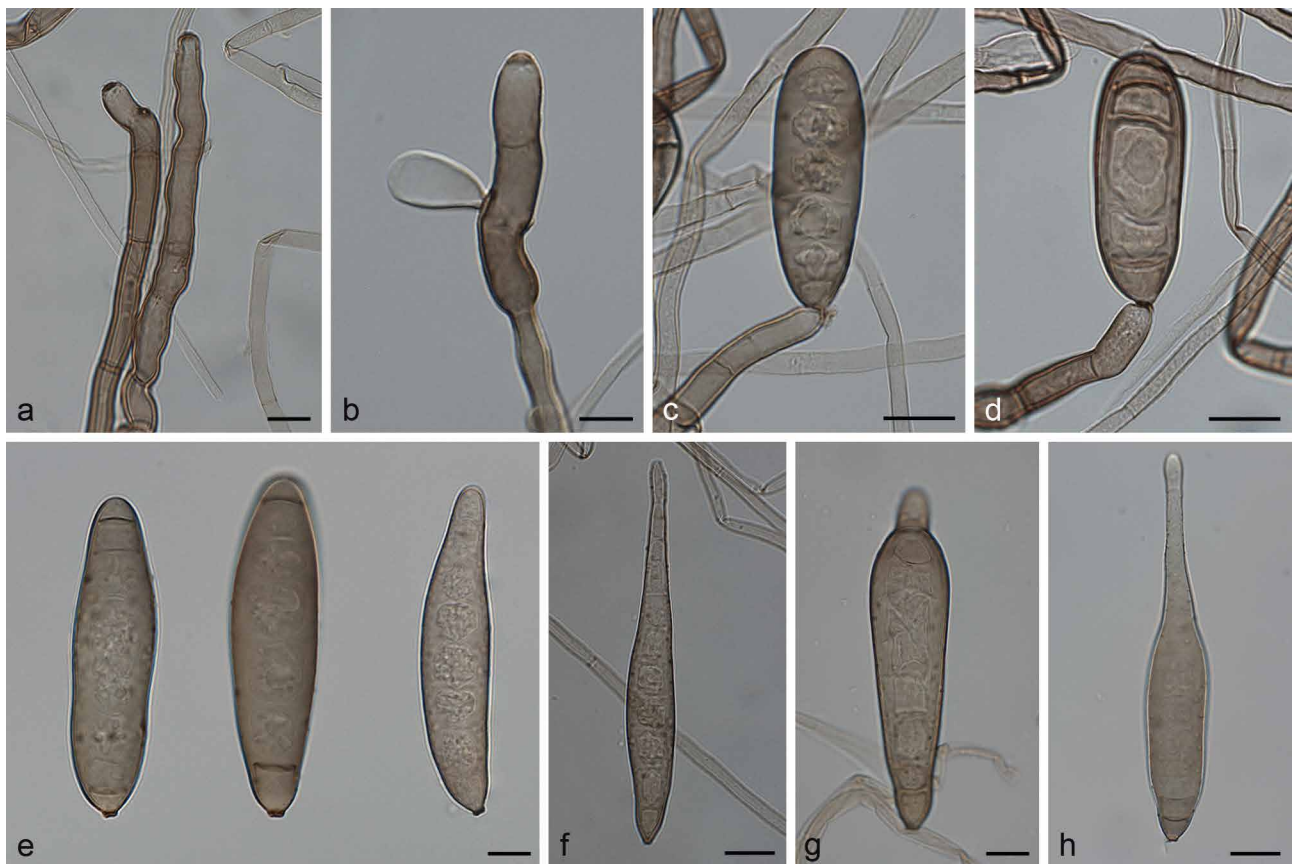


Fig. 3 *Exserohilum corniculatum* (BRIP 11426 ex-type). a. Conidiophores; b–d. conidiogenous cells and conidia; e–h. conidia. — Scale bars: 10 µm.

fusoid with obtuse ends, obovoid to clavate, obclavate rostrate, straight to moderately curved, mid olivaceous brown, with a small paler area at each pole, finely asperulate, but apical cell usually smooth, 3–9-distoseptate, $38.5\text{--}117.5 \times 16.5\text{--}32 \mu\text{m}$, with a strongly protruding hilum 2–4 µm wide. *Sexual morph* adapted from Luttrell (1963a) and Sivanesan (1987). *Ascogonia* globose, 262–644 µm diam, unilocular, black, covered by rigid setae on the upper part, and a ostiole surrounded by short, rigid, dark brown setae; peridium composed of an outer layer of dark brown, thick-walled, pseudoparenchymatous polyhedral cells, which become thin-walled and hyaline towards the inner wall. *Pseudoparaphyses* numerous, hyaline, filiform, branched, sometimes anastomosing. *Asci* 1–8-spored, thick-walled when young, clavate, $174\text{--}232 \times 28\text{--}36 \mu\text{m}$. *Ascospores* fusoid, straight to curved, hyaline, (2–)3(–6)-septate, not or slightly constricted at the septa, surrounded by a mucilaginous sheath which may extend beyond either end after discharge, $47\text{--}78 \times 12\text{--}20 \mu\text{m}$.

Culture characteristics — Colonies on SNA + sterilized maize leaves at 24 °C reaching 48–70 mm diam after 7 d, flat, translucent toward the periphery, hairy to powdery and greenish black at the centre and on the maize leaves, with a fimbriate margin; reverse concolorous with obverse.

Additional materials examined. AUSTRALIA, Queensland, Goondiwindi, on leaf spot of *Dactyloctenium radulans*, 25 Apr. 1979, Y. Brouwer No. 7795b2 (BRIP 12679). — THAILAND, Nakhon Pathom, on *Dactyloctenium aegyptium*, 19 Sept. 1990, J.L. Alcorn No. 9084b (CBS 128053). — UNKNOWN COUNTRY, on *Dactyloctenium aegyptium*, unknown date, R.R. Nelson (CBS 318.64); on *Dactyloctenium aegyptium*, unknown date, R.R. Nelson (CBS 319.64). — VENEZUELA, on seed of *Sorghum vulgare*, 24 Oct. 1983, M.C. Muthaiyan (culture ex-type of *E. curvatum* CBS 505.90).

Notes — *Exserohilum holmii*, originally described as *Helminthosporium*, was the cause of leaf blight of *Dactyloctenium aegyptium* in Georgia, USA (Luttrell 1963a). Luttrell (1963a) obtained the sexual morph in culture by mating compatible conidial strains on Sach's agar supporting sterilized barley grains. In the

protologue, conidial size were longer and with more number of septa than those observed in this study ($56\text{--}134 \times 14\text{--}31 \mu\text{m}$, 5–11-distoseptate vs $38.5\text{--}117.5 \times 16.5\text{--}32 \mu\text{m}$, 3–9-distoseptate). *Exserohilum holmii* has also been isolated from other grasses and other hosts including *Coffea*, *Cymbopogon*, *Gossypium*, *Musa*, *Oryza*, *Psidium*, *Triticum*, *Solanum*, etc. Besides the USA, *E. holmii* has been reported from Australia, India and Nigeria (Sivanesan 1987, Farr & Rossman 2017). Later, *E. curvatum* was introduced for a fungus growing on *Sorghum vulgare* in Venezuela (Sivanesan 1984). It was distinguished from other species by the distinctively curved conidia (Sivanesan 1984). Nevertheless, *E. curvatum* appears to be a morphological variant. With the culture media and growth conditions used in our study, the conidia of this fungus were predominantly asymmetrical to slightly curved. Based on a culture on tap water agar (TWA) + wheat straw, conidia in the protologue of *E. curvatum* are longer (up to 120 µm vs 92.5 µm) and distinctly curved (Sivanesan 1984) than those observed in our study. In culture, *E. curvatum* is morphologically similar to *E. holmii* which also produces elongated conidia with end cells usually delimited by an accentuated distoseptum. Based on these morphological similarities and supported by the multi-locus sequence data analysis (Fig. 2), we consider *E. curvatum* as a synonym of *E. holmii*.

Exserohilum khartoumensis (El Shafie & J. Webster) P.M. Kirk, Index Fungorum 269: 1. 2015 — Fig. 5

Basionym. *Setosphaeria khartoumensis* El Shafie & J. Webster, Trans. Brit. Mycol. Soc. 77: 442. 1981.

Type material. SUDAN, Khartoum, on seed of *Sorghum bicolor* var. *mayo* (HME 4006 holotype, not seen; IMI 249194 (= CBS 132708) culture ex-isotype (of *Setosphaeria khartoumensis*)).

On maize meal agar with autoclaved *Sorghum* grains. *Vegetative hyphae* branched, septate, pale to mid-brown. *Asexual morph.* *Conidiophores* macronematous single or in small



Fig. 4 *Exserohilum holmii* (CBS 413.65 ex-isotype (a–d), CBS 128053 (e–h), CBS 505.90 (i–l), BRIP 12679 (m–p)). a–b, e–g, i–j, m–n, p. Conidiophores and conidia; c–d, h, k–l, o. conidia. — Scale bars: a = 50 μ m; e, m–o = 20 μ m; b–d, f–l, p = 10 μ m.

groups, straight to flexuous, geniculate above, septate, unbranched, brown to mid-brown, paler towards the apex, smooth, up to $240 \times 5\text{--}7.5$ μ m thick. *Conidia* variable, broadly obclavate-rostrate, broadly ellipsoidal to cylindrical, straight sometimes slightly curved, end cells often rather pale and often cut off by a thick, dark septum, intermediate cells mid-dark golden brown, smooth, (6–)7–10(–12)-distoseptate, $55\text{--}160 \times 15\text{--}25$ μ m, with a distinctly protuberant hilum. *Sexual morph* adapted from El Shafie & Webster (1981) and Sivanesan (1987). *Asco-*

mata unilocular, globose to ellipsoid, $200\text{--}300 \times 190\text{--}300$ μ m, sometimes with a short cylindrical ostiolate beak, surrounded by rigid setae which also occur scattered over the upper surface of the ascogonia. *Setae* dark brown, thick-walled, septate, bluntly rounded at the end, swollen at the base, $50\text{--}180 \times 5\text{--}6$ μ m. *Pseudoparaphyses* filamentous, hyaline, septate, branched and anastomosing. *Asci* 1–8-spored, clavate to clavate-cylindrical, bitunicate, tapered at the base, thick-walled when young, $100\text{--}155 \times 25\text{--}32.5$ μ m. *Ascospores* always 3-septate, con-

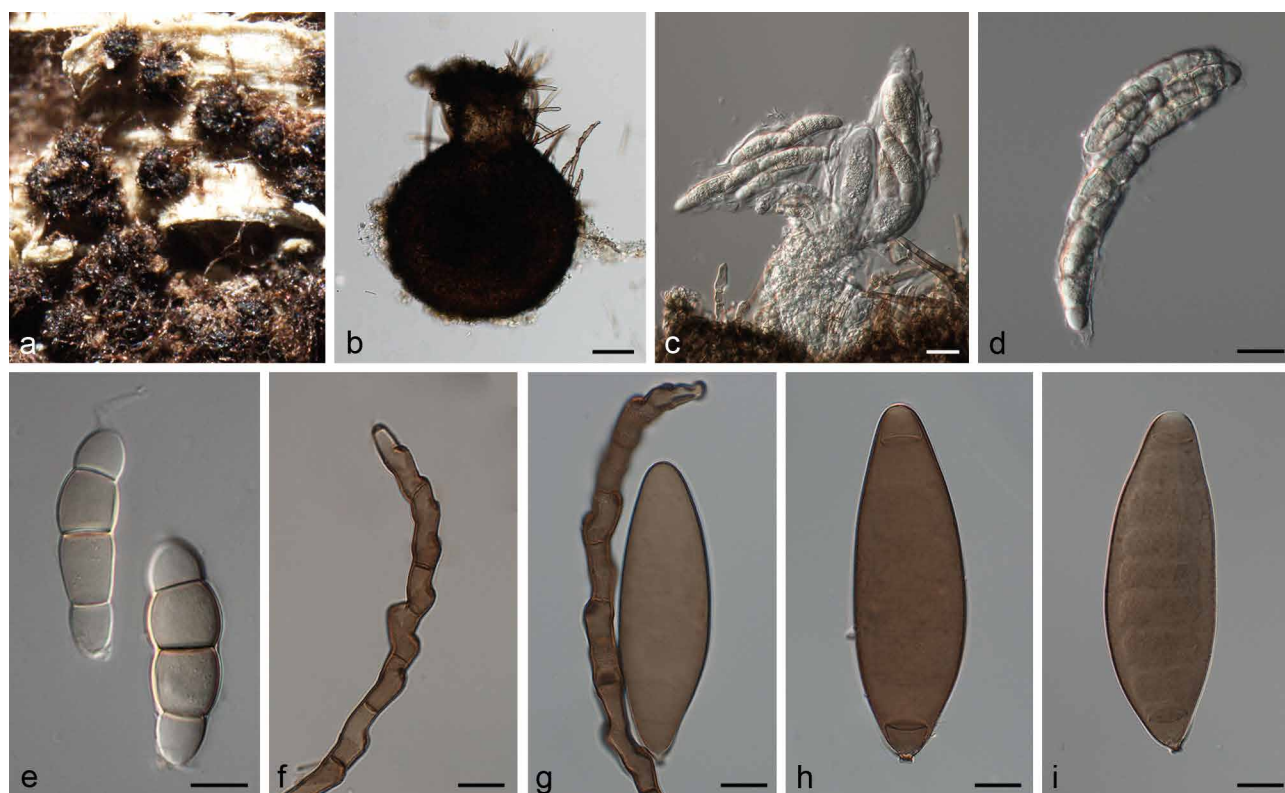


Fig. 5 *Exserohilum khartoumensis* (CBS 132708 ex-isotype). a–e. Sexual morph: a. habit; b. ascoma; c, d. asci; e. ascospores; f–i. asexual morph: f. conidiophore; g. conidiophore and conidia; h–i. conidia. — Scale bars: b = 50 μ m; c–d = 20 μ m; e–i = 10 μ m.

stricted at the septa, fusoid, curved to straight, hyaline to pale brown, middle cells darker than the end cells, 42–44 \times 10–15 μ m, surrounded by hyaline, thin mucilaginous sheath which extends beyond the end of the spore after discharge.

Culture characteristics — Colonies on SNA + sterilized maize leaves at 24 $^{\circ}$ C reaching 52 mm diam after 7 d, hairy, with scarce aerial mycelium, translucent at the periphery, except for sparse strands of dark brown hyphae, cottony and pale mouse grey on maize leaves, with a fimbriate margin; reverse concolorous with obverse.

Notes — *Exserohilum khartoumensis* is a homothallic species isolated from *Sorghum*, and only known from the type locality, Khartoum, Sudan, (El Shafie & Webster 1981). In the protologue, both the sexual and asexual morphs were described under the name *Setosphaeria khartoumensis*. Recently, Kirk (2015) proposed the new combination in *Exserohilum*. In our phylogenetic tree, this species is represented by the isotype strain IMI 249194 which forms a basal clade of *E. holmii* (Fig. 2).

Exserohilum minor Alcorn, Trans. Brit. Mycol. Soc. 86: 313. 1986 — Fig. 6

Synonym. *Setosphaeria minor* Alcorn, Trans. Brit. Mycol. Soc. 86: 313. 1986.

Type material. AUSTRALIA, Queensland, Saibai Island, on leaf spot of *Dactyloctenium aegyptium*, 1 June 1981, J.L. Alcorn (BRIP 14616 holotype; IMI 294530a isotype; BRIP 14616 culture ex-type).

Vegetative hyphae septate, branched, pale olivaceous to pale olivaceous brown, smooth to asperulate, 3–8.5 μ m wide. **Asexual morph** based on IMI 294530b. **Conidiophores** macronematous, mononematous, rather straight, septate, unbranched, olivaceous brown, often paler at the apex, smooth to verruculose, length indeterminate, 3.5–7.5 μ m wide, sometimes with a bulbous base up to 9.5 μ m wide. **Conidiogenous cells** integrated, intercalary and terminal, mono- or polytretic, proliferating sympodially, mostly subcylindrical to slightly swollen, 13–48.5 \times

3.5–7.5 μ m, with scars up to 4.5 μ m wide. **Conidia** fusiform, straight to slightly curved, pale olivaceous brown, smooth to verruculose, 6–8-distoseptate, 63.5–86 \times 12–19.5 μ m, with a strongly protruding hilum 2–3 μ m wide. **Sexual morph** based on IMI 294530a. **Ascospores** fusoid with obtuse ends, straight to slightly curved, pale olivaceous to pale olivaceous brown, 3(–5) septate, with central cells darker than the polar ones, constricted at the septa, 35.5–51.5 \times 10–14.5 μ m, enveloped by a mucilaginous sheath that extends from each end as a simple tubular appendage up to 47.5 μ m long (in lactic acid mounts).

Culture characteristics — Colonies on SNA + sterilized maize leaves at 24 $^{\circ}$ C reaching 40–50 mm diam after 7 d, flat with scarce hairy aerial mycelium and whitish at the periphery, becoming cottony and pale olivaceous grey on the maize leaves, with a fimbriate to feathery margin; reverse concolorous with obverse.

Additional materials examined. AUSTRALIA, Queensland, Saibai Island, ascocarps formed by BRIP 13597 in the laboratory (no culture), Mar. 1985, J.L. Alcorn (BRIP 14612); Queensland, Saibai Island, ascocarps formed by BRIP 13597 in the laboratory (no culture), Mar. 1985, J.L. Alcorn (BRIP 14614); Queensland, Saibai Island, on leaf spot of *Dactyloctenium aegyptium*, 1 June 1981, J.L. Alcorn (holotype of *Setosphaeria minor* BRIP 14615, isotype IMI 294530b, culture ex-type BRIP 14615).

Notes — *Exserohilum minor* is a homothallic species known only from Australia (Alcorn 1986). It is the cause of leaf spots on *Dactyloctenium aegyptium*. The isolates included in the present

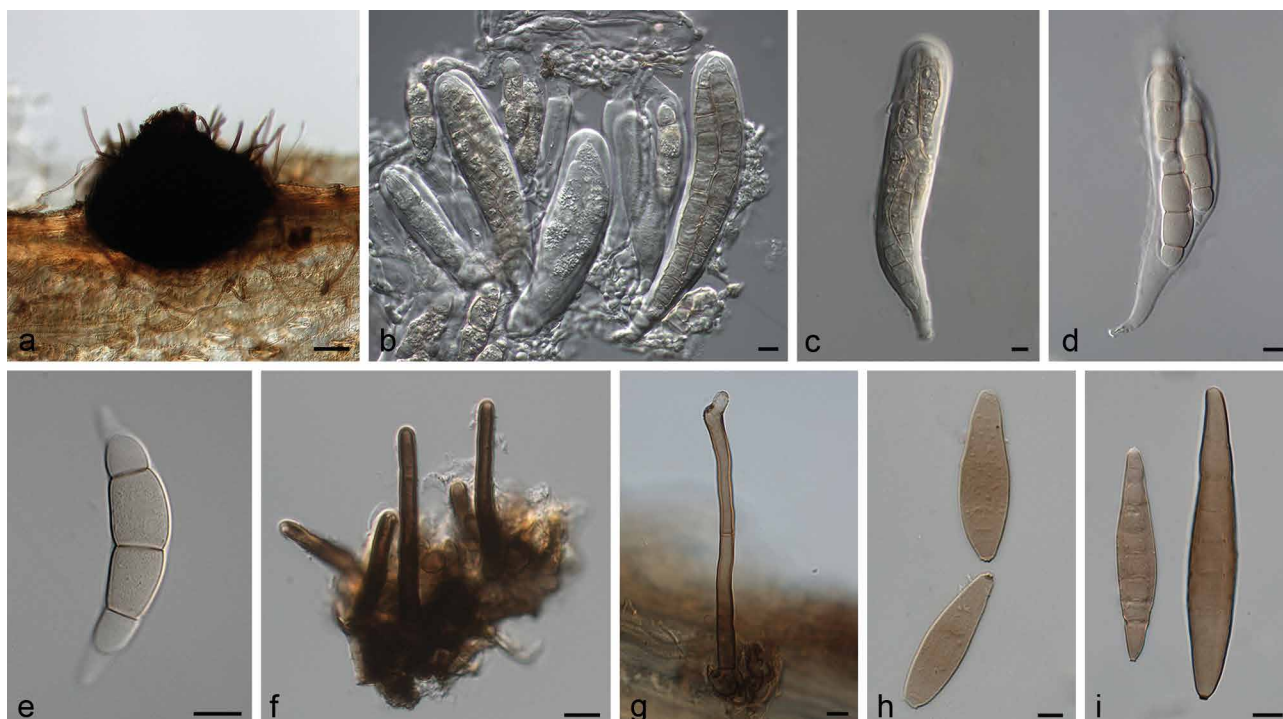


Fig. 6 *Exserohilum minor* (IMI 294530 isotype). a–f. Sexual morph: a. ascoma; b–d. asci; e. ascospore; f. setae of the ascoma; g–i. asexual morph: g. conidiophore; h–i. conidia. — Scale bars: a = 50 μ m; b–i = 10 μ m.

study appear to be degenerated since none of them produced the asexual morph in culture and the ascomata showed few short setae and ascospores with abnormal morphology. Therefore, in our study the description of microscopic features are based on the isotypes of *E. minor* IMI 294530a and *S. minor* IMI 294530b. However, in the protologue conidia were longer and with more distosepta (up to 135 μ m long; 5–11-distoseptate) (Alcorn 1986). *Exserohilum minor* was phylogenetically placed in a separate basal clade to *E. corniculatum*, *E. holmii*, *E. khartoumensis*, *E. neoregeliae* and *E. rostratum*.

Exserohilum monoceras (Drechsler) K.J. Leonard & Suggs, *Mycologia* 66: 291. 1974 — Fig. 7, 8

Basionym. *Helminthosporium monoceras* Drechsler, *J. Agric. Res.* 24: 706. 1923.

Synonyms. *Bipolaris monoceras* (Drechsler) Shoemaker, *Canad. J. Bot.* 37: 883. 1959.

Drechslera monoceras (Drechsler) Subram. & B.L. Jain, *Curr. Sci.* 35: 354. 1966.

Setosphaeria monoceras Alcorn, *Mycotaxon* 7: 411. 1978.

Luttrellia monoceras (Drechsler) Khokhr., as '*Lutrellia*', *Vodorosii*, *Griby i Mkhi Dal'nego Vostoka* [Algae, Fungi and Mosses of the Soviet Far-East] (Vladivostok): 80. 1978.

Setomelanomma monoceras (Alcorn) S.A. Ahmed et al., *Persoonia* 33: 144. 2014 (nom. invalid Art. 41.1).

Helminthosporium crus-galli Y. Nisik. & C. Miyake, *Ber. Ohara Inst. Landw. Forsch. Kurashiki* 2: 597. 1925.

Type material. USA, New York, Long Island, Port Washington, on *Echinochloa crus-galli*, 20 Sept. 1922, C. Drechsler (BPI 429633 holotype, not seen (of *Helminthosporium monoceras*)).

Asexual morph adapted from Drechsler (1923). *Conidiophores* macronematous, single or in groups of 2–3, straight to flexuous, sometimes geniculate above, dark brown to olivaceous, paler at the apex, 120–325 \times 6–9 μ m. *Conidiogenous cells* integrated, terminal and intercalary, mono- to polytretic, proliferating sympodially, mostly subcylindrical. *Conidia* fusoid, mainly straight, yellowish when young, becoming dark olivaceous when fully matured, smooth, 3–10-septate, 40–150 \times 15–22 μ m, with a protruding hilum. On SNA + maize leaves (this study). *Vegeta-*

tive hyphae septate, branched, pale olivaceous to pale olivaceous brown, smooth, 3–6.5 μ m wide. *Conidiophores* macronematous, mononematous, straight to flexuous, occasionally geniculate towards the apex, septate, mostly unbranched, pale to dark olivaceous brown, smooth, with cell walls often thicker than those of the vegetative hyphae, 181–743 \times 4.5–10.5 μ m, with occasional subnodulose intercalary swellings up to 11.5 μ m wide. *Conidiogenous cells* terminal and intercalary, mostly subcylindrical, mono- to polytretic, proliferating sympodially, 33.5–103.5 μ m long, conidiogenous loci with scars up to 6 μ m wide. *Conidia* fusiform, straight to slightly curved, pale to dark olivaceous brown, smooth slightly verruculose near the hilum, 3–9-distoseptate, 76–119(–139.5) \times 16–31 μ m, hilum strongly protruding, 2.5–4.5 μ m wide. *Sexual morph* adapted from Sivanesan (1987). *Ascomata* immersed, erumpent or superficial on the substrate, dark brown to black, globose to ellipsoid or ovoid, 300–500 \times 260–400 μ m, ostiolate, sometimes with a short broad beak, setose, especially on the upper half. *Setae* dark brown, unbranched, straight, paler towards the apex, septate, up to 450 μ m long, 6–15 μ m wide at the base which is sometimes swollen. *Pseudoparaphyses* filiform, hyaline, septate, branched and anastomosing. *Asci* 1–8-spored, cylindrical to clavate, sometimes with a short pedicel, 135–245 \times 21–35 μ m. *Ascospores* hyaline, fusoid to oblong, straight to mostly slightly curved, 2–5(usually 3-)septate, constricted at the septa, 45–75 \times 11–20 μ m, surrounded by a thin, hyaline mucilaginous sheath.

Culture characteristics — Colonies on SNA + sterilized maize leaves at 24 $^{\circ}$ C reaching 60–92 mm diam after 7 d, hairy to cottony or floccose, whitish to iron grey on maize leaves or olivaceous black, with a fimbriate margin; reverse concolorous with obverse.

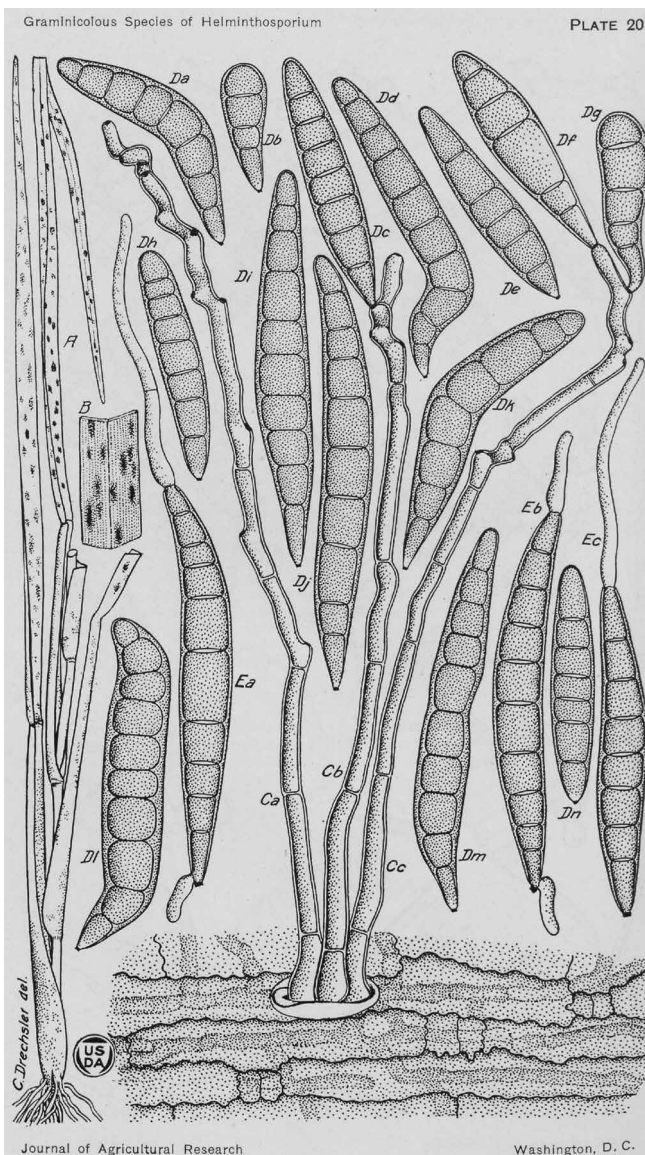
Specimens examined. AUSTRALIA, Queensland, Beerwah, on *Echinochloa colona*, Apr. 1972, J.L. Alcorn No. 19677 (BRIP 11418, CBS 239.77); Brisbane, on leaf spot of *Setaria italica*, 20 Mar. 1973, B. Champion No. 20020a (BRIP 11542); from pairing single-spore cultures 77163-1 \times 77163-5 on leaf sheaths of *Triticum aestivum* on modified Sach's agar, 23 Feb. 1978, J.L. Alcorn No. 7804b (holotype specimen of *Setosphaeria monoceras* BRIP 12567); Biloela, on leaf spot of *Echinochloa colona*, 13 Apr. 1977, M. Vincent

No. 7792a (BRIP 12236); Biloela, on leaf spot of *Echinochloa colona*, 30 May 1977, J.L. Alcorn No. 77163 (paratype specimen of *Setosphaeria monoceras* BRIP 12271, culture ex-type BRIP 12271); Biloela, on leaf spot of *Echinochloa colona*, 30 May 1977, J.L. Alcorn No. 77163-1 (CBS 209.78). – JAPAN, on *Echinochloa crus-galli*, Nov. 1929, Y. Nisikado (CBS 198.29).

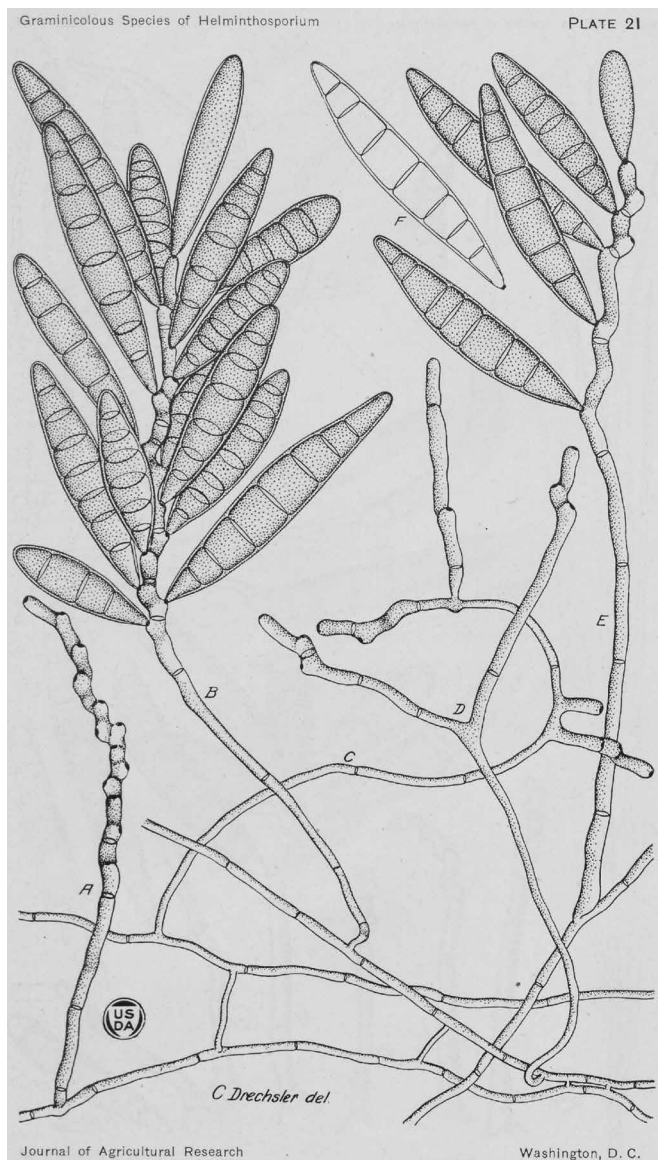
Notes — This species, formerly introduced as *Helminthosporium monoceras*, was isolated from a splotch in the grass *Echinochloa crus-galli* in Long Island, USA (Drechsler 1923) (Fig. 7). The holotype of *H. monoceras* (BPI 429633) is preserved in the US National Fungus Collection. The sexual morph, *S. monoceras* was obtained by Alcorn (1978) in Australia by pairing compatible single conidial isolates in modified Sach's agar media supporting sterilized wheat leaf sheaths. Unfortunately, none of the strains of *E. monoceras* serves as epitype, since they were collected in Australia and Japan, very distant geographically from the type locality in the USA. The type specimens of *H. monoceras* and *S. monoceras* are different

and yet to be confirmed as the same using molecular phylogenetic studies. The correct phylogenetic position of *E. monoceras* is still unclear until molecular data from type material of *H. monoceras* becomes available.

It has been reported from *Dichanthelium clandestinum*, *Echinochloa* spp., *Eragrostis* spp., *Panicum* spp., *Oryza sativa* and *Setaria viridis* (Farr & Rossman 2017). In our phylogenetic tree, *E. monoceras* is represented by five Australian strains, which were isolated mainly from *Echinochloa*, but also from *Setaria*, and one strain isolated from *Echinochloa crus-galli* in Japan. *Exserohilum monoceras* formed a clade together with *E. turcicum* (Fig. 2). These two species are also similar in conidial morphology, dimensions and septation. Nevertheless, we consider them as different species based on substrate preferences; *E. monoceras* is mainly isolated from *Echinochloa*, *Panicum* and *Setaria*, while *E. turcicum* is mainly isolated from *Zea mays* and *Sorghum*.



a PLATE 20
Helminthosporium monoceras
A.—Portion of plant of *Echinochloa crus-galli* attacked by *H. monoceras* showing presence of spots on leaf blades and of diffused discoloration on basal sheaths. $\times 34$.
B.—Portion of leaf blade of *Echinochloa crus-galli* attacked by *H. monoceras* showing variation in size of spots. $\times 34$.
Ca-b.—Group of conidiophores emerging from stoma of host; showing also mycelium ramifying in mesophyll as revealed in glycerine preparations stained with eosin. $\times 500$.
Da-n.—Conidia from *Echinochloa crus-galli* collected at Port Washington, N. Y., September 20, 1920, showing variation in size, shape, and septation. $\times 500$.
Ea-c.—Conidia from *Echinochloa crus-galli* germinating by the production of two polar germ tubes. $\times 500$.



b PLATE 21
Helminthosporium monoceras
A-E.—Conidiophores of *H. monoceras* arising from imbedded anastomosing mycelium, showing habit of growth, irregular ramifications and production of conidia in racemose arrangement. $\times 500$. Drawn from 20-day old culture on tap-water agar.
F.—Outline of conidium from pure culture, showing attenuated regions in peripheral wall at apex and at basal end. $\times 500$.

Fig. 7 Original drawing of *Helminthosporium monoceras* (reproduced from Drechsler 1923). a. From natural substrate *Echinochloa crus-galli*; b. from culture.



Fig. 8 *Exserohilum monoceras* CBS 198.29 (a–h), CBS 239.77 (i, j, l, m) and BRIP 11542 (k, n, o). a, c–g, k–m. Conidiogenous cells with conidia; b, i–j. conidiogenous cells; h, n–o. conidia. — Scale bars: 10 µm.

***Exserohilum neoregeliae* Sakoda & Tsukib., Mycotaxon 118: 214. 2011 — Fig. 9**

Type material. JAPAN, Chiba, Narita, from living leaves of *Neoregelia carolinae* (imported from the Netherlands), 24 May 2006, T. Sakoda IM201-D (NIAESH 20605 holotype, not seen; CBS 132832 culture ex-type; NIAESH 20606 isotype, not seen; CBS 132833 culture ex-isotype).

On SNA + maize leaves. *Vegetative hyphae* septate, branched, pale olivaceous to pale olivaceous brown, smooth to verruculose, 2.5–6.5 µm wide. *Asexual morph.* *Conidiophores* macro-nematous, mononematous, straight to flexuous, often strongly geniculate towards the apex, septate, almost always unbranched, pale olivaceous brown to dark brown, paler at the apex, smooth, with cell walls often thicker than those of the vegetative hyphae, 14–596 × 5.5–10 µm, often with a bulbous basal cell up to 22.5 µm wide. *Conidiogenous cells* integrated, terminal and intercalary, mono- to polytretic, proliferating sympodially, mostly subcylindrical, 9.5–52 µm long, conidiogenous loci with scars 2–4.5 µm wide. *Conidia* ellipsoidal, clavate, subcylindrical or fusiform, often appearing strongly rostrate at maturity, straight to more or less curved, pale olivaceous to

dark brown, smooth to verruculose, 2–11-distoseptate, 22–161(–191.5) × (10.5–)12–24.5(–33.5) µm, with the basal (and sometimes also the apical) cell delimited by a dark septum; hilum usually strongly protruding, 2.5–4.5 µm wide. *Sexual morph* not reported.

Culture characteristics — Colonies on SNA + sterilized maize leaves at 24 °C reaching 61–72 mm diam after 7 d, flat, with scarce aerial mycelium, hairy, becoming cottony on the maize leaves, grey olivaceous to olivaceous black, with a fimbriate margin; reverse concolorous with obverse.

Notes — *Exserohilum neoregeliae* caused leaf spots on *Neoregelia carolinae* plants imported from the Netherlands to Japan (Sakoda & Tsukiboshi 2011). It has not been reported from other countries or hosts since its original description. As in other members of *Exserohilum*, conidial size in this species can vary greatly depending on growth conditions. Based on colonies on V8 juice agar, the protologue describes conidia much longer (up to 285 µm in length) and with more septa (6–26-distosepta) than those obtained on SNA + maize leaves in our study.

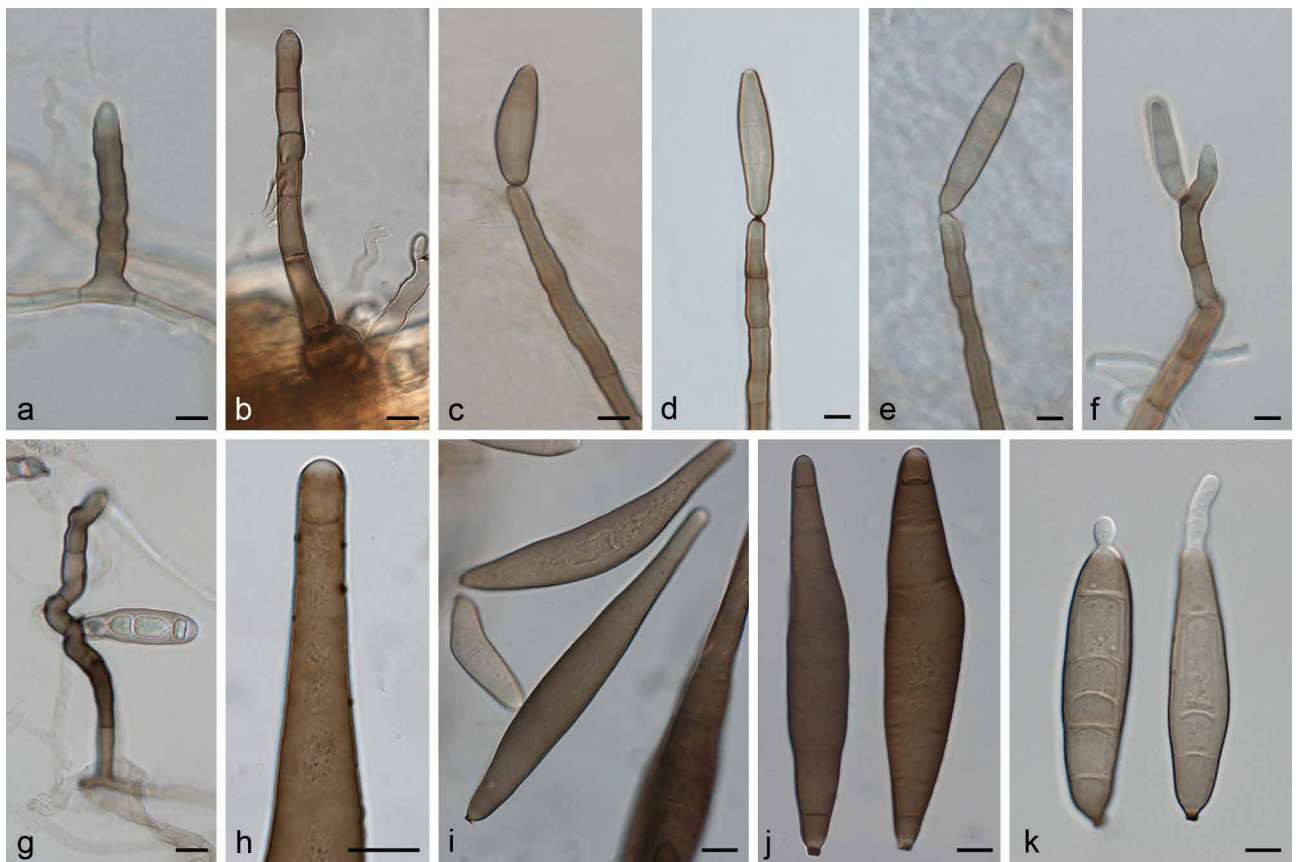


Fig. 9 *Exserohilum neoregeliae* (CBS 132832 ex-type and CBS 132833). a–b. Conidiophores; c–g. conidiophores and conidia; h. upper part of conidium; i–k. conidia. — Scale bars: 10 μ m.

Exserohilum oryzicola Sivan., Trans. Brit. Mycol. Soc. 83: 325. 1984 — Fig. 10

Synonym. *Exserohilum fusiforme* Alcorn, Mycotaxon 41: 337. 1991.

Type material. COLOMBIA, Meta, Villavicencio, on leaves of *Oryza sativa*, 2 Nov. 1982, E.A. Urresta (IMI 273194 holotype; CBS 502.90 culture ex-isotype).

On SNA + maize leaves. *Vegetative hyphae* septate, branched, pale olivaceous to pale olivaceous brown, smooth to verruculose, 2.5–7.5 μ m wide. *Conidiophores* macronematous, mononematous, straight to flexuous, geniculate at the fertile part, septate, unbranched, pale olivaceous brown to dark brown, often paler at the apex, smooth to finely verruculose, with cell walls often thicker than those of the vegetative hyphae, 180–1436 \times 4.5–8.5 μ m, with subnodulose and nodulose intercalary swellings up to 11 μ m wide, sometimes with a swollen basal cell up to 15.5 μ m wide. *Conidiogenous cells* integrated, terminal and intercalary, mostly subcylindrical, mono- to polytretic, proliferating sympodially, 14.5–86.5 μ m long, conidiogenous loci with scars up to 5.5 μ m wide. *Conidia* fusiform, straight to slightly curved, pale to dark olivaceous brown, smooth to finely verruculose near the hilum, 4–10-distoseptate, (41.5–) 67–179(–221) \times (11–) 16.5–22(–30) μ m; hilum strongly protruding, 2.5–5 μ m wide. *Chlamydospores* (only produced by isolate CBS 376.76) terminal and intercalary, ellipsoidal to subglobose, pale olivaceous brown, smooth, 7.5–22.5 μ m wide. *Sexual morph* not reported.

Culture characteristics — Colonies on SNA + sterilized maize leaves at 24 $^{\circ}$ C reaching 44–94 mm diam after 7 d, hairy to cottony, grey olivaceous to olivaceous black, greenish black on maize leaves, with a fimbriate margin; reverse concolorous with obverse.

Additional materials examined. AUSTRALIA, Queensland, Beaudesert, on leaf of *Echinochloa crus-galli*, 17 Mar. 1988, J.L. Alcorn (culture ex-holotype

of *E. fusiforme* BRIP 16229 = CBS 132709). — TURKEY, Ege Region, on *Oryza sativa*, July 1976, J. Oktar (CBS 376.76).

Notes — *Exserohilum oryzicola* was described growing on leaves of *Oryza sativa* from Colombia, characterized by long, tapered and fusiform conidia (Sivanesan 1984). Later, a morphologically similar fungus named *E. fusiforme* was introduced, but was distinguished from *E. oryzicola* by having smaller conidia (up to 141 μ m) (Alcorn 1991). *Exserohilum fusiforme* is pathogenic to *Echinochloa crus-galli* causing numerous small leaf lesions and also can produce a few small linear spots on *O. sativa* (Alcorn 1991). In the phylogenetic tree, *E. oryzicola* represented by the ex-isotype strain CBS 502.90 and *E. fusiforme* represented by two isolates CBS 132709 (the ex-type strain) and CBS 376.76 were placed in the same clade, representing the same phylogenetic species (Fig. 2). Since both species are morphologically similar, they are known from the same substrate *O. sativa*, and their phylogenetic affinities, we consider *E. fusiforme* conspecific with *E. oryzicola*.

Exserohilum pedicellatum (A.W. Henry) K.J. Leonard & Suggs, Mycologia 66: 291. 1974 — Fig. 11

Basionym. *Helminthosporium pedicellatum* A.W. Henry, Tech. Bull. Minn. Agric. Exp. Stn. 22: 42. 1924.

Synonyms: *Bipolaris pedicellata* (A.W. Henry) Shoemaker, Canad. J. Bot. 37: 884. 1959.

Drechslera pedicellata (A.W. Henry) Subram. & B.L. Jain, Curr. Sci 35: 354. 1966.

Trichometasphaeria pedicellata R.R. Nelson, Mycologia 57: 665. 1965.
Setosphaeria pedicellata (R.R. Nelson) K.J. Leonard & Suggs, Mycologia 66: 295. 1974.

Type material. USA, Minnesota, St. Paul, University Farm, substrate unknown, 23 Sept. 1925, A.W. Henry (BPI 429735 lectotype of *Helminthosporium pedicellatum* designated here (MBT379822)); on *Triticum aestivum*, Sept. 1964, R.R. Nelson (CBS H-12242 epitype designated here (MBT378850); CBS 322.64 culture ex-epitype).



Fig. 10 *Exserohilum oryzaicola* CBS 502.90 ex-isotype (a–j) and BRIP 16229 (k–t). a–h, k–o. Conidiophores, conidiogenous cells with conidia; i–j, q–t. conidia; p. chlamydospore. — Scale bars: a = 50 μ m; b–t = 10 μ m.



Fig. 11 *Exserohilum pedicellatum* (CBS 375.76 (a–i) and BRIP 12040 (j–p)). a–c. Conidiophores; d–g, j–n. conidiophores and conidia; h–i, o–p. conidia. — Scale bars: 10 µm.

On SNA + maize leaves. *Vegetative hyphae* septate, branched, subhyaline to pale olivaceous brown, smooth, 2.5–6 µm wide. *Asexual morph.* *Conidiophores* semi- to macronematous, mononematous, usually strongly geniculate towards the apex, unbranched to branched, septate, pale olivaceous brown to dark brown, smooth to asperulate, with cell walls usually thicker than those of the vegetative hyphae, 16–196 × 4–8 µm, with subnodulose to nodulose intercalary swellings up to 9 µm wide, swellings with conidiogenous loci. *Conidiogenous cells* integrated, terminal and intercalary, mostly subcylindrical, mono- and polytretic, proliferating sympodially, 10–43.5 µm

long, with pores up to 1 µm wide, surrounded by scars 3.5–4.5 µm wide. *Conidia* mostly fusiform, straight to more or less curved, occasionally sigmoid, pale olivaceous brown to dark brown, paler in the area around the hilum, smooth, 4–8-distoseptate, (37–)44–88(–89) × (18–)19.5–29(–32) µm, with a basal pedicel-like, subcylindrical extension, 6–15.5 × 4–6 µm, often delimited by a dark septum; hilum usually strongly protruding, 2.5–3.5 µm wide. *Sexual morph* adapted from Sivanesan (1987). *Ascospores* black, globose to ellipsoid, 250–625 × 210–600 µm, ostiolate, non-beaked, with rigid, dark brown setae surrounding the ostiole and also on the upper surface of

the ascomata. *Pseudoparaphyses* filiform, hyaline, branched, septate and anastomosing. Asci 1–8-spored, cylindrical to cylindrical-clavate, short pedicellate, $125\text{--}210 \times 21\text{--}32 \mu\text{m}$. Ascospores fusoid, straight to curved, hyaline, (2–)3(–)6-septate, $40\text{--}60 \times 11\text{--}18 \mu\text{m}$, surrounded by a thin, hyaline mucilaginous sheath which may extend beyond the ends of the spore after discharge.

Culture characteristics — Colonies on SNA + sterilized maize leaves at 24°C reaching 80 mm diam after 7 d, hairy to powdery, grey olivaceous to olivaceous black, with a fimbriate margin; reverse concolorous with obverse.

Additional materials examined. AUSTRALIA, Queensland, Clare, on root of *Oryza sativa*, 11 Oct. 1976, M. Finlay (BRIP 12040). — TURKEY, Ege region, on *Oryza sativa*, July 1976, J. Oktar (CBS 375.76).

Notes — This species was originally described as *Helminthosporium pedicellatum* from wheat roots in the USA (Henry 1924). It has been reported from root rots of various hosts, including *Echinochloa*, *Oryza*, *Paspalum*, *Setaria*, *Sorghum*, *Triticum* and *Zea* in Egypt, India, Pakistan, South Africa and the USA (Henry 1924, Sivanesan 1987, Gilbert 2002). It causes brown lesions on wheat roots and root rot of maize (Sivanesan 1987). The isolate CBS 322.64 was chosen as the epitype since it was collected in the same country and substrate as stated in the protologue. Unfortunately, CBS 322.64 no longer sporulate, so the morphology was described from CBS 375.76, which shows good sporulation, fits well with the description given in

the protologue, and it is conspecific with CBS 322.64 (Fig. 2). In this species, some morphological variation among strains was observed; conidia in the strain BRIP 12040 were mostly clavate with rounded apex, while those of CBS 375.76 were mostly fusiform with acute apex. *Exserohilum pedicellatum* is easy to identify on account of its mostly broadly fusiform conidia with a basal, cylindrical, pedicel-like extension.

Exserohilum protrudens Alcorn, Trans. Brit. Mycol. Soc. 90: 146. 1988 — Fig. 12

Type material. AUSTRALIA, Queensland, Torres Strait, Yorke Island, on leaf spot of *Dactyloctenium aegyptium*, 30 May 1985, R.A. Peterson (BRIP 14814 holotype; BRIP 14814 culture ex-type; IMI 316693 isotype).

Asexual morph adapted from Alcorn (1988b). *Conidiophores* macronematous, mononematous, straight to flexuous, geniculate, septate, unbranched, cylindrical, mid to dark olivaceous brown, paler towards the apex, smooth, basal cell commonly swollen, $11\text{--}21 \mu\text{m}$ wide, $6\text{--}10 \mu\text{m}$ wide near the base, $5\text{--}7.5 \mu\text{m}$ wide at the apex, up to $2100 \mu\text{m}$ long. *Conidiogenous cells* terminal and intercalary, mono- and polytretic, cicatrized, verruculose and slightly swollen at the conidiogenous nodes. *Conidia* fusoid to obclavate-fusoid, sometimes shortly and broadly rostrate, straight or curved, (5–)7–8(–)9-distoseptate, $55\text{--}105 \times 14\text{--}27 \mu\text{m}$, smooth, olivaceous brown, concolorous except for the hilar protrusion which is paler; hilum is borne on

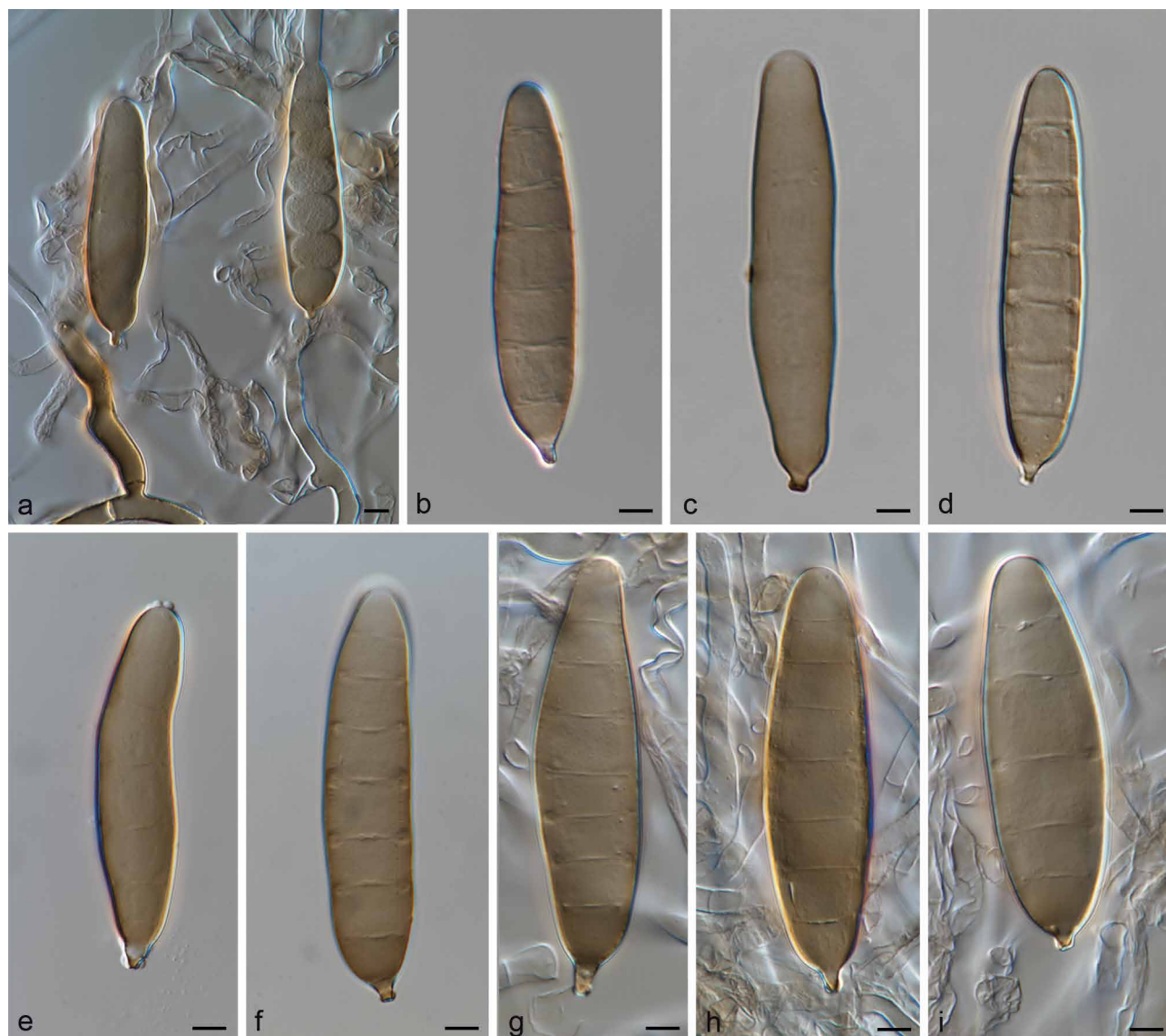


Fig. 12 *Exserohilum protrudens* (BRIP 14816). a. Conidiophore and conidia; b–i. conidia. — Scale bars: 10 μm .

a distinct truncate conical protrusion 2.5–5 µm long, 2.5–4 µm wide proximal to the body of the spore, and 2–3 µm wide at the hilar extremity. *Sexual morph* not reported.

Culture characteristics — Colonies on SNA + sterilized maize leaves at 24 °C reaching 40–61 mm diam after 7 d, mycelium mostly immersed, with scarce aerial mycelium, whitish, becoming pale mouse grey to mouse grey and cottony on the maize leaves, with a fimbriate margin; reverse concolorous with obverse.

Additional material examined. AUSTRALIA, Queensland, Coconut Island, 1 June 1985, R.A. Peterson (BRIP 14816).

Notes — This species is only known from two specimens causing leaf spot on *Dactyloctenium aegyptium* from the Torres Strait Islands (Yorke Island and Coconut Island). Attempts to produce the sexual morph were not successful (Alcorn 1988b). *Exserohilum protrudens* is phylogenetically placed in a basal clade to *E. monoceras*, *E. oryzicola*, *E. pedicellatum* and *E. turcicum*.

Exserohilum rostratum (Drechsler) K.J. Leonard & Suggs, *Mycologia* 66: 290. 1974 — Fig. 13–17

Basionym. *Helminthosporium rostratum* Drechsler, *J. Agric. Res.* 24: 724. 1923.

Synonyms: *Bipolaris rostrata* (Drechsler) Shoemaker, *Canad. J. Bot.* 37: 883. 1959.

Drechslera rostrata (Drechsler) M.J. Richardson & E.M. Fraser, *Trans. Brit. Mycol. Soc.* 51: 148. 1968.

Luttrellia rostrata (Drechsler) Gornostaï, as '*Luttrellia*', *Vodorosli, Gribyi i Mkhi Dal'nego Vostoka [Algae, Fungi and Mosses of the Soviet Far-East] (Vladivostok)*: 81. 1978.

Helminthosporium halodes Drechsler, *J. Agric. Res.* 24 (8): 709. 1923.

Helminthosporium halodes Drechsler var. *tritici* Mitra, *Trans. Brit. Mycol. Soc.* 15 (3-4): 287. 1931.

Helminthosporium halodes Drechsler var. *elaeicola* Kovachich, *Trans. Brit. Mycol. Soc.* 37 (4): 423. 1954.

Bipolaris halodes (Drechsler) Shoemaker, *Canad. J. Bot.* 37: 883. 1959.

Drechslera halodes (Drechsler) Subram. & B.L. Jain, *Curr. Sci.* 35: 354. 1966.

Drechslera halodes (Drechsler) Subram. & B.L. Jain var. *halodes* (Drechsler) Subram. & B.L. Jain, *Curr. Sci.* 35: 354. 1966.

Drechslera halodes (Drechsler) Subram. & B.L. Jain var. *elaeicola* Kovachich, *Trans. Brit. Mycol. Soc.* 37: 423. 1954.

Exserohilum halodes (Drechsler) K.J. Leonard & Suggs, *Mycologia* 66: 290. 1974.

Helminthosporium leptochloae Y. Nisik. & C. Miyake, *Ber. Ohara Inst. Landw. Forsch. Kurashiki* 2: 483. 1924.

Helminthosporium longirostratum Subram., *J. Indian Bot. Soc.* 35: 463. 1957.

Exserohilum longirostratum (Subram.) Sivan., *Trans. Brit. Mycol. Soc.* 83 (2): 328. 1984.

Exserohilum prolatum K.J. Leonard & Suggs, *Mycologia* 66: 290. 1974.

Setosphaeria prolata K.J. Leonard & Suggs, *Mycologia* 66: 294. 1974.

Setosphaeria rostrata K.J. Leonard, *Mycologia* 68: 409. 1976.

Exserohilum gedarefense (El Shafie) Alcorn, as '*gedarefensis*', *Mycotaxon* 17: 68. 1983.

Exserohilum mcginnisii A.A. Padhye & Ajello, as '*mcginnisii*', *J. Clin. Microbiol.* 24: 247. 1986.

Exserohilum antillanum R.F. Castañeda, Guarro & Cano, *Mycol. Res.* 99: 825. 1995.

Setomelanomma rostrata Green et al., *Allergy, Asthma & Clinical Immunology* 10: 3. 2014 (nom. invalid Art. 41.1).

Type material. USA, Washington DC, on dry leaves of *Eragrostis major*, Sept. 1921, C. Drechsler (BPI 430144 holotype (of *Helminthosporium rostratum*)).

Adapted from Leonard (1976). **Vegetative hyphae** septate, branched, pale olivaceous to pale olivaceous brown, smooth to verruculose, 2.5–8 µm wide. **Asexual morph.** *Conidiophores* macronematous, mononematous, straight to flexuous, geniculate towards the apex, septate, unbranched, subcylindrical, pale olivaceous brown to dark olivaceous brown, with cell walls usually thicker than those of the vegetative hyphae, smooth,

becoming finely verruculose around the conidiogenous loci, 65–395.5 × 4–7.5 µm, base up to 9 µm wide. *Conidiogenous cells* integrated, terminal and intercalary, mono- to polytretic, proliferating sympodially, irregularly pigmented, mostly subcylindrical, 5.5–27.5 µm long, pores surrounded by scars up to 3–4.5 µm wide. *Conidia* ellipsoid, clavate, obclavate or subcylindrical, rostrate or not, straight to moderately curved, pale olivaceous brown to dark olivaceous brown, basal and apical cells often delimited by a dark septum, smooth to verruculose, 1–15-distoseptate, 15–190 × 7–29 µm, hilum 3–4 µm wide. **Sexual morph.** *Ascomata* superficial, globose to ellipsoid, black, 340–600 × 330–580 µm, ostiolate, sometimes with a short, cylindrical, beak, with rigid, dark brown, septate setae surrounding the ostiole, and the upper surface of the ascomata. *Pseudoparaphyses* filiform, hyaline, septate, branched and anastomosing. *Asci* 1–8-spored, clavate to cylindrical-clavate, short stalked, 105–260 × 26–42 µm. *Ascospores* hyaline to

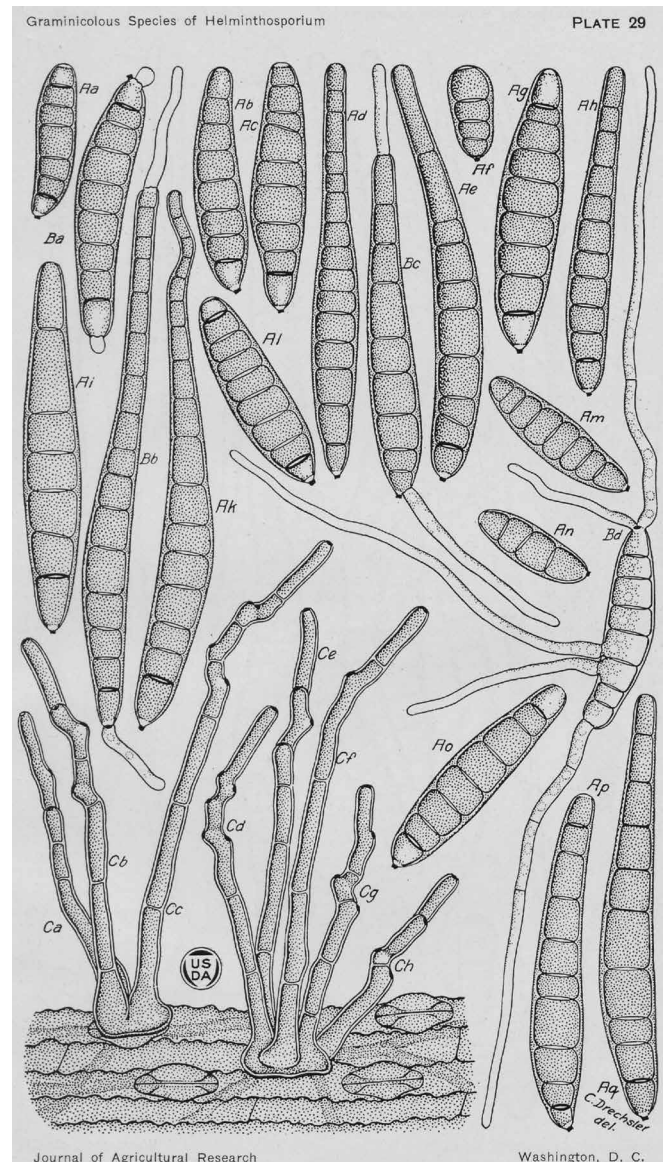


PLATE 29
Helminthosporium rostratum
Aa–q.—Conidia of *H. rostratum* from dry leaves of *Eragrostis major* collected near Washington, D. C., October 13, 1921, showing variation in size, shape, and septation. × 500.
Ba–d.—Conidia from dry leaf of *Eragrostis major* germinating in tap water, the mature spores (Ba–c) by the production of two polar germ tubes; the newly proliferated spore (Bd) by the production of two lateral germ tubes in addition to polar tubes. × 500.
Ca–h.—Conidiophores showing origin in groups from an expanded base and relation of latter to stomata or epidermal cells. × 500.

Fig. 13 Original drawing of *Helminthosporium rostratum* from dry leaves of *Eragrostis major* collected near Washington (lectotype) (reproduced from Drechsler 1923).



Fig. 14 *Exserohilum rostratum* (BPI 429032 (holotype of *Helminthosporium halodes*) (a–f), CBS 128061 (g–j), CBS 120380 (k–n)). a. Conidiophore; b–f, j, n. conidia; g–i, k–m. conidiophores and conidia. — Scale bars: a, k = 20 μ m; b–j, l–n = 10 μ m.

pale brown, fusoid, straight to curved, (2–)3(–5)-septate, constricted at the septa, 29–85 \times 9–21 μ m, surrounded by a thin, hyaline mucilaginous sheath which may extend beyond the ends of the spore after discharge.

Culture characteristics — Colonies on SNA + sterilized maize leaves at 24 °C reaching 64–108 mm diam after 7 d, hairy, grey olivaceous to olivaceous black, with patches of cottony whitish to olivaceous grey mycelium on maize leaves and a fimbriate margin; reverse concolorous with obverse.

Additional materials examined. AUSTRALIA, New South Wales, Broken Head, on leaf spot of *Spinifex hirsutus*, 6 Jan. 1988, J.L. Alcorn (BRIP 16078); Leadville, on *Hordeum vulgare*, 19 July 2002, G. Platz (BRIP 29236c); Sydney, on *Sorghum* sp., 1998, F. Benyon (BRIP 28001); Northern Territory, Howard Springs, on leaf spot of *Areca catechu*, 28 July 1986, M. Connelly (BRIP 15274); Queensland, Atherton, on stalk rot of *Zea mays*, 9 Apr. 1985, M.D. Ramsey (BRIP 14916); Bamaga, on leaf spot of *Eragrostis tenella*, 29 May 1981, J.L. Alcorn (BRIP 10724); Biloela, on leaf lesion of *Zea mays*, 12 Apr. 1972, N.T. Vock (BRIP 11416); Brisbane, on leaf blight of *Cymbopogon citratus*, 22 Feb. 1988, J.L. Alcorn (BRIP 16114); on leaf spot of *Croton* sp., 7 June 2010, L.I. Forsberg (BRIP 53634b); from pairing single-spore cultures BRIP 12220 (USA, North Carolina, from *Zea mays*,

14 Jan. 1977, K.J. Leonard SrA3) \times BRIP 11761 (Kingaroy, from stalk rot of *Zea mays*, 13 Apr. 1976, P.E. Mayers) on *Barley* seeds on Sach's agar, 22 Mar. 1997, J.L. Alcorn (BRIP 12224, culture CBS 128062); Gatton, on crown rot of *Triticum aestivum*, Oct. 1986, R.L. Dodman (BRIP 15489); Goomeri, on leaf spot of *Zea mays*, 26 Apr. 1972, C. Euler (BRIP 11422); Gympie, on leaf spot of *Megathyrsus maximus*, 6 July 1992, D.S. Loch (BRIP 20144b); Lawes, on leaf spot of *Dinebra retroflexa*, 4 Apr. 1977, J.L. Alcorn (BRIP 12147); Mundubbera, on leaf spot of *Vitis vinifera*, 11 Feb. 2005, C.M. Horlock and P. Jackson (BRIP 46107); Nebo, on undetermined *Poaceae*, 6 Sept. 1972, unknown collector (BRIP 11432); Norwin, on leaf spot of *Zea mays*, 28 Mar. 1972, K.M. Middleton (BRIP 10995); Parada, on ear rot of *Zea mays*, 13 Apr. 1972, W. Pont (BRIP 11417); Peregrin Beach, on leaf spot of *Paspalidium distans*, 7 Mar. 1982, J.L. Alcorn No. 8230b (BRIP 13560); Rockhampton, on leaf spot of *Chrysalidocarpus lutescens*, 23 July 1986, unknown collector (BRIP 15403); Sabai Island, on leaf spot of *Eragrostis brownii*, 28 Feb. 1977, J.L. Alcorn No. 7728 (BRIP 12090); Sabai Island, on leaf spot of *Ischaemum villosum*, 1 June 1982, J.L. Alcorn No. 8194a (BRIP 13592); Saibai Island, on leaf of *Dactyloctenium aegyptium*, 1 June 1981, J.L. Alcorn (BRIP 13599); Samford, on leaf spot of *Eragrostis pilosa*, 25 May 1977, J.L. Alcorn No. 77162 (BRIP 12270); Warwick, on *Hordeum vulgare*, 22 June 2009, K. Stephen (BRIP 52639). — CUBA, Ciudad de la Habana, Santiago de las Vegas, on plant debris from forest soil, 10 Feb. 1993, R.F. Castañeda-Ruiz (culture ex-isotype of *E. antillanum* CBS 412.93). — GUATEMALA,

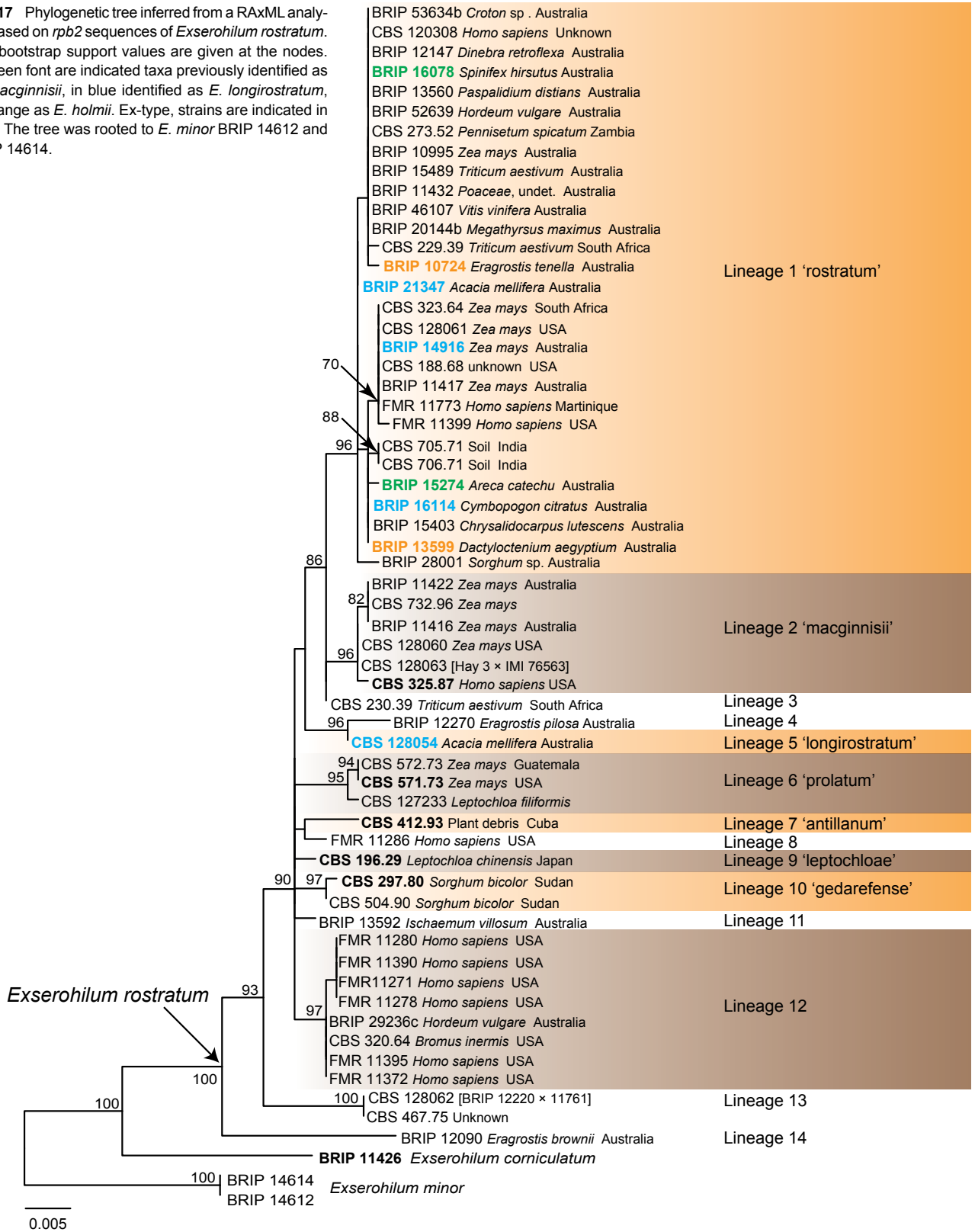


Fig. 15 *Exserohilum rostratum* (CBS 325.87 (ex-type of *E. macginnisii*) (a–d), BRIP 11416 (e–h), CBS 128060 (i–k), BRIP 11422 (l–n), CBS 128054 (o–q), CBS 412.93 (ex-type of *E. antillanum*) (r–t)). a–b, r–t. Conidiophores and conidia; c. chlamydospore; d–q. conidia. — Scale bars: a–n, p–t = 10 μ m; o = 40 μ m.



Fig. 16 *Exserohilum rostratum* (CBS 572.73 (as *E. prolatum*) (a–f), CBS 127233 (g–j), CBS 196.29 (ex-syntype of *H. leptochloae*) (k–n), CBS 320.64 (o–r)). a–d, g–i, k–m, o–p. Conidiophores and conidia; e–f, j, n, q–r. conidia. — Scale bars: a–j, l–r = 10 μm; k = 20 μm.

Fig. 17 Phylogenetic tree inferred from a RAxML analysis based on *rpb2* sequences of *Exserohilum rostratum*. The bootstrap support values are given at the nodes. In green font are indicated taxa previously identified as *E. macginnisii*, in blue identified as *E. longirostratum*, in orange as *E. holmii*. Ex-type, strains are indicated in bold. The tree was rooted to *E. minor* BRIP 14612 and BRIP 14614.



on seed of *Zea mays*, Feb. 1972, unknown collector, No. Ep1 (authentic mating type 'minus' of *Setosphaeria prolata* CBS 572.73). – INDIA, Poona, from soil, unknown date, P.G. Patwardhan (CBS 705.71, CBS 706.71). – JAPAN, Okayama, Kurashiki, on *Leptochloa chinensis*, Oct. 1919, Y. Nisikado (syntype of *H. leptochloae* CBS H-7220; culture ex-syntype of *H. leptochloae* CBS 196.29). – MARTINIQUE, on heart valve prosthesis of *Homo sapiens*, 1980, unknown collector (FMR 11773). – NAMIBIA, Windhoek, endophytic on 5-mo-old seedlings of *Acacia mellifera* subsp. *detinens*, Apr. 1993, G. Holz (CBS 128054); Windhoek, endophytic on 5-mo-old seedlings of *Acacia mellifera* subsp. *detinens*, Apr. 1993, G. Holz (CBS 128055). – SOUTH AFRICA, Gauteng Province, Johannesburg, unknown substrate, unknown date, P. Martin No. 1323 (CBS 188.68); Free State Province, Bethlehem, on *Triticum aestivum*, Apr. 1939, K. Putterill No. 30456 (CBS 230.39); Gauteng Province, on

Triticum aestivum, Apr. 1939, K. Putterill No. 30434 (CBS 229.39). – SUDAN, on grains of *Sorghum bicolor*, Apr. 1979, A.E. El Shafie (culture ex-type of *E. gedarefense* CBS 297.80); 21 Mar. 1983, J.L. Alcorn (as *E. gedarefense* CBS 504.90). – UNKNOWN COUNTRY, on *Zea mays*, unknown date, J.L. Alcorn (CBS 732.96); from nasal mucosa of 45-yr-old male with acute myelogenous leukemia, unknown date, dep. I. Polachek (as *E. macginnisii* CBS 120308); unknown substrate, unknown date, unknown collector (CBS 467.75 = ATCC 32198). – USA, Florida, Gainesville, on *Zea mays*, 27 May 1972, E.S. Luttrell 8868 'mating type A' (CBS 128061); Georgia, Decatur County, on *Zea mays*, 8 June 1971, E.S. Luttrell 8686 'mating type A' (CBS 128060); Georgia, from eye (wood splinter) of *Homo sapiens*, 2009, S.A. Sutton (FMR 11399); Mississippi, State College, on leaf of *Zea mays*, Oct. 1971, M.C. Futrell No. Ep3 (authentic mating type 'plus' of *Setosphaeria prolata* CBS 571.73); Montana,

from maxillary sinus of *Homo sapiens*, 2009, S.A. Sutton (FMR 11395); New York, Douglaston, on *Distichlis spicata*, 26 Sept. 1920, C. Drechsler (holotype of *Helminthosporium halodes* BPI 429032); North Carolina, ascospore isolate from Hay3 × IMI 76563, 14 Jan. 1977, K.J. Leonard (CBS 128063); North Carolina, on barley grains on Sach's agar by mating compatible isolates *Ep1* × *Ep3*, 1974, K.J. Leonard (holotype specimen of *Setosphaeria prolata* BPI 622161); Oklahoma, Stillwater, on *Leptochloa filiformis*, 29 Aug. 1960, R.A. Shoemaker (CBS 127233); Texas, on elbow tissue of *Homo sapiens*, 2008, D.A. Sutton (FMR 11028); sinus, 2005, D.A. Sutton (FMR 11271); from cornea of *Homo sapiens*, 2006, D.A. Sutton (FMR 11278); great toe, 2006, D.A. Sutton (FMR 11280); shin skin of *Homo sapiens*, 2007, D.A. Sutton (FMR 11286); nasal inferior turbinate, 2008, D.A. Sutton (FMR 11390); unknown tissue of *Homo sapiens*, 2007, D.A. Sutton (FMR 11372); Tucson, Arizona, from nasal polyp from *Homo sapiens*, unknown date, A.A. Padhye (culture ex-type of *E. macginnisii* CBS 325.87); unknown state, on *Bromus inermis*, unknown date, R.R. Nelson (CBS 320.64); unknown state, on *Zea mays*, unknown date, R.R. Nelson No. 26 (CBS 323.64); Utah, maxillary sinus of *Homo sapiens*, 2008, D.A. Sutton (FMR 11392). — ZAMBIA, on seed of *Pennisetum spicatum*, 1951, W.E. Kerr, No G. 32 (CBS 273.52).

Notes — *Exserohilum rostratum* is by far the most commonly recorded and known species of the genus. This cosmopolitan species has been recorded from numerous hosts, especially *Poaceae* and other monocots, causing leaf spot and foot rot of wheat and other grasses, blight, damping-off, rots including leaf spot of banana (Sivanesan 1987, Farr & Rossman 2017). Clinical human reports of this species have also been increasing (Aquino et al. 1995, Adler et al. 2006, Al-Attar et al. 2006, Derber et al. 2010, Da Cunha et al. 2012, Kainer et al. 2012, Smith et al. 2013).

Exserohilum rostratum was first described as *Helminthosporium rostratum*, isolated from *Eragrostis major* in the USA (Drechsler 1923). The holotype, BPI 430144, is preserved at the US National Fungus Collection. Unfortunately, no culture is linked to the holotype. Among the specimens examined in our study, none of them were suitable to serve as an epitype, since there are no isolates from *E. major* from the USA. In the protologue, Drechsler (1923) described ellipsoidal conidia with 3–9 septa and rostrate conidia with 8–15 septa, measuring 32–184 × 14–22 µm (Fig. 13). Leonard (1976) noticed the wide morphological variability of this species when he introduced the synonymy of *E. halodes* (conidial size after emendation 15–190 × 7–29, 1–15-septate). He pointed out that isolates of *E. rostratum* that originally produce strongly rostrate conidia may lose that characteristic in culture. Another factor that influences the conidial morphology was the light. Isolates that were exposed to light formed strongly rostrate conidia, but in the dark they formed only ellipsoidal conidia (Leonard 1976). During our study, conidial morphology in the specimens examined was also highly variable (Fig. 14–16). Furthermore, phylogenetic analysis based on multi-locus data show that *E. antillanum*, *E. gedarefense*, *E. longirostratum*, *E. macginnisii*, *E. prolatum* and *Helminthosporium leptochloae* are conspecific to *E. rostratum*, and therefore they are listed here as synonyms (Fig. 1).

In *E. rostratum*, 14 lineages were discerned with the individual analysis of the most informative gene, *rpb2* (Fig. 17). The clinical isolates were mainly distributed in three lineages, i.e., 'rostratum', 'macginnisii' and lineage 12, except for the isolate FMR 11286 which formed an independent lineage. The lineage 'rostratum' includes 26 strains isolated mainly from monocotyledon plants (Fig. 17, Table 1) but also include four clinical isolates (FMR 11773, FMR 11028, FMR 11399 and CBS 120308) from Australia, USA, South Africa, India and Zambia. The lineage 'macginnisii' includes CBS 325.87 (the ex-type of *E. macginnisii*) isolated from a clinical sample, CBS 128060 (the mating type A used by Luttrell to produce the sexual morph), CBS 128063 (ascospore isolate from crossing: Hay 3 (R.R. Nelson) × IMI 76563), and three isolates from *Zea mays* CBS 732.96, BRIP 11422 and BRIP 11416 from Australia and the

USA. The lineage 12 includes mostly clinical isolates from the USA (FMR 11390, FMR 11287, FMR 11271, FMR 11280, FMR 11372, FMR 11395, FMR 11392) and two isolates from plants BRIP 29236 (*Hordeum vulgare*, Australia) and CBS 320.64 (*Bromus inermis*, USA). The lineage 'prolatum' includes three isolates, two of them CBS 571.73 and CBS 572.73, isolated from *Zea mays* in the USA and Guatemala, respectively, and CBS 127233 deposited as '*Drechslera micropus*' isolated from *Leptochloa filiformis* in the USA. The lineage 'gedarefense' includes two isolates identified as *E. gedarefense* including the type strain CBS 297.80 and CBS 504.90, both isolated from *Sorghum bicolor* in Sudan. The lineage 'antillanum' includes CBS 412.93 (ex-type strain of *E. antillanum*) isolated from plant debris in Cuba. The clade 'leptochloae' includes CBS 196.29 (ex-type strain of *H. leptochloae*) isolated from *Leptochloae chinensis* in Japan. Other lineages were formed by individual strains CBS 230.39, BRIP 13592, BRIP 12090, CBS 128054, and BRIP 12270. Interestingly, the isolate CBS 128062 (= BRIP 12224) which was the offspring of a cross among BRIP 12220 (USA, North Carolina, from *Zea mays*, 14 Jan. 1977, K.J. Leonard SrA3) × BRIP 11761 (Kingaroy, from stalk rot of *Zea mays*, 13 Apr. 1976, P.E. Mayers) formed a basal lineage together with CBS 467.75 (= ATCC 32198 = IMI 197560), which is labelled at the ATCC database as SrA3. However, with the information available in the CBS and IMI database we cannot corroborate this data.

***Exserohilum turcicum* (Pass.) K.J. Leonard & Suggs, Mycologia 66: 291. 1974 — Fig. 18**

Basionym. *Helminthosporium turcicum* Pass., Boln Comiz. Agr. Parmense 10: 3. 1876.

Synonyms. *Bipolaris turcica* (Pass.) Shoemaker, as '*turcicum*', Canad. J. Bot. 37: 884. 1959.

Drechslera turcica (Pass.) Subram. & B.L. Jain, Curr. Sci. 35: 355. 1966.

Luttrellia turcica (Pass.) Khokhr., as '*Luttrellia*', Vodorosli, Griby i Mkhi Dal'nego Vostoka [Algae, Fungi and Mosses of the Soviet Far-East] (Vladivostok): 81. 1978.

Trichometasphaeria turcica Luttr., Phytopathology 48: 282. 1958.

Keissleriella turcica (Luttr.) Arx, Gen. Fungi Sporul. Cult. (Lehr): 126. 1970.

Setosphaeria turcica (Luttr.) K.J. Leonard & Suggs, Mycologia 66: 295. 1974.

Helminthosporium inconspicuum Cooke & Ellis, Grevillea 6 (no. 39): 88. 1878.

Type material. ITALY, Parma, on *Zea mays*, date unknown, G. Passerini (BPI 431157 lectotype designated here (of *Helminthosporium turcicum* MBT379823)). — GERMANY, Lower Saxony, Einbeck, on *Zea mays*, unknown date, D. Heitmann No. W64A (CBS H-23323 epitype designated here, MBT378854; CBS 690.71 culture ex-epitype).

On *Zea mays* leaves (BPI 431157). *Vegetative hyphae* mostly immersed, septate, branched, pale olivaceous to pale olivaceous brown, smooth, 3–7.5 µm wide. *Asexual morph.* *Conidiophores* macronematous, single to caespitose, usually emerging from stomata, straight to flexuous, often geniculate above, septate, mostly unbranched, subcylindrical, septate, mostly simple, olivaceous brown, becoming paler towards the apex, finely verruculose, with cell walls thicker than those of the vegetative hyphae, length indeterminate, 5.5–10.5 µm wide, often with a bulbous base up to 19.5 µm wide, rarely with subnodulose and nodulose intercalary swellings up to 15 µm wide. *Conidiogenous cells* integrated, terminal and intercalary, mostly subcylindrical, mono- and polytretic, proliferating sympodially, 10–86.5 µm long; pores up to 1 µm wide, surrounded by scars 4–5.5 µm wide. *Conidia* ellipsoidal, obclavate to fusiform, straight to slightly curved, pale olivaceous brown, smooth, sometimes asperulate at the base, (1–)3–9-distoseptate, (51–)60.5–126(–140) × (16.5–)19.5–31(–33) µm, with a slightly to strongly protruding hilum 2–4.5 µm wide.



Fig. 18 *Exserohilum turcicum* (BPI 431157 holotype (a–j), CBS 690.71 ex-epitype (k–s)). a–e. Conidiophores and conidiogenous cells; f–j. conidia; k–s. conidiophores and conidia. — Scale bars: a–j = 10 μ m; k–s = 20 μ m.

On SNA + maize leaves. *Vegetative hyphae* septate, branched, pale olivaceous to pale olivaceous brown, smooth to verruculose, with anastomoses, 2–9 µm wide. *Asexual morph.* *Conidiophores* semi-macronematous to macronematous, straight to flexuous, often geniculate at the fertile part, septate, often unbranched, subcylindrical, pale olivaceous brown to dark brown, paler at the apex, smooth to asperulate, with cell walls thicker than those of the vegetative hyphae, 169–1324.5 × 5.5–10 µm, often with a swollen, sometimes bulbous base up to 22 µm wide, with subnodulose to nodulose intercalary swellings up to 12.5 µm wide, swellings with conidiogenous loci. *Conidiogenous cells* integrated, terminal and intercalary, mostly subcylindrical, mono- to polytretic, proliferating sympodially, 11–74 µm long, with scars up to 4.5 µm wide. *Conidia* fusoid, straight to more or less curved, pale to dark olivaceous brown, smooth to finely verruculose, (1–)4–7-distoseptate, (43–)76–135.5(–141) × (10–)16.5–22(–25) µm, with a strongly protruding hilum 2–4.5 µm wide. *Microcyclic conidiation* occasionally observed. *Sexual morph* (setosphaeria-like) adapted from Sivanesan (1987). *Ascomata* globose to ellipsoid, black, 350–725 × 345–500 µm, ostiolate, with rigid, dark brown, septate setae surrounding the ostiole, and the upper surface of the ascomata. *Pseudoparaphyses* filiform, hyaline, septate, branched and anastomosing. *Asci* 1–8-spored, cylindrical-clavate, short stalked, 175–250 × 24–31 µm. *Ascospores* hyaline, fusoid, straight to curved, (1–)3(–6)-septate, constricted at the septa, 40–78 × 12–18 µm, surrounded by a thin, hyaline mucilaginous sheath which may extend beyond the ends of the spore after discharge.

Culture characteristics — Colonies on SNA + sterilized maize leaves at 24 °C reaching 50–80 mm diam after 7 d, hairy to floccose, olivaceous grey to olivaceous black, cottony on maize leaves, with a fimbriate margin; reverse concolorous with obverse.

Additional materials examined. AUSTRALIA, Queensland, Samford, on leaf blight of *Sorghum bicolor*, 25 May 1977, J.L. Alcorn No. 77159 (BRIP 12267); on leaf speckle of *Sorghum sudanense*, 6 Apr. 1981, R. Jones No. 22233 (BRIP 13326). — INDONESIA, Lembang, on leaf of *Zea mays*, June 1926, M.B.

Schwarz (CBS 195.26). — USA, on leaf spot of *Zea mays*, Sept. 1964, R.R. Nelson (CBS 330.64); Georgia, dried culture of a crossing of compatible isolates on Sach's agar with *Hordeum vulgare* straw, 1954, E.S. Luttrell No. 6001 (holotype of *Setosphaeria turcica* BPI 623931); single ascospore isolate, Mar. 1958, E.S. Luttrell No. 1198-9 ('plus' strain of *S. turcica* CBS 384.58); E.S. Luttrell No. 1198-6 ('minus' strain of *S. turcica* CBS 385.58); on leaf of *Sorghum halepense*, Mar. 1958, E.S. Luttrell (CBS 386.58); Tifton, on leaf of *Zea mays*, Mar. 1958, E.S. Luttrell (CBS 387.58).

Notes — *Helminthosporium turcicum* was described on maize from Italy (Passerini 1876, Saccardo 1886). Luttrell (1958) obtained the ascomata by mating opposite compatible sexual strains, and introduce *Trichometasphaeria turcica* for the sexual morph. Later, Leonard & Suggs (1974) introduce *Exserohilum* with *E. turcicum*, based on *H. turcicum*, as the generic type and introduce the sexual morph as *Setosphaeria*. The herbarium material preserved at the US National Fungal Collection, BPI 431157 bears the label 'Type?'. This material was collected by G. Passerini from the same locality and host as the type, and is therefore designated here as the lectotype. To stabilize the name, the isolate CBS 690.71 from *Zea mays* in Germany, is proposed as the ex-epitype, being from the same host and geographically close to the type locality, Italy, and its morphology fits well with the description of the species. This species causes the disease known as northern leaf blight of maize. It has also been reported on *Euchlaena*, *Sorghum* and other graminicolous plants. It is widespread in both tropical and subtropical areas. In the phylogenetic tree, *E. turcicum* is represented by eight strains isolated from *Zea mays* and *Sorghum* spp. collected from different geographical origins, i.e., Australia, Germany, Indonesia and the USA (Fig. 2).

DOUBTFUL OR EXCLUDED SPECIES

In this section are included species retained in *Exserohilum* based on morphology (without molecular data), and species transferred to other genera based on molecular and/or morphological data.



Fig. 19 *Exserohilum curvisporum* (IMI 356632 holotype). a–e. Conidiophores and conidiogenous cells; f–j. conidia. — Scale bars: 10 µm.

Exserohilum curvisporum Sivan., Abdullah & B.A. Abbas, Mycol. Res. 97: 1486. 1993 — Fig. 19

Type material. IRAQ, Basrah, isolated from sediments of Shat-al-Arab River, 15 Dec. 1991, S.K. Abdullah & A. Abbas BSRA 10260 (IMI 356632 holotype).

Adapted from Sivanesan et al. (1993). *Colonies* effuse, pale brown. *Vegetative hyphae* pale brown, branched, septate, smooth, 4–5 µm wide. *Conidiophores* commonly unbranched, straight to flexuous, geniculate above, cicatrized, cylindrical, olivaceous brown, paler towards the apex, 125–450 × 6–8 µm. *Conidia* cylindrical to cylindrical-fusiform, mostly strongly curved, sometimes slightly curved or sigmoid, rarely straight, concolorous, pale brown, surface often granulose, 1–12-distoseptate, 65–165 × 12.5–22 µm, mostly 80–125 × 14–15 µm, with a basal distinctly protruding hilum up to 1 µm wide.

Notes — *Exserohilum curvisporum* is only known from the type locality, isolated from sediments of a river in Iraq. Although no molecular data exist for *E. curvisporum*, this species is retained in *Exserohilum* based on the characteristic hilum structure and conidial morphology.

Exserohilum echinochloae Sivan., Trans. Brit. Mycol. Soc. 83: 319. 1984 — Fig. 20

Type material. BANGLADESH, on leaves of *Echinochloae colona*, 10 Apr. 1979, M.A. Miah (IMI 237838 holotype).

Herbarium material. *Colonies* dark brown, effuse, sporulating abundantly. *Vegetative hyphae* septate, branched, pale olivaceous to pale olivaceous brown, 2.5–6 µm wide. *Conidiophores* macronematous, mononematous, straight, more or less bent or flexuous, septate, mostly unbranched, subcylindrical, brown, becoming paler and sometimes appearing geniculate toward the apex, smooth to asperulate, with cell walls thicker than those of the vegetative hyphae, 216–812.5 × 5.5–9.5 µm, and with a bulbous base up to 14.5 µm wide, often with subnodulose and nodulose intercalary swellings up to 13 µm wide, swellings with

conidiogenous loci. *Conidiogenous cells* integrated, terminal and intercalary, mostly subcylindrical, mono- and polytretic, proliferating sympodially, 26–88 µm long, pores 0.5–1 µm wide, surrounded by scars 4.5–5 µm wide. *Conidia* fusiform, straight to curved, olivaceous brown, smooth, asperulate at the base, 7–11-distoseptate, 111–197.5 × 19–37 µm, basal cell often bulging a little, with a strongly protruding hilum 2.5–3.5 µm wide.

Notes — *Exserohilum echinochloae* is morphologically similar to *E. monoceras* and *E. turcicum*, but differs from them by having longer and wider conidia (Sivanesan 1984). Although no molecular data exist for *E. echinochloae*, this species is retained in *Exserohilum* based on the characteristic hilum structure and conidial morphology.

Exserohilum elongatum Hern.-Restr. & Crous, *sp. nov.* — MycoBank MB823162; Fig. 21

Synonym. *Exserohilum elongatum* Del Serrone et al., Phytopath. Mediterr. 30: 152. 1991 [nom. invalid Art. 40.1].

Type material. ITALY, Piemonte, Cherasco (Cuneo), on leaves of *Echinochloa crus-galli*, 1979, Porta-Puhglia, IMI 321829 holotype designated here.

Herbarium material. *Colonies* brown, effuse, with abundant sporulation. *Vegetative hyphae* septate, branched, pale olivaceous to pale olivaceous brown, smooth to asperulate, 2–6 µm wide. *Conidiophores* macronematous, straight to flexuous, septate, mostly unbranched, subcylindrical, pale olivaceous brown to dark brown, often paler toward the apex, smooth to asperulate, with cell walls thicker than those of the vegetative hyphae, 168.5–1190 × 7–9.5 µm, often with a bulbous base up to 18.5 µm wide, with subnodulose intercalary swellings up to 11.5 µm wide, swellings with conidiogenous loci. *Conidiogenous cells* integrated, terminal and intercalary, mostly subcylindrical, mono- and polytretic, proliferating sympodially, 19.5–97 µm long, pores 0.5–1 µm wide, surrounded by scars 4–6 µm wide. *Conidia* clavate, cylindrical to fusiform, olivaceous brown, often somewhat paler at the apex or at the ends, smooth, asperulate

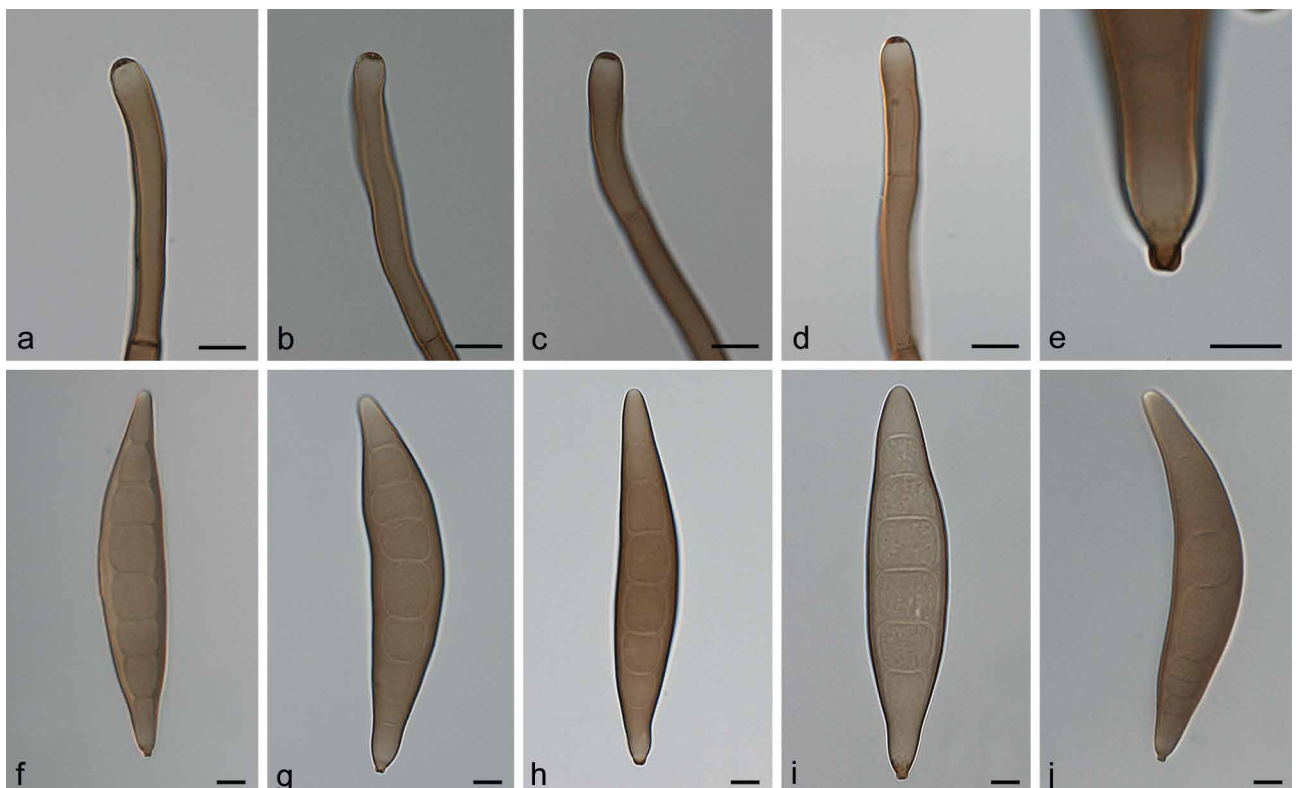


Fig. 20 *Exserohilum echinochloae* (IMI 237838 holotype). a–d. Conidiogenous cells; e. lower part of conidium; f–j. conidia. — Scale bars: 10 µm.

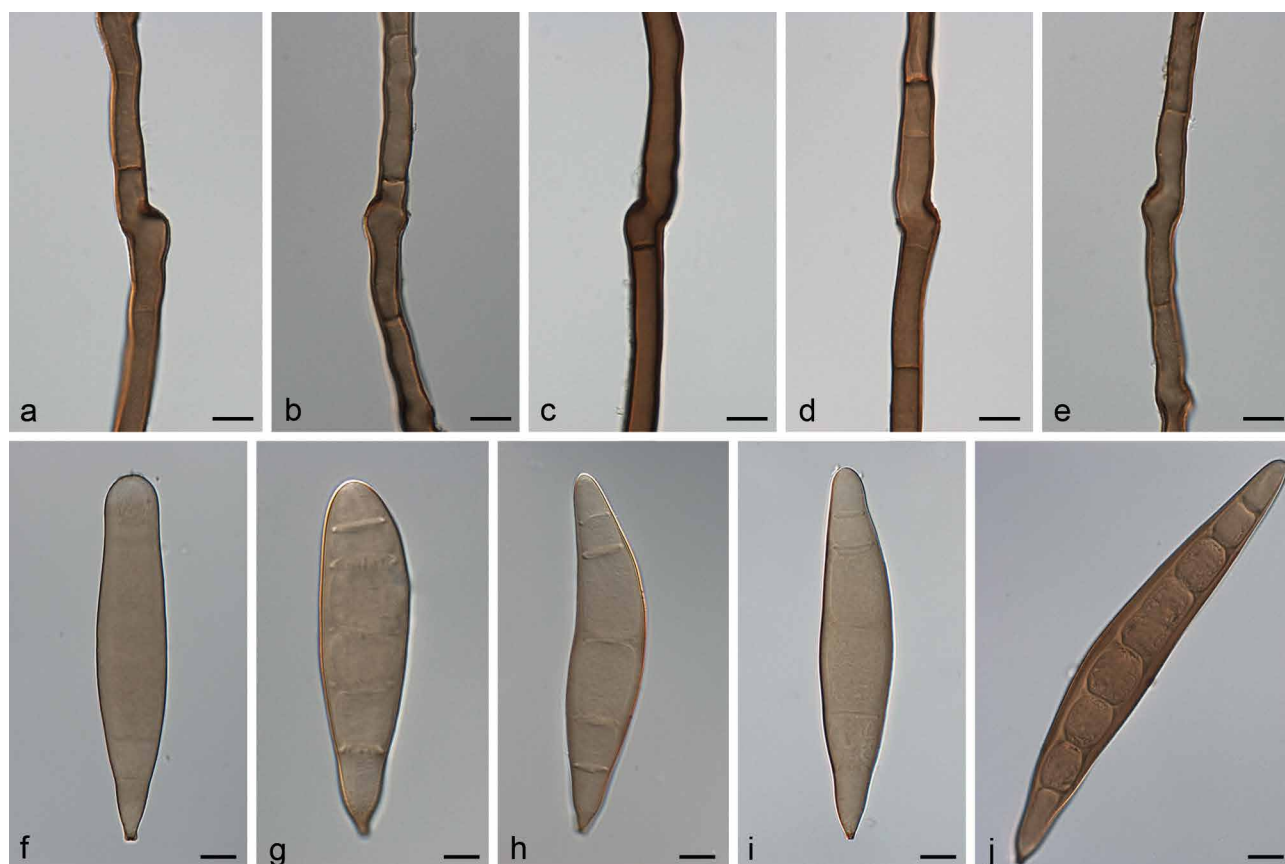


Fig. 21 *Exserohilum elongatum* (IMI 321829 holotype). a–e. Conidiogenous cells; f–j. conidia. — Scale bars: 10 μ m.

at the base, 4–8-distoseptate, (42–)81–168 \times 19–28.5 μ m, with a strongly protruding hilum 2–3.5 μ m wide.

Notes — *Exserohilum elongatum* is morphologically comparable with *E. echinochloae* and *E. oryzicola*. However, the protologue of the former (Del Serrone et al. 1991) describes longer conidia in respect to the other two species (i.e., 114–247 \times 28–30 μ m vs 150–210 \times 25–35 μ m and 170–210 \times 20–28 μ m, respectively). Nevertheless, we examined the material deposited at Kew Botanical Garden (IMI 321829) and conidia were shorter (42–168 \times 19–28.5 μ m) than those described in the original description (Del Serrone et al. 1991). The high morphological variation in species of *Exserohilum*, and the lack of molecular data in this species, make the correct placement of *E. elongatum* problematic.

Exserohilum frumentacei (Mitra) K.J. Leonard & Suggs, as '*frumentaceum*', *Mycologia* 66: 291. 1974

Basionym. *Helminthosporium frumentacei* Mitra, *Trans. Brit. Mycol. Soc.* 15: 288. 1931.

Type material. INDIA, Pusa, leaf-sheaths of *Panicum frumentaceum*, unknown date, Mitra.

Notes — This species was described from *Panicum frumentaceum* in India (Mitra 1931). *Exserohilum frumentacei* resembles *E. monoceras* in conidial size and morphology and probably represents the same species. However, culture of this species is not available for phylogenetic comparison.

Exserohilum glycinea (L.S. Srivast. et al.) P.M. Kirk, *Index Fungorum* 269: 1. 2015

Basionym. *Setosphaeria glycinea* L.S. Srivast. et al., *Indian J. Mycol. Pl. Pathol.* 12: 241. 1983.

Type material. INDIA, Meghalaya, on leaves of *Glycine max*, 11 Aug. 1976 (IMI 209021 holotype, not seen).

Notes — The inclusion of this species in *Exserohilum* is doubtful. Originally, *E. glycinea* was described as the causal agent of leaf spot and blight of leaves of *Glycine max* (Srivastava et al. 1983), an uncommon substrate for *Exserohilum* species. It is only known by the sexual morph and was distinguished from other species of *Setosphaeria* by the presence of well-developed, long and septate setae on the ascomata, ascospores 5–6-septate, the enlargement of the third cell from the top of the ascospore and by the absence of asexual morph (Srivastava et al. 1983).

Exserohilum heteromorphum G.Y. Sun, *Mycotaxon* 92: 174. 2005

Type material. CHINA, Shaanxi, on leaves of *Echinochloa crus-galli* var. *mitis*, unknown date, unknown collector (HMUABO 20579 holotype, not seen).

Notes — *Exserohilum heteromorphum* was differentiated from other species of the genus by the presence of strongly curved conidia (Sun et al. 2005). However, *E. heteromorphum* is morphologically similar to *E. monoceras*, which also has curved conidia (Drechsler 1923). Furthermore, *E. heteromorphum* was described from leaves of *Echinochloa crus-galli*, the same substrate as *E. monoceras*, and therefore likely represent the same species. Unfortunately, no cultures are available to confirm the phylogenetic relationship.

Exserohilum israeli Steiman et al., *Antonie van Leeuwenhoek* 78: 155. 2000

Type material. ISRAEL, Timna Park, Negev desert, Arava valley, from soil, Aug. 1994 (CMPG 1339 holotype, not seen).

Notes — *Exserohilum israeli* was described from soil in Israel (Steiman et al. 2000). According to the protologue, this fungus is morphologically compatible with *E. rostratum*. No living culture of *E. israeli* is available for study.

Exserohilum lagenarioides Pachkhede, Geobios, New Rep. 8: 64. 1989

Notes — This name is currently considered as invalid in Index Fungorum following Art. 40.1, 40.4 and 8.4 of the International Code of Nomenclature for algae, fungi and plants (Melbourne Code).

Exserohilum longisporum G.Y. Sun, Mycol. Res. 101: 776. 1997

Type material. CHINA, Hunan, Changsha, on *Miscanthus sinensis*, 12 Oct. 1992 (HMUABO 100133 holotype, not seen; HMAS 73782 isotype, not seen).

Notes — *Exserohilum longisporum* was described from *Miscanthus sinensis* in China (Sun et al. 1997). According to the protologue, this fungus is morphologically compatible with *E. rostratum*. No living culture of *E. longisporum* is available for study.

Exserohilum oryzae Sivan., Mycol. Pap. 158: 231. 1987 — Fig. 22

Type material. YUGOSLAVIA (CURRENTLY MACEDONIA), Kočani, on *Oryza sativa*, June 1977, *Karov Ilija 5* (IMI 214168 holotype).

Herbarium material. *Vegetative hyphae* septate, branched, pale olivaceous to pale brown, smooth-walled, 3.5–5.5 µm wide, anastomosing. *Conidiophores* macronematous, mononematous, straight, curved or geniculate, mostly unbranched, subcylindrical, pale olivaceous brown to dark brown, becoming paler towards the apex, smooth to asperulate, with cell walls usually thicker than those of the vegetative hyphae, 21–720 × 3.5–7.5 µm, sometimes slightly swollen at the base up to 10 µm wide, often with subnodulose and nodulose intercalary swellings up to

10 µm wide, swellings with conidiogenous loci. *Conidiogenous cells* integrated, terminal and intercalary, mostly subcylindrical, mono- and polytretic, proliferating sympodially, 10–54 µm long, with pores up to 1 µm wide, surrounded by scars 3–5 µm wide. *Conidia* fusiform with an obtuse apex and a truncate obconic base, rarely clavate, straight to more or less curved, pale olivaceous brown to dark brown, often paler at both poles, smooth to asperulate with the ornamentation more evident at the base, (3–)7–9-distoseptate, (34–)61–150 × 10–24 µm, with a protruding hilum, 2.5–5.5 µm wide. Germination unipolar or bipolar. *Microcyclic conidiation* frequent.

Notes — The protologue describes narrower hyphae (up to 4.5 µm wide), conidiophores slightly shorter and narrower (up to 600 µm long, 5–6 µm wide) and conidia slightly longer and wider, 96–160 × 18–25 µm (Sivanesan 1987) than those observed here (34–150 × 10–24 µm). Sivanesan possibly excluded short conidia from his description because he might have considered them immature. They were included here because even these short conidia were able to germinate. *Exserohilum oryzae* and *E. oryzicola* are very similar species isolated from the same substrate. According to Sivanesan (1987), they differ in conidial size. Nevertheless, the high morphological variation in species of *Exserohilum*, and the lack of molecular data in this species, makes the correct placement of *E. oryzae* difficult to assess.

Exserohilum oryzinum Sivan., Trans. Brit. Mycol. Soc. 83: 325. 1984 — Fig. 23

Type material. EGYPT, Alexandria, from leaves of *Oryza* sp., 8 Nov. 1970, *M.K. El-Kazaz* (IMI 152682 holotype).

Herbarium material. *Vegetative hyphae* septate, branched, pale olivaceous to medium brown, smooth to asperulate 3–7.5 µm

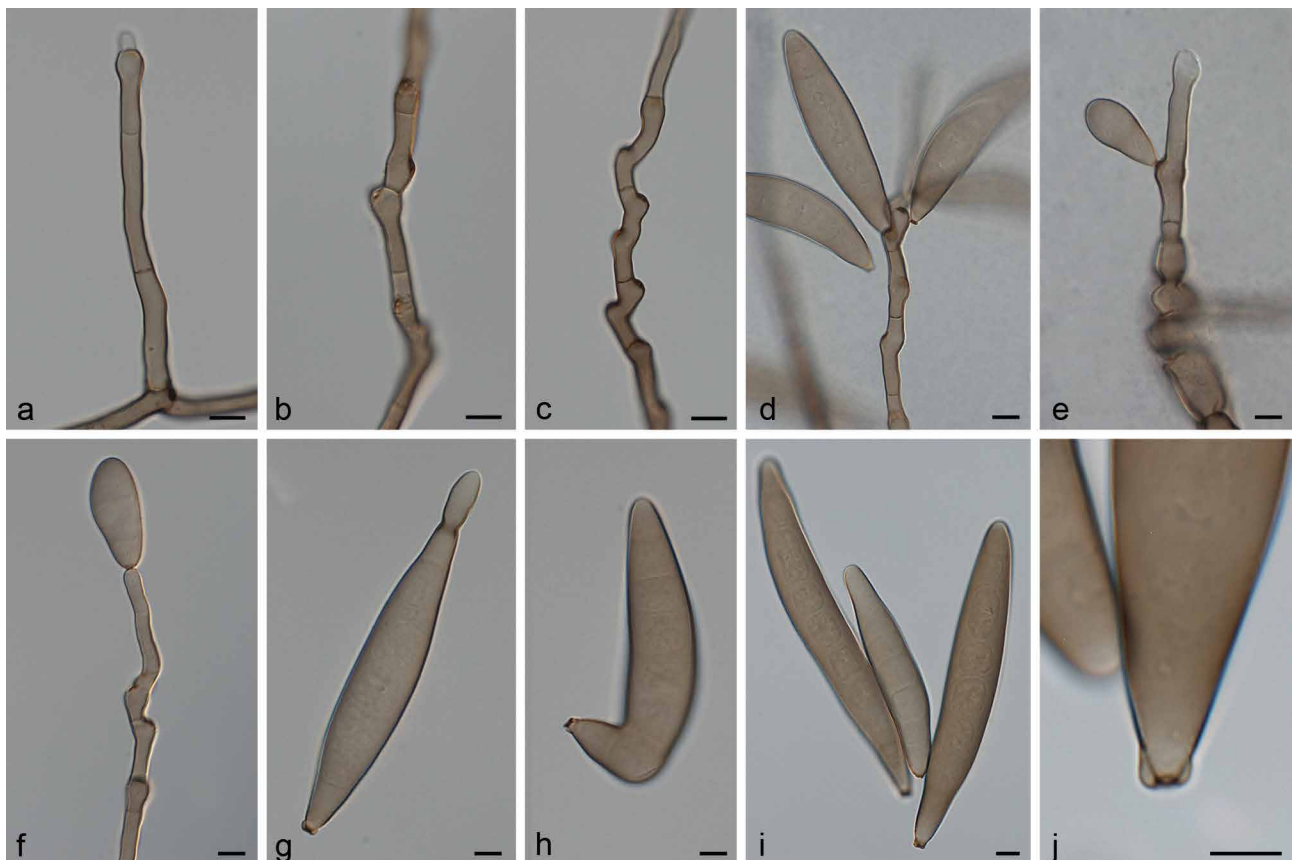


Fig. 22 *Exserohilum oryzae* (IMI 214168 holotype). a–c. Conidiophores and conidiogenous cells; d–f. conidiogenous cells and conidia; g–i. conidia; j. lower part of conidium. — Scale bars: 10 µm.

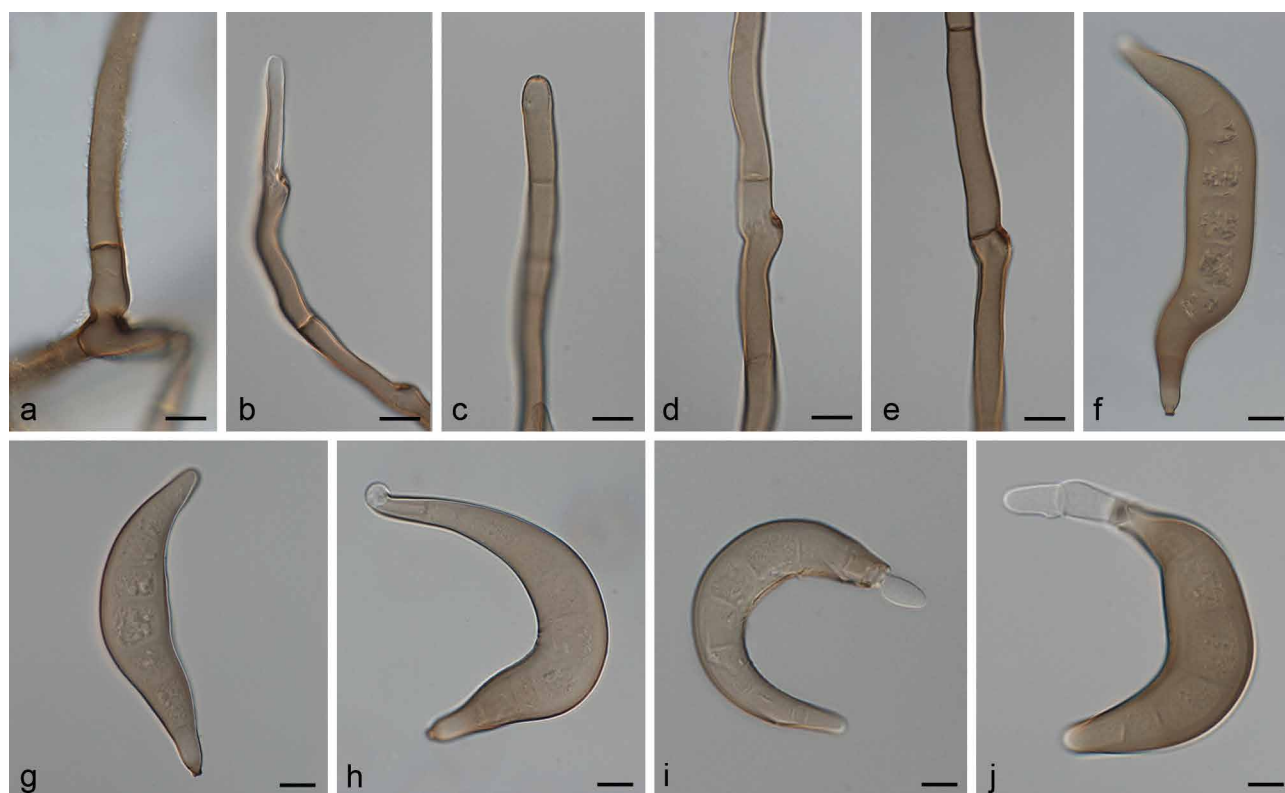


Fig. 23 *Exserohilum oryzinum* (IMI 152682 holotype). a. Conidiophore with a swelling base; b–e. conidiogenous cells; f–j. conidia. — Scale bars: 10 μm .

wide, anastomosing. *Conidiophores* macronematous, straight to flexuous, septate, mostly unbranched, subcylindrical, pale olivaceous brown to dark brown, becoming paler towards the apex, smooth to asperulate, with cell walls thicker than the vegetative hyphae, up to 810 μm long, 4–8 μm wide, sometimes swollen at the base up to 9 μm wide, with subnodulose and nodulose intercalary swellings up to 11 μm wide, swellings with conidiogenous loci. *Conidiogenous cells* integrated, terminal and intercalary, mostly subcylindrical, mono- and polytretic, proliferating sympodially, 9–61.5 μm long, pores up to 1 μm wide, surrounded by scars 3.5–5.5 μm wide. *Conidia* mostly falcate or sigmoid, rarely fusiform or clavate, pale to medium olivaceous brown, smooth to asperulate with the ornamentation more evident at the base, (4–)6–10-distoseptate, (56–)80–155 \times 14–27 μm , with a protruding hilum, 2.5–4 μm wide. Germination uni- or bipolar. *Microcyclic conidiation* frequent.

Notes — *Exserohilum oryzinum* is only known from Egypt growing on *Oryza* sp. This species is distinguished from other *Exserohilum* spp. by the distinctively curved to sigmoid, pale to mid-brown conidia. Although no molecular data exist for *E. oryzinum*, this species is retained in *Exserohilum* based on the characteristic hilum structure and conidial morphology (Sivanesan 1984).

Exserohilum parlierense W.Q. Chen & Michailides, as '*parlierensis*', Mycotaxon 83: 153. 2002

Type material. USA, California, on leaves of *Pistacia vera*, 16 Aug. 2001, Q.W. Chen (ATCC MYA-2456 holotype, not seen; CH-26 culture ex-type).

Notes — *Exserohilum parlierense* was described from *Pistacia vera* in the USA (Chen et al. 2002). According to the protologue, this fungus is morphologically compatible with *E. rostratum*.

Exserohilum phragmitis W.P. Wu, as '*phragmatis*', J. Hebei Acad. Sci., Selected papers: 60. 1990

Type material. CHINA, Hebei, on leaves of *Phragmites* (IBHAS 4150 holotype, not seen).

Notes — This name we considered here as invalid following Art. 8 and 40 of the International Code of Nomenclature for algae, fungi and plants (Melbourne Code). The data of the type material listed here is accordingly to information in Index Fungorum. However, the publication linked to the protologue did not describe a new species.

Exserohilum psidii Sivan., Mycol. Res. 96: 489. 1992 — Fig. 24

Type material. INDIA, Warangal, on *Psidium* sp., 15 Oct. 1985, Madhukar D2 (IMI 299549 holotype, not seen).

Herbarium material. *Colonies* on TWA + wheat straw effuse floccose, dark brown. Vegetative hyphae septate, branched, subhyaline to mid olivaceous brown, smooth to asperulate, 3–7 μm wide. *Conidiophores* macronematous, straight to flexuous, septate, unbranched, subcylindrical, pale olivaceous brown to dark brown, smooth to asperulate, with cell walls thicker than those of the vegetative hyphae, up to 1086 μm long, 5.5–11 μm wide, often swollen at the base up to 18 μm wide, with subnodulose and nodulose intercalary swellings up to 12 μm wide, swellings with conidiogenous loci. *Conidiogenous cells* integrated, terminal and intercalary, mostly subcylindrical, mono- and polytretic, proliferating sympodially, 16.5–118.5 μm long, with pores up to 1 μm wide, surrounded by scars up to 4.5–5.5 μm wide. *Conidia* mostly fusiform, rarely clavate, with an obtuse apex and a truncate obconic base, straight to slightly curved, pale to mid olivaceous brown, smooth, asperulate at the base, (5–)6(–7)-distoseptate, (53–)112.5–148 \times 16–23 μm , with a protruding hilum 2.5–3.5 μm wide. Germination uni- or bi-polar.

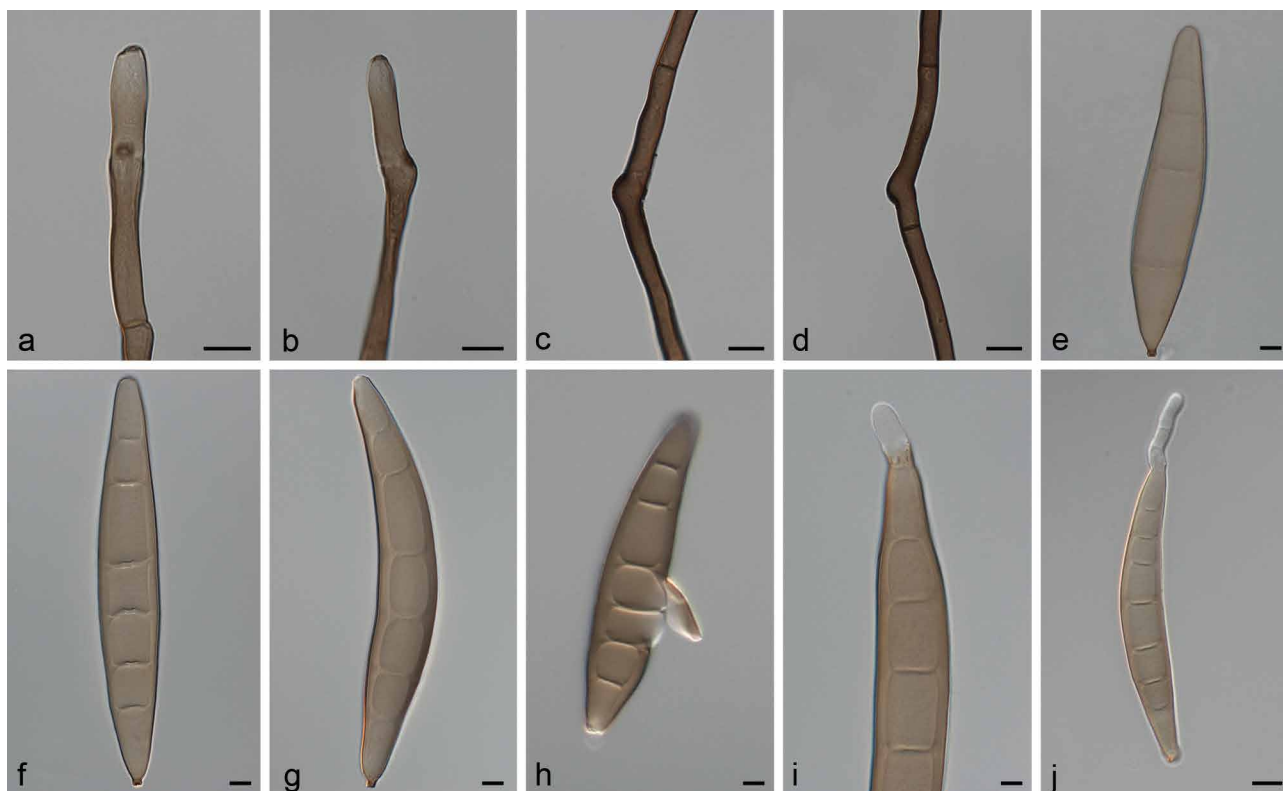


Fig. 24 *Exserohilum psidii* (IMI 299549 holotype). a–d. Conidiogenous cells; e–j. conidia. — Scale bars: a–i = 10 μm ; j = 20 μm .

Notes — The protologue describes narrower conidiophores (up to 6 μm wide) and conidia much longer and wider 150–175 (–190) \times 27–30 (–35) μm (Sivanesan 1992) than those observed here (53–148 \times 16–23 μm). The morphology of this species resembles *E. monoceras* and *E. turcicum*. Nevertheless, the high morphological variation in species of *Exserohilum* and the lack of molecular data in this species, make the correct placement of *E. psidii* difficult.

Exserohilum sodomii Guiraud et al., Antonie van Leeuwenhoek 72: 318. 1997

Type material. ISRAEL, Neguev desert, Dead Sea (road of Sodom), from soil, Aug. 1994, unknown collector (CMPG1340 holotype, not seen).

Notes — *Exserohilum sodomii* was described from soil in Israel, as well as *E. israeli* by the same authors (Guiraud et al. 1997, Steiman et al. 2000). According to the protologue, this fungus is morphological compatible with *E. rostratum*. No living culture of *E. sodomii* is available for study.

Curvularia micropus (Drechsler) Hern.-Restr., Y.P. Tan & Crous, *comb. nov.* — MycoBank MB822994; Fig. 25

Basionym. *Helminthosporium micropus* Drechsler, J. Agric. Res. 24: 722. 1923.

Synonyms. *Bipolaris micropus* (Drechsler) Shoemaker, Canad. J. Bot. 37: 884. 1959.

Drechslera micropus (Drechsler) Subram. & B.L. Jain, as '*micropa*', Curr. Sci. 35: 354. 1966.

Exserohilum paspali J.J. Muchovej & Nesio, Trans. Brit. Mycol. Soc. 89: 126. 1987.

Type material. USA, Florida, Wauchula, on *Paspalum boscianum* (?), 2 May 1921, C. Drechsler (IMI 296605, not seen (holotype of *Helminthosporium micropus*); BPI 429621, syntype (of *Helminthosporium micropus*)); Georgia, Tifton, on *Paspalum notatum*, 17 July 1970, E.S. Luttrell No. Lutt. 8530 (BRIP 6520 epitype designated here (MBT378847); CBS 127235 = BRIP 6520 culture ex-epitype.

On SNA + banana leaf. *Vegetative hyphae* pale brown, septate. *Conidiophores* macronematous, single or in small groups, erect, septate, unbranched, cylindrical, brown, smooth, 80–335 \times 4–8 μm . *Conidiogenous cells* terminal and intercalary, geniculate, mono- and polytretic, 8–37.5 \times 3.5–6.5 μm . *Conidia* cylindrical (longer ones) to ellipsoid (shorter ones) or sigmoid, straight or slightly curved, subhyaline to pale brown, verruculose, 3–9-distoseptate, 30–70 \times 10–18.5 μm , protruding hilum 1–3.5 μm long, 1.5–3 μm wide. *Sexual morph* not observed.

Culture characteristics — On SNA + sterilized maize leaf after 7 d at 24 $^{\circ}\text{C}$ in the dark, hairy to floccose, olivaceous grey to olivaceous black, cottony on maize leaves, with a fimbriate margin; reverse concolorous with obverse.

Additional materials examined. BRAZIL, Minas Gerais, Viçosa, on *Paspalum conjugatum*, 10 May 1986, J.J. Muchovej (authentic culture of *E. paspali* BRIP 16070 = CBS 128057). — USA, Florida, Lakeland, on *Paspalum notatum*, 3 Apr. 1970, E.S. Luttrell, Lutt. 8452 (BRIP 6516 = CBS 127234); Georgia, Tifton, on *Paspalum notatum*, 3 Apr. 1987, A.Y. Rossman (BRIP 15689a = CBS 127236).

Notes — *Curvularia micropus* attacks leaf blades of young plants of *Paspalum*, killing the foliar tissues (Drechsler 1923, Muchovej & Ribeiro Nesio 1987, Sivanesan 1987). *Curvularia micropus*, originally described as *Helminthosporium* (Drechsler 1923), was transferred to *Bipolaris* (Shoemaker 1959) and later to *Drechslera* (Subramanian & Jain 1966). Other species listed as synonyms of *B. micropus* are *Helminthosporium leptochloae* (Sivanesan 1987) and *E. paspali* (Alcorn 1991). However, molecular data generated in this study revealed that *H. leptochloae* is conspecific with *E. rostratum* (Fig. 2), whereas *E. paspali* and *B. micropus* are conspecific (Fig. 1). Nevertheless, this species is better placed in *Curvularia*. In the multi-gene tree, three strains isolated from *Paspalum* in the USA and one from Brazil, are placed in a basal clade of *Curvularia* (Fig. 1). Type material of *H. micropus* is preserved at the IMI (holotype IMI 296605) and at the US National Fungal Collection (BPI 429620, BPI 429621, BPI 429615, as syntype), unfortunately there is no culture available. The strain CBS 127234 was collected from

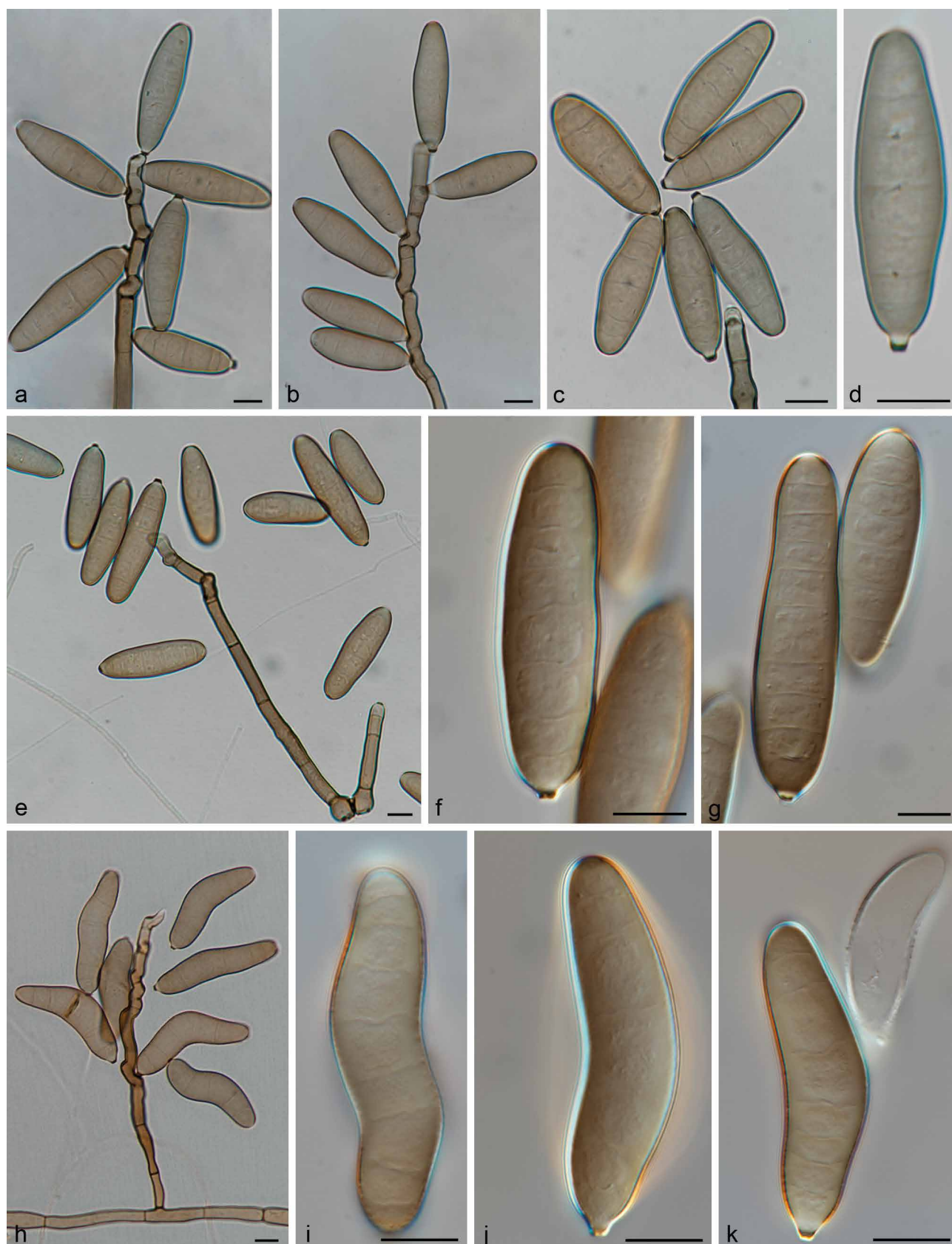


Fig. 25 *Curvularia micropus* (CBS 127235 ex-epitype (a–d), CBS 127236 (e–g), CBS 128057 (h–k)). a–c, e, h. Conidiophores and conidia; d, f–g, i–k. conidia. — Scale bars: 10 μ m.

the same state as the type material (Florida) but this isolate was sterile under the culture conditions tested. It is, however, genetically identical to the strain CBS 127235. In order to stabilize the use of the name, we propose CBS 127235 as the ex-epitype strain of *C. micropus*, since it fits well with the description given in the protologue and it was collected in a neighbouring state.

Curvularia sorghicola (Sivan.) Madrid & Crous, *comb. nov.* — MycoBank MB822997; Fig. 26

Basionym. *Exserohilum sorghicola* Sivan., *Mycol. Pap.* 158: 237. 1987.

Type material. ETHIOPIA, on leaves of *Sorghum* sp., 15 Sept. 1976, unknown collector (IMI 225559 holotype).

Adapted from Sivanesan (1987). *Leaf spots* irregularly elongate, running parallel to the midrib, surrounded by a thick dark purple border. *Vegetative hyphae* mostly immersed, septate, branched, pale olivaceous to pale olivaceous brown, sometimes with purplish tinges, smooth, 2.5–7.5 µm wide, giving rise to chains and clumps of swollen subcylindrical, globose to irregularly shaped cells up to 24 µm wide. *Conidiophores* macronematous, single to fasciculate, straight to flexuous, often geniculate above, septate, mostly unbranched, subcylindrical, olivaceous brown, becoming paler towards the apex and sometimes also toward the base, smooth to asperulate, with cell walls thicker than those of the vegetative hyphae, 28.5–112 × 3–7.5 µm, often with a bulbous base up to 14 µm wide. *Conidiogenous cells* integrated, intercalary and terminal, mostly subcylindrical, mono- and polytretic, proliferating sympodially, 7–46 × 3–7.5 µm, with pores up to 1 µm wide, surrounded by scars 3–4.5 µm wide. *Conidia* mostly clavate, straight to curved, pale olivaceous brown, often paler towards both ends, smooth to asperulate, 3(–5)-distoseptate, often constricted at the septa, 30–57 × 11–19 µm, with a protruding hilum, 1.5–3 µm wide.

Notes — This fungus was originally described as an atypical species of *Exserohilum* (Sivanesan 1987), and examination of the holotype revealed that its conidia produce hila which are delimited from the basal cell by a septum, different from other *Exserohilum* species. This kind of hilum is produced by many *Curvularia* species (Alcorn 1991, Zhang et al. 2004, Madrid et al.

2014), and therefore this is the correct genus for *E. sorghicola*. Morphologically, this fungus resembles members of the trifolii-clade of *Curvularia* in producing predominantly 4-celled conidia with a strongly protruding hilum (Madrid et al. 2014). However, there is no culture available for DNA sequence analyses, and its exact phylogenetic placement in *Curvularia* still has to be assessed.

Sporidesmiella novae-zelandiae (S. Hughes) Madrid, Hern.-Restr. & Crous, *comb. nov.* — MycoBank MB822998; Fig. 27

Basionym. *Sporidesmium hyalospermum* var. *novae-zelandiae* S. Hughes, *New Zealand J. Bot.* 16: 349. 1978.

Synonym. *Sporidesmiella hyalosperma* var. *novae-zelandiae* (S. Hughes) P.M. Kirk, *Trans. Brit. Mycol. Soc.* 79: 479. 1982.

Exserohilum novae-zelandiae (S. Hughes) H.P. Upadhyay & Mankau, *Mycologia* 83: 373. 1991.

Type material. NEW ZEALAND, Canterbury Province, Okuti Valley, near Little River, on rotten wood, 17 May 1963, S.J. Hughes (PDD 30420 holotype (of *Sporidesmium hyalospermum* var. *novae-zealandiae*), not seen; DAOM 159962 isotype).

Vegetative hyphae septate, branched, subhyaline to pale brown, smooth and thin-walled, 1–2.5 µm wide. *Conidiophores* macronematous, mononematous, septate, unbranched, straight or flexuous, showing either percurrent or sympodial proliferations and sometimes both, dark brown, becoming paler towards the apex, smooth to asperulate, thick-walled, length undetermined, 4.5–9 µm wide, often with a bulbous base up to 13 µm wide. *Conidiogenous cells* integrated, terminal, mostly subcylindrical, often flexuous, holoblastic, mono- and polyblastic, 7.5–38 µm long, with flat or slightly convex, non-darkened scars 3.5–5 µm wide. *Conidia* solitary, mostly clavate with an obconically truncate base, pale olivaceous to pale golden brown, smooth, 3–4-distoseptate, 20.5–28 × 11.5–15 µm, 3–5.5 µm wide at the base, basal cell cut-off by a dark-brown septum.

Additional material examined. MEXICO, Laguna de Zempoala, Morelos, plant debris (of grass), 22 Feb. 1989, R. Mankau (CBS 135842).

Notes — This species was originally described as *Sporidesmium hyalospermum* var. *novae-zelandiae* by Hughes (1978).



Fig. 26 *Curvularia sorghicola* (IMI 225559 holotype). a–f. Conidiophores; g–i. conidia. — Scale bars: 10 µm.

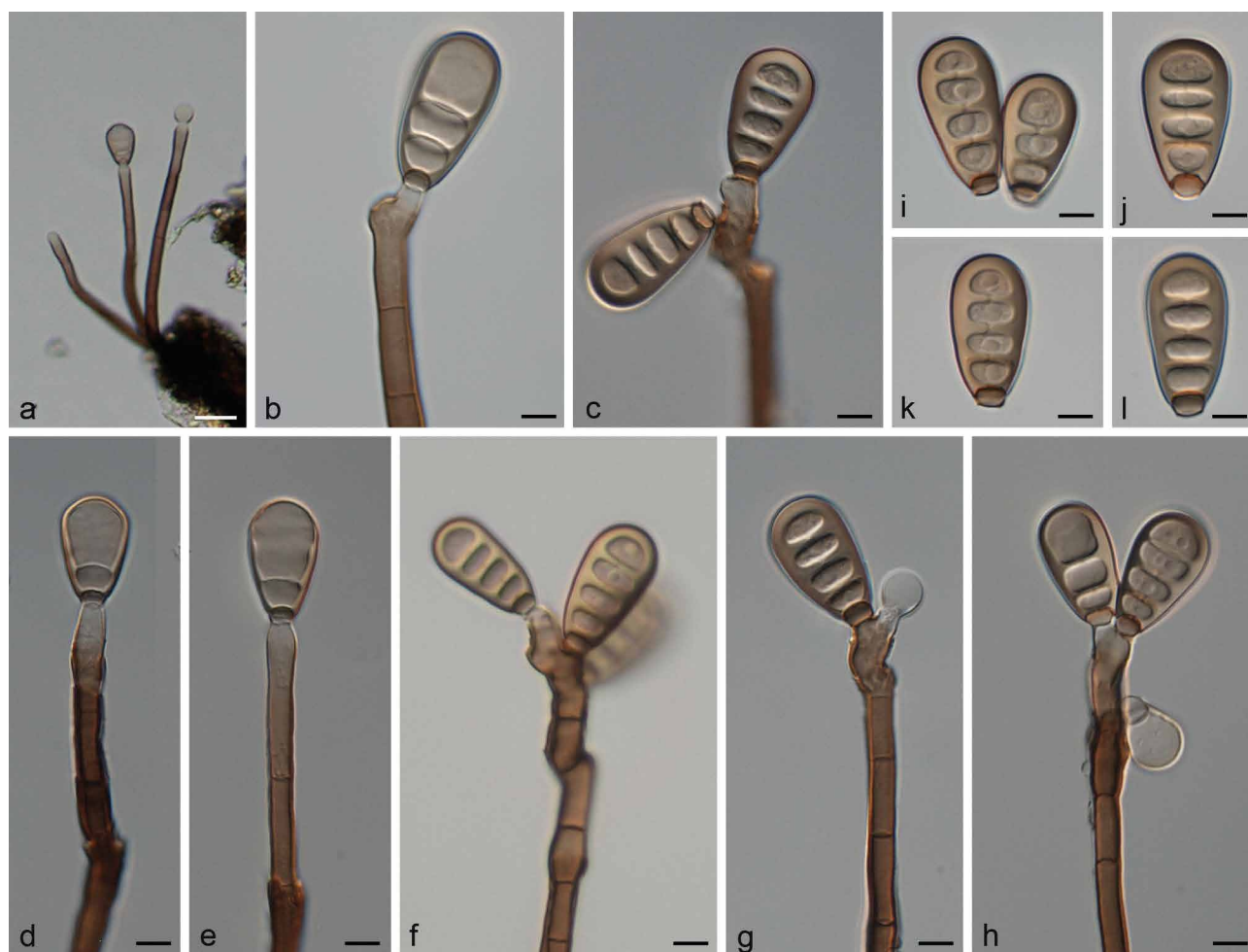


Fig. 27 *Sporidesmiella novae-zelandiae* (DAOM 159962 isotype). a–h. Conidiophores and conidia; i–l. conidia. — Scale bars: a = 20 μm ; b–h = 10 μm .

This and the type variety were reallocated to *Sporidesmiella* by Kirk (1982) and var. *novae-zelandiae* was later transferred to *Exserohilum* by Upadhyay & Mankau (1991) as *E. novae-zelandiae*. The combination proposed by the latter authors is not appropriate since the conidiogenous cells in the holotype lack the darkened scars and conspicuous pores typical of *Exserohilum* spp. and produce conidia with an obconically truncate base, not with a truly protruding hilum. Although DNA sequence data are lacking for the type specimens of the varieties of *S. hyalosperma*, morphological differences indicate that *S. hyalosperma* var. *novae-zelandiae* and *S. hyalosperma* var. *hyalosperma* are different fungi. The latter differs from the variety *novae-zelandiae* in having conidiophores that proliferate almost always percurrently, with numerous conspicuous annellations and narrower (9–12 μm wide) conidia (Morgan-Jones & Cole 1964, Kirk 1982, Wu & Zhuang 2005). Furthermore, the isolate CBS 135842, identified as *Exserohilum novae-zelandiae* by Upadhyay & Mankau (1991), proved to be related to *Annulatascaceae*, *Sordariomycetes* (unpubl. data), revealing that the fungus is phylogenetically distant from *Exserohilum* (*Pleosporaceae*, *Dothideomycetes*). Based on morphological and molecular evidence we consider that ‘*Exserohilum*’ *novae-zelandiae* should be, at least provisionally, retained in *Sporidesmiella*. Currently, *Sporidesmiella* comprises 24 species (Seifert et al. 2011). However, *Sporidesmiella fusiformis* is the only species with molecular data available in this genus, and it belongs to *Didymosphaeriaceae* (*Dothideomycetes*) (Shenoy et al. 2006) rather than *Annulatascaceae*, like *S. novae-zelandiae*. Further studies are needed in order to establish generic boundaries in *Sporidesmiella*.

DISCUSSION

In this study, we have reviewed the taxonomic circumscription of *Exserohilum* (= *Setosphaeria*) using molecular and morphological data. This is the first study that presents a robust phylogeny using a broad distribution of *Exserohilum* isolates from different hosts and geographic origins. Furthermore, we also studied the holotype material of several species and prototypes of species listed in the genus to provide a statement of their placement in the genus. The phylogenetic analysis based on four genes *gapdh*, *rpb2*, LSU and ITS (Fig. 1), shows that the morphologically atypical species *E. paspali* is conspecific with *B. micropus*, as previously noticed by Alcorn (1991), but belongs in *Curvularia* rather than in *Exserohilum* or *Bipolaris*. This phylogenetic analysis also confirms that *C. crassiseptum* and *C. heteropogonicola*, previously known as *Exserohilum* species, are correctly placed in *Curvularia* (Alcorn 1991, Zhang et al. 2004). Furthermore, excluding those species or others such as *E. novae-zelandiae*, *Exserohilum* is highly supported as a monophyletic clade, which is clearly different from other helminthosporoid genera such as *Bipolaris*, *Curvularia*, *Johnnalcornia*, *Porocercospora* and *Pyrenophora*.

Exserohilum species are defined as pathogenic fungi to humans and plants, mainly grasses, as well as, saprobic, endophytic and soil-borne fungi. Species of this genus are frequently found as asexual morphs in nature, although the sexual morph was often obtained by combining compatible strains, except for *E. minor* and *E. khartoumsensis* (Drechsler 1923, Luttrell 1963a, Nelson 1965, Alcorn 1978, 1986, El Shafie & Webster 1981). The setosphaeria-like sexual morph of different *Exserohilum*

species can be morphologically very similar and therefore morphology of the asexual morph is considered more reliable for identification purposes (Leonard 1976, Alcorn 1986, Sivanesan 1987). The traditional morphological attributes of conidia that have been used as taxonomical criteria at the generic rank for *Bipolaris*, *Curvularia*, *Exserohilum* and *Pyrenophora* are mainly the germination patterns of the conidia, septum ontogeny and hilum morphology (Leonard & Suggs 1974, Alcorn 1983, 1990, 1991, Sivanesan 1987). Among those features, the hilum morphology is the most valuable criteria to delineate *Exserohilum* species. The hilum is characterised by an enveloping structure around the hilar protrusion which is often thickened basally or laterally (Alcorn 1983). However, in some *Curvularia* species, a structure resembling that of the hilum in *Exserohilum* can be present, but in *Curvularia*, the hilum is separated from the conidial body by a septum.

By combining morphological data with multi-locus analysis from ITS, *act*, *gapdh*, *his*, *rpb2*, *tef1* and *tub2* sequences, we were able to delimit 11 species in *Exserohilum*, one of which is formally proposed as a new species, *E. corniculatum*, in addition to other previously described species, i.e., *E. holmii*, *E. khar-toumensis*, *E. minor*, *E. monoceras*, *E. neoregeliae*, *E. oryzicola*, *E. pedicellatum*, *E. protrudens*, *E. rostratum* and *E. turcicum*. The phylogenetic position of *E. monoceras* is still unresolved, since molecular data from type material was not available. The phylogenetic tree shows a clade of *E. turcicum*, closely related to strains identified as *E. monoceras*; however, more study is needed on members of these clades in order to resolve their relationship (Fig. 2). This study demonstrated that some species can be morphologically highly variable, but molecularly they are very closely related and they are treated here as synonyms, *E. curvatum* with *E. holmii* and *E. fusiforme* with *E. oryzicola*. *Exserohilum rostratum* was an exceptional case, where this species is shown as conspecific to *E. antillanum*, *E. gedarefense*, *E. longirostratum*, *E. macginnisii*, *E. prolatum* and *H. leptochloae*. Morphological variability in conidial shape, size and pigmentation of *E. rostratum* has been already noticed in natural substrate (Drechsler 1923), as well as in culture, which is influenced by external factors like carbon source, glucose concentration, type of culture media, light exposure and pH, among others (Mitra 1931, Kafi & Tarr 1966, Tarr & Kafi 1968, Leonard 1976, Anahosur & Sivanesan 1978, Honda & Aragaki 1978). Previously, Leonard & Suggs (1974) observed morphological similarities among *E. rostratum*, *H. leptochloae* and *E. longirostratum*. More recently, Da Cunha et al. (2012) demonstrated that *E. rostratum*, *E. longirostratum* and *E. macginnisii* are very closely related based on multigene sequence analysis of clinical isolates, but did not propose any synonymy. Here we propose them as synonyms of *E. rostratum*.

For an accurate species identification of *Exserohilum* species, a molecular analysis is required. Among the nine loci used in this study, ITS, *act* and *rpb2* were able to resolve 11, 13 and 12 OTUs, respectively, with varying statistical support. Although each of these loci proved to be suitable barcoding markers for species identification, a combined analysis is highly recommended. The *gapdh* gene is recommended for species resolution in *Bipolaris* and *Curvularia* (Da Cunha et al. 2012, Manamgoda et al. 2012,) but in *Exserohilum* this region showed *E. rostratum* (including *E. corniculatum*) as a polyphyletic group. However, the other nine species were well-supported.

Besides the 11 phylogenetic species recognised here, the taxonomic placement at species and generic level of other 15 species listed as 'doubtful' (i.e., *E. curvisporum*, *E. echinochloae*, *E. elongatum*, *E. frumentacei*, *E. glycinea*, *E. heteromorphum*, *E. israeli*, *E. lagenarioides*, *E. longisporum*, *E. oryzae*, *E. oryzinum*, *E. parlierense*, *E. phragmitis*, *E. psidii* and

E. sodomii) have to be confirmed as members of *Exserohilum* by molecular data.

The present investigation significantly extends the knowledge of the taxonomy of *Exserohilum*. Nevertheless, extensive sampling of uncommon species and inclusion of additional data like chemical compounds (i.e., secondary metabolites), ecology and host range for species are needed in order to resolve some taxonomic and phylogenetic aspects.

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REFERENCES

- Adler A, Yaniv I, Samra Z, et al. 2006. *Exserohilum*: an emerging human pathogen. *European Journal of Clinical Microbiology and Infectious Diseases* 25: 247–253.
- Al-Attar A, Williams CG, Redett RJ. 2006. Rare lower extremity invasive fungal infection in an immunosuppressed patient: *Exserohilum longirostratum*. *Plastic and Reconstructive Surgery* 117: 44e–47e.
- Alcorn JL. 1978. *Setosphaeria monoceras* sp. nov., ascigerous state of *Exserohilum monoceras*. *Mycotaxon* 7: 411–414.
- Alcorn JL. 1983. *Cochliobolus ellisii* sp. nov. *Transactions of the British Mycological Society* 81: 172–174.
- Alcorn JL. 1986. A new homothallic *Setosphaeria* species and its *Exserohilum* anamorph. *Transactions of the British Mycological Society* 86: 313–317.
- Alcorn JL. 1988a. The taxonomy of *Helminthosporium* species. *Annual Review of Phytopathology* 26: 37–56.
- Alcorn JL. 1988b. A new species of *Exserohilum*. *Transactions of the British Mycological Society* 90: 146–148.
- Alcorn JL. 1990. Additions to *Bipolaris*, *Cochliobolus* and *Curvularia*. *Mycotaxon* 39: 361–392.
- Alcorn JL. 1991. New combinations and synonymy in *Bipolaris* and *Curvularia*, and a new species of *Exserohilum*. *Mycotaxon* 41: 329–343.
- Alcorn JL. 1996. *Cochliobolus heliconiae* sp. nov. *Australian Systematic Botany* 9: 813–817.
- Alloub H, Juraimi AS, Kadir J, et al. 2009. Field efficacy of *Exserohilum prolatum*-A potential mycoherbicide for biological control of itchgrass (*Rottboelia cochinchinensis*). *Journal of Biological Sciences* 9: 119–127.
- Altschul SF, Gish W, Miller W, et al. 1990. Basic local alignment search tool. *Journal of Molecular Biology* 215: 403–410.
- Amaradasa BS, Madrid H, Groenewald JZ, et al. 2014. *Porocercospora seminalis* gen. et comb. nov. the causal organism of buffalograss false smut. *Mycologia* 106: 77–85.
- Anahosur KH, Sivanesan A. 1978. *Setosphaeria rostrata*. *CMI Descriptions of Pathogenic Fungi and Bacteria* 587.
- Aquino VM, Norvell JM, Krisher K, et al. 1995. Fatal disseminated infection due to *Exserohilum rostratum* in a patient with aplastic anemia: case report and review. *Clinical Infectious Diseases* 20: 176–178.
- Berbee ML, Pirseyedi M, Hubbard S. 1999. *Cochliobolus* phylogenetics and the origin of known, highly virulent pathogens, inferred from ITS and glyceraldehyde-3-phosphate dehydrogenase gene sequences. *Mycologia* 91: 964–977.
- Bhigjee AI, Parmanand V, Hoosen AA, et al. 1993. Disseminated *Exserohilum* infection. *Journal of Infection* 26: 336–337.
- Bolle PC. 1924. Die durch Schwärzepilze (Phaeodictyae) erzeugten Pflanzenkrankheiten. *Mededelingen Phytopathologisch Laboratorium 'Willie Commelin Scholten'* 7: 1–77.
- Bouchon CL, Greer DL, Genre CF. 1994. Corneal ulcer due to *Exserohilum longirostratum*. *American Journal of Clinical Pathology* 101: 452–455.
- Bunker RN, Mathur K. 2006. Host range of leaf blight pathogen (*Exserohilum turcicum*) of Sorghum. *Indian Phytopathology* 59: 370–372.
- Carbone I, Kohn LM. 1999. A method for designing primer sets for speciation studies in filamentous ascomycetes. *Mycologia* 91: 553–556.
- Castañeda-Ruiz RF, Guarro J, Cano J. 1995. A new species of *Exserohilum* from Cuba. *Mycological Research* 99: 825–826.

- Chen W-Q, Ntahimpera N, Morgan DP, et al. 2002. Mycoflora of *Pistacia vera* in the Central Valley, California. *Mycotaxon* 83: 147–158.
- Crous PW, Groenewald JZ, Risede J-M, et al. 2004. *Calonectria* species and their *Cylindrocladium* anamorphs: species with sphaeropedunculate vesicles. *Studies in Mycology* 50: 415–429.
- Da Cunha KC, Sutton DA, Gené J, et al. 2012. Molecular identification and in vitro response to antifungal drugs of clinical isolates of *Exserohilum*. *Antimicrobial Agents and Chemotherapy* 56: 4951–4954.
- De Hoog GS, Gerrits van den Ende AHG. 1998. Molecular diagnostics of clinical strains of filamentous Basidiomycetes. *Mycoses* 41: 183–189.
- De Hoog GS, Guarro J, Gené J, et al. 2000. *Atlas of Clinical Fungi*. 2nd ed. Centraalbureau voor Schimmelcultures, Utrecht.
- Del Serrone P, Porta-Puglia A, Sivanesan A. 1991. A new species of *Exserohilum* on barnyardgrass. *Phytopathologia Mediterranea* 30: 151–154.
- Derber C, Elam K, Bearman G. 2010. Invasive sinonasal disease due to dematiaceous fungi in immunocompromised individuals: case report and review of the literature. *International Journal of Infectious Diseases* 14, supplement 3: e329–e332.
- Drechsler C. 1923. Some graminicolous species of *Helminthosporium*: I. *Journal of Agricultural Research* 24: 641–739.
- Drechsler C. 1934. Phytopathological and taxonomic aspects of *Ophiobolus*, *Pyrenophora* and *Helminthosporium* and a new genus, *Cochliobolus*. *Phytopathology* 24: 953–983.
- El Shafie AE. 1980. *Drechslera gedarefensis* sp. nov. from Sorghum grains. *Transactions of the British Mycological Society* 74: 437–438.
- El Shafie AE, Webster J. 1981. *Setosphaeria khartoumensis* sp. nov. and its *Exserohilum* conidial state. *Transactions of the British Mycological Society* 77: 442–446.
- Ellis MB. 1971. Dematiaceous Hyphomycetes. Commonwealth Mycological Institute, Kew.
- Ellis MB. 1976. More dematiaceous Hyphomycetes. Commonwealth Mycological Institute, Kew.
- Farr DF, Rossman AY. 2017. Fungal databases, U.S. National Fungus Collections, ARS, USDA. <https://nt.ars-grin.gov/fungaldatabases/>. Accessed October 2017.
- Friedman GC, Hartwick RW, Ro JY, et al. 1991. Allergic fungal sinusitis. Report of three cases associated with dematiaceous fungi. *American Journal of Clinical Pathology* 96: 368–372.
- Gilbert RL. 2002. First report of *Exserohilum pedicellatum* on *Zea mays* in Australia. *New Disease Reports* 6: 3.
- Glass NL, Donaldson GC. 1995. Development of primer sets designed for use with PCR to amplify conserved genes from filamentous ascomycetes. *Applied and Environmental Microbiology* 61: 1323–1330.
- Guiraud P, Steiman R, Seigle-Murandi F, et al. 1997. *Exserohilum sodomii*, a new species isolated from soil near the Dead Sea (Israel). *Antonie van Leeuwenhoek* 72: 317–325.
- Henry AW. 1924. Root-rots of wheat. University of Minnesota Agricultural Experiment Station Technical Bulletin 22: 1–71.
- Honda Y, Aragaki M. 1978. Photosporogenesis in *Exserohilum rostratum*. Temperature effects on sporulation and spore morphology. *Mycologia* 70: 343–354.
- Hsu ML, Lee JY. 1993. Cutaneous and subcutaneous phaeohyphomycosis caused by *Exserohilum rostratum*. *Journal of the American Academy of Dermatology* 28: 340–344.
- Hughes SJ. 1978. New Zealand fungi 25. Miscellaneous species. *New Zealand Journal of Botany* 16: 311–370.
- Ito S. 1930. On some ascigerous stages of the species of *Helminthosporium* parasitic on cereals. *Proceedings of the Imperial Academy of Tokyo* 6: 352–355.
- Joseph NM, Kumar MA, Stephen S, et al. 2012. Keratomycosis caused by *Exserohilum rostratum*. *Indian Journal of Pathology and Microbiology* 55: 248–249.
- Kafi A, Tarr SAJ. 1966. Growth, sporulation and conidial characteristics of five graminicolous species of *Helminthosporium*: I. Effect of nutrients. *Transactions British Mycological Society* 49: 327–337.
- Kainer MA, Reagan DR, Nguyen DB, et al. 2012. Fungal infections associated with contaminated methylprednisolone in Tennessee. *New England Journal of Medicine* 367: 2194–2203.
- Katoh K, Standley DM. 2013. MAFFT multiple sequence alignment software version 7: improvements in performance and usability. *Molecular Biology and Evolution* 30: 772–780.
- Kirk PM. 1982. New or interesting microfungi VI. *Sporidesmiella* gen. nov. (Hyphomycetes). *Transactions of the British Mycological Society* 79: 479–489.
- Kirk PM. 2015. Index Fungorum no. 269. www.indexfungorum.org.
- Kodsueb R, Dhanasekaran V, Aptroot A, et al. 2006. The family Pleosporaceae intergeneric relationships and phylogenetic perspectives based on analyses of partial 28S rDNA. *Mycologia* 98: 571–583.
- Lasala PR, Smith MB, McGinnis MR, et al. 2005. Invasive *Exserohilum* sinusitis in a patient with aplastic anemia. *The Pediatric Infectious Disease Journal* 24: 939–941.
- Leonard KJ. 1976. Synonymy of *Exserohilum halodes* with *E. rostratum*, and induction of the ascigerous state, *Setosphaeria rostrata*. *Mycologia* 68: 402–411.
- Leonard KJ, Suggs EG. 1974. *Setosphaeria prolata*, the ascigerous state of *Exserohilum prolatum*. *Mycologia* 66: 281–297.
- Levy I, Stein J, Ashkenazi S, et al. 2003. Ecthyma gangrenosum caused by disseminated *Exserohilum* in a child with leukemia: a case report and review of the literature. *Pediatric Dermatology* 20: 495–497.
- Lin SC, Sun PL, Ju YM, et al. 2009. Cutaneous phaeohyphomycosis caused by *Exserohilum rostratum* in a patient with cutaneous T-cell lymphoma. *International Journal of Dermatology* 48: 295–298.
- Lin S-H, Huang S-L, Li Q-Q, et al. 2011. Characterization of *Exserohilum rostratum*, a new causal agent of banana leaf spot disease in China. *Australasian Plant Pathology* 40: 246–259.
- Link HF. 1809. Observaciones en ordines plantarum naturales. *Dissertatio I. Magazin der Gesellschaft Naturforschenden Freunde Berlin* 3: 3–42.
- Liu F, Dian-Ming H, Cai L. 2012. *Conlarium duplumascospora* gen. et sp. nov. and *Jobellisia guangdongensis* sp. nov. from freshwater habitats in China. *Mycologia* 104: 1178–1186.
- Luttrell ES. 1958. The perfect stage of *Helminthosporium turcicum*. *Phytopathology* 48: 281–287.
- Luttrell ES. 1963a. A *Trichometasphaeria* perfect stage of a *Helminthosporium* causing leaf blight of *Dactyloctenium*. *Phytopathology* 53: 281–285.
- Luttrell ES. 1963b. Taxonomic criteria in *Helminthosporium*. *Mycologia* 55: 643–674.
- Madrid H, Da Cunha KC, Gené J, et al. 2014. Novel *Curvularia* species from clinical specimens. *Persoonia* 33: 48–60.
- Manamgoda DS, Cai L, Bahkali AH, et al. 2011. *Cochliobolus*: an overview and current status of species. *Fungal Diversity* 51: 3–42.
- Manamgoda DS, Cai L, McKenzie EHC, et al. 2012. A phylogenetic and taxonomic re-evaluation of the *Bipolaris-Cochliobolus-Curvularia* complex. *Fungal Diversity* 56: 131–144.
- Mathews MS, Maharajan SV. 1999. *Exserohilum rostratum* causing keratitis in India. *Medical Mycology* 37: 131–132.
- McGinnis MR, Rinaldi MG, Winn RE. 1986. Emerging agents of phaeohyphomycosis: pathogenic species of *Bipolaris* and *Exserohilum*. *Journal of Clinical Microbiology* 24: 250–259.
- McNeill J, Barrie FF, Buck WR, et al. 2012. International Code of Nomenclature for algae, fungi, and plants (Melbourne Code). Koeltz Scientific Books, Königstein (Regnum Vegetabile no. 154).
- Miller MA, Pfeiffer W, Schwartz T. 2010. Creating the CIPRES Science Gateway for inference of large phylogenetic trees. *Proceedings of the Gateway Computing Environments Workshop (GCE)*, November 14, 2010, New Orleans, Louisiana: 1–8.
- Mitra M. 1931. A comparative study of species and strains of *Helminthosporium* on certain Indian cultivated crops. *Transactions of the British Mycological Society* 15: 254–293.
- Morgan-Jones G, Cole ALJ. 1964. Concerning *Endophragmia hyalosperma* (Corda) comb. nov. *Transactions of the British Mycological Society* 47: 489–495.
- Muchovej JJ, Ribeiro Nesio ML. 1987. A new *Exserohilum* from Brazil. *Transactions of the British Mycological Society* 89: 126–128.
- Nelson RR. 1964. The perfect stage of *Helminthosporium cynodontis*. *Mycologia* 56: 64–69.
- Nelson RR. 1965. The perfect stage of *Helminthosporium pedicellatum*. *Mycologia* 57: 665–668.
- Nirenberg HI. 1976. Untersuchungen über die morphologische und biologische Differenzierung in der *Fusarium*-Sektion *Liseola*. *Mitteilungen aus der Biologischen Bundesanstalt für Land- und Forstwirtschaft Berlin-Dahlem* 169: 1–117.
- Nisikado Y. 1928. Studies on *Helminthosporium* diseases of Gramineae in Japan. *Special Report of the Ohara Institute for Agricultural Research* 4: 111–126.
- Nylander JAA. 2004. MrModeltest v. 2. Program distributed by the author. Evolutionary Biology Centre, Uppsala University.
- O'Donnell K, Cigelnik E. 1997. Two divergent intragenomic rDNA ITS2 types within a monophyletic lineage of the fungus *Fusarium* are non-orthologous. *Molecular Phylogenetics and Evolution* 7: 103–116.
- O'Donnell K, Sarver BAJ, Brandt M, et al. 2007. Phylogenetic diversity and microsphere array-based genotyping of human pathogenic fusaria including isolates from the 2005–06 multistate contact lens-associated U.S. keratitis outbreaks. *Journal of Clinical Microbiology* 45: 2235–2248.
- Olivier C, Berbee ML, Shoemaker RA, et al. 2000. Molecular phylogenetic support from ribosomal DNA sequences for origin of *Helminthosporium* from *Leptosphaeria*-like ancestors *Mycologia* 92: 736–746.

- Pachkhede AU. 1989. A new species of *Exserohilum* from India. *Geobios New Reports* 8: 64–65.
- Padhye AA, Ajello L, Wieden MA, et al. 1986. Phaeohyphomycosis of the nasal sinuses caused by a new species of *Exserohilum*. *Journal of Clinical Microbiology* 24: 245–249.
- Passerini G. 1876. La nebbia del grano turco. *Bolletino del Comizio Agrario Parmense* 10: 1–3.
- Paul AR. 1972. *Pyrenophora erythrospila* sp. nov., the perfect state of *Drechslera erythrospila*. *Transactions of the British Mycological Society* 59: 97–102.
- Paul AR, Parbery DG. 1968. *Pyrenophora dictyoides* sp. nov. the perfect state of *Helminthosporium dictyoides*. *Transactions of the British Mycological Society* 51: 707–710.
- Rehner SA, Buckley E. 2005. A *Beauveria* phylogeny inferred from nuclear ITS and EF-1 α sequences: evidence for cryptic diversification and links to *Cordyceps* teleomorphs. *Mycologia* 97: 84–98.
- Ronquist F, Teslenko M, Van der Mark P, et al. 2012. MrBayes 3.2: efficient Bayesian phylogenetic inference and model choice across a large model space. *Systematic Biology* 61: 539–542.
- Rossman AY, Crous PW, Hyde KD, et al. 2015. Recommended names for pleomorphic genera in Dothideomycetes. *IMA Fungus* 6: 507–523.
- Rossman AY, Farr DF, Castlebury LA, et al. 2002. *Setomelanomma holmii* (Pleosporales, Phaeosphaeriaceae) on living spruce twigs in Europe and North America. *Canadian Journal of Botany* 80: 1209–1215.
- Saccardo PA. 1886. *Sylogae Fungorum* IV: 420–421.
- Sakoda T, Tsukiboshi T. 2011. *Exserohilum neoregeliae* sp. nov., a new pathogen of *Neoregelia carolinae*. *Mycotaxon* 118: 213–218.
- Seifert K, Morgan-Jones G, Gams W, et al. 2011. The genera of hyphomycetes. CBS Biodiversity Series 9. CBS-KNAW Fungal Biodiversity Centre, Utrecht.
- Shenoy BD, Jeewon R, Wu WP, et al. 2006. Ribosomal and RPB2 DNA sequence analyses suggest that *Sporidesmium* and morphologically similar genera are polyphyletic. *Mycological Research* 110: 916–928.
- Shoemaker RA. 1959. Nomenclature of *Drechslera* and *Bipolaris*, grass parasites segregated from 'Helminthosporium'. *Canadian Journal of Botany* 37: 879–887.
- Shoemaker RA. 1961. *Pyrenophora phaeocomes* (Reb. ex Fr.) Fr. *Canadian Journal of Botany* 39: 901–908.
- Simmons EG. 1971. *Helminthosporium allii* as type of a new genus. *Mycologia* 63: 380–386.
- Simmons EG. 2007. *Alternaria*. An identification manual CBS Biodiversity Series 6. CBS Fungal Biodiversity Centre, Utrecht, The Netherlands.
- Sivanesan A. 1984. New species of *Exserohilum*. *Transactions of the British Mycological Society* 83: 319–329.
- Sivanesan A. 1987. Graminicolous species of *Bipolaris*, *Curvularia*, *Drechslera*, *Exserohilum* and their teleomorphs. *Mycological Papers* 158: 1–261.
- Sivanesan A. 1992. New *Bipolaris*, *Curvularia* and *Exserohilum* species. *Mycological Research* 96: 485–489.
- Sivanesan A, Abdullah SK, Abbas BA. 1993. *Exserohilum curvisporum* sp. nov., a new hyphomycete from Iraq. *Mycological Research* 97: 1486–1488.
- Smith IM, Dunez J, Lelliott RA, et al. 1988. *European Handbook of Plant Diseases*. Blackwell Scientific Publications, Oxford.
- Smith RM, Schaefer MK, Kainer MA, et al. 2013. Fungal infections associated with contaminated methylprednisolone injections. *New England Journal of Medicine* 369: 1598–1609.
- Srivastava LS, Dhar V, Shambi HS, et al. 1983. A new leaf spot disease of soybean in India. *Indian Journal of Mycology and Plant Pathology* 12: 240–242.
- Stamatakis A. 2014. RAxML version 8: a tool for phylogenetic analysis and post-analysis of large phylogenies. *Bioinformatics* doi: <https://doi.org/10.1093/bioinformatics/btu033>.
- Steiman R, Guiraud P, Seigle-Murandi F, et al. 2000. *Exserohilum israeli*, a new species isolated from soil near Timna Park (Israel), and its physiological properties. *Antonie van Leeuwenhoek* 78: 153–161.
- Subramanian CV. 1956. Hyphomycetes – II. *Journal of the Indian Botanical Society* 35: 446–494.
- Subramanian CV, Jain BL. 1966. A revision of some graminicolous Helminthosporia. *Current Science* 35: 352–355.
- Sun GY, Zhang R, Zhou W, et al. 2005. *Exserohilum heteromorphum* sp. nov., a new helminthosporioid fungus from *Echinochloa* in China. *Mycotaxon* 92: 173–176.
- Sun GY, Zhang R, Zhu MQ, et al. 1997. A new species of *Exserohilum* from China. *Mycological Research* 101: 776–779.
- Tamura K, Stecher G, Peterson D, et al. 2013. MEGA6: Molecular Evolutionary Genetics Analysis version 6.0. *Molecular Biology and Evolution* 30: 2725–2729.
- Tanaka K, Hirayama K, Yonezawa H, et al. 2015. Revision of the Massarineae (Pleosporales, Dothideomycetes). *Studies in Mycology* 82: 75–136.
- Tarr SAJ, Kafi A. 1968. Growth, sporulation and conidial characteristics of five graminicolous species of *Helminthosporium*. *Transactions of the British Mycological Society* 51: 771–777.
- Togitani K, Kobayashi M, Sakai M, et al. 2007. Ethmoidal sinusitis caused by *Exserohilum rostratum* in a patient with malignant lymphoma after non-myeloablative allogeneic peripheral blood stem cell transplantation. *Transplant Infectious Disease* 9: 137–141.
- Torres C, Ro JY, el-Naggar AK, et al. 1996. Allergic fungal sinusitis: a clinicopathologic study of 16 cases. *Human Pathology* 27: 793–799.
- Tosiah S, Kadir J, Sariah M, et al. 2011. Efficacy of *Exserohilum monoceras*, a potential fungus for biocontrol of *Echinochloa* species. *Journal of Tropical Agriculture and Food Science* 39: 117–124.
- Upadhyay HP, Mankau R. 1991. *Dactylaria nervicola* sp. nov. and *Exserohilum novae-zelandiae* comb. nov. from Mexico. *Mycologia* 83: 371–376.
- Vaidya G, Lohman DJ, Meier R. 2011. SequenceMatrix: concatenation software for the fast assembly of multi-gene datasets with character set and codon information. *Cladistics* 27: 171–180.
- Vilgaly R, Hester M. 1990. Rapid genetic identification and mapping of enzymatically amplified ribosomal DNA from several species of *Cryptococcus*. *Journal of Bacteriology* 172: 4238–4246.
- Voglmayr H, Jaklitsch WM. 2017. *Corynespora*, *Exserohilum* and *Helminthosporium* revisited – New species and generic reclassification. *Studies in Mycology* 87: 43–76.
- Voigt K, Wöstemeyer J. 2000. Reliable amplification of actin genes facilitates deep-level phylogeny. *Microbiological Research* 155: 179–195.
- Wei CT. 1950. Notes on *Corynespora*. *Mycological Papers* 34: 1–10.
- White TJ, Bruns TD, Lee S, et al. 1990. Amplification and direct sequencing of fungal ribosomal genes for phylogenetics. In: Gelfand M, Sninsky JI, White TJ (eds), *PCR protocols: a guide to methods and applications*: 315–322. New York, Academic Press.
- Whitford HW, Schwartz WL, Richards H. 1989. *Exserohilum* dermal granulomas in a bovine. *Journal of Veterinary Diagnostic Investigation* 1: 78–81.
- Wu W. 1990. Contribution to the knowledge of graminicolous 'Helminthosporium' species in Hebei Province (II). *Journal of the Hebei Academy of Sciences Selected Papers* 60: 49–64.
- Wu W, Zhuang W. 2005. *Sporidesmium*, *Endophragmiella* and related genera from China. Fungal Diversity Press, University of Hong Kong, Hong Kong.
- Zhang G, Berbee ML. 2001. *Pyrenophora* phylogenetics inferred from ITS and glyceraldehyde-3-phosphate dehydrogenase gene sequences. *Mycologia* 93: 1048–1063.
- Zhang M, Zhang TY, Wu YM. 2004. A new name and a new variety in *Curvularia*. *Mycosystema* 23: 177–178.
- Zhang W, Watson AK. 1997. Efficacy of *Exserohilum monoceras* for the control of *Echinochloa* species in rice (*Oryza sativa*). *Weed Science* 45: 144–150.
- Zhang Y, Crous PW, Schoch CL, et al. 2012. Pleosporales. *Fungal Diversity* 53: 1–221.
- Zhang Y, Schoch CL, Fournier J, et al. 2009. Multi-locus phylogeny of Pleosporales: a taxonomic, ecological and evolutionary re-evaluation. *Studies in Mycology* 64: 85–102.