



Re-evaluation of *Mycoleptodiscus* species and morphologically similar fungi

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Key words

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Muyocoprion
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Abstract *Mycoleptodiscus* includes plant pathogens, animal opportunists, saprobic and endophytic fungi. The present study presents the first molecular phylogeny and revision of the genus based on four loci, including ITS, LSU, *rpb2*, and *tef1*. An extensive collection of *Mycoleptodiscus* cultures, including ex-type strains from the CBS, IMI, MUCL, BRIP, clinical isolates from the USA, and fresh isolates from Brazil and Spain, was studied morphologically and phylogenetically to resolve their taxonomy. The study showed that *Mycoleptodiscus* sensu lato is polyphyletic. Phylogenetic analysis places *Mycoleptodiscus* in *Muyocoprionales* (*Dothideomycetes*), together with *Arxiella*, *Leptodiscella*, *Muyocoprion*, *Neocochlearomyces*, and *Paramycoleptodiscus*. *Mycoleptodiscus terrestris*, the type species, and *M. sphaericus* are reduced to synonyms, and one new species is introduced, *M. suttonii*. *Mycoleptodiscus atromaculans*, *M. coloratus*, *M. freycinetiae*, *M. geniculatus*, *M. indicus*, *M. lateralis* (including *M. unilateralis* and *M. variabilis* as its synonyms) and *M. taiwanensis* belong to *Muyocoprion* (*Muyocoprionales*, *Dothideomycetes*), and *M. affinis*, and *M. lunatus* to *Omnidemptus* (*Magnaporthales*, *Sordariomycetes*). Based on phylogenetic analyses we propose *Muyocoprion alcornii* sp. nov., a fungus associated with leaf spots on *Epidendrum* sp. (*Orchidaceae*) in Australia, *Muyocoprion zamiae* sp. nov. associated with leaf spots on *Zamia* (*Zamiaceae*) in the USA, and *Omnidemptus graminis* sp. nov. isolated from a grass (*Poaceae*) in Spain. Furthermore, *Neomycoleptodiscus venezuelense* gen. & sp. nov. is introduced for a genus similar to *Mycoleptodiscus* in *Muyocoprionaceae*.

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INTRODUCTION

Mycoleptodiscus was proposed to accommodate *M. terrestris*, a species previously included in the invalid genus *Leptodiscus* (Gerdemann 1953), and *M. sphaericus* (Ostazeski 1967). Species of *Leptodiscus* were originally characterised by sporodochial conidiomata, thick-walled holoblastic conidiogenous cells that produce hyaline, 1-septate conidia with appendages at each end. Subsequently, Sutton & Alcorn (1990) emended the generic concept to include species with 0–2-septate conidia with polar and lateral appendages or lacking appendages, and frequently producing appressoria (Sutton & Hodges 1976, Sutton & Alcorn 1990, Alcorn 1994, Whitton et al. 2012). Currently, *Mycoleptodiscus* comprises 18 species (Ostazeski 1967, Sutton & Hodges 1976, Sutton & Alcorn 1985, 1990, Matsushima 1987, 1993, Bills & Polishook 1992a, Alcorn 1994, Ando 1996,

Whitton et al. 2012, Tibpromma et al. 2018). The sexual morph has not been described for any species of the genus, except for *M. affinis*, which was introduced as *Omnidemptus affinis* by Cannon & Alcorn (1994). *Omnidemptus* is a monotypic genus characterised by having superficial, perithecial ascomata, cylindrical-clavate asci, with an apical pore, and a small ring which stains dark blue with Melzer's reagent and ascospores that are fusiform, 1–3-septate and hyaline (Cannon & Alcorn 1994).

The first phylogenetic approach of a *Mycoleptodiscus* species was based on LSU rDNA sequences from *M. coloratus* (Thongkantha et al. 2009), retaining this genus in *Magnaporthales* (*Sordariomycetes*). Later, Luo & Zhang (2013) established that *M. affinis* (= *O. affinis*) was also related to *Magnaporthaceae*. However, Klaubauf et al. (2014) demonstrated that *M. coloratus* and *M. affinis* were unrelated, the former affine to *Ophiocercaceae* and the latter affine to *Magnaporthaceae*.

Recently, Crous et al. (2018) showed that *Mycoleptodiscus*, based on *M. terrestris*, the type species, was a member of *Muyocoprionales*, a newly proposed order in *Dothideomycetes* (Mapook et al. 2016a). Furthermore, analyses of sequences deposited in the GenBank database as *M. indicus* or *Mycoleptodiscus* sp. (Dewar & Sigler 2010, Metry et al. 2010, Koo et al. 2012) showed that they are related to *Muyocoprion* (*Muyocoprionales*). *Muyocoprion* was proposed by Spegazzini (1881), re-described by Saccardo (1883), and its taxonomical placement treated initially in *Microthyriaceae* (Von Arx & Müller 1975, Lumbsch & Huhndorf 2007) and later in *Muyocoprionaceae* (Hyde et al. 2013, Pang et al. 2013, Mapook et al. 2016a). *Muyocoprion* is characterised by pseudo-thyriothelial, superficial, flattened, carbonaceous, brittle ascomata, with pseudoparaphyses that are longer than the asci and ellipsoidal to ovate, unicellular ascospores (Hyde et al. 2013, Mapook et al.

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Table 1 GenBank accession numbers included in the alignments of Dothideomycetes and Sordariomycetes.

Species ¹	Old names	Strains ²	Other collections	GenBank accession numbers ³				References
				ITS	LSU	<i>rpb1</i>	<i>rpb2</i>	
Dothideomycetes								
<i>AcrospERMum compressum</i>		M151†		EU940161	EU940084	–	–	Sternoos et al. (2010)
<i>A. gramineum</i>		M152†		EU940162	EU940085	–	–	Sternoos et al. (2010)
<i>Arxiella dolichandrae</i>		CBS 138853 ^T	CPC 22951	NR_137930	KP004477	–	MK492710	MK495954 Crous et al. (2014), this study
<i>A. terrestris</i>		CBS 268.65 ^T		MH858565	MH870201	–	–	Vu et al. (2019)
<i>Asterodiscus tamaricis</i>		CBS 136918	L113	KU234100	KU234100	–	KU234115	Voglmayr et al. (2016)
<i>Corynespora cassiicola</i>		CBS 100822		–	GU301808	–	GU371742	Schoch et al. (2009)
<i>Dothidea sambuci</i>		DAOM 231303	AFTOL-ID 274	NR_111220	AY544681	–	DQ522854	Schoch et al. (2014)
<i>Dyfolromyces tiomanensis</i>		NTOU 3636†		KC692156	KC692156	–	–	Pang et al. (2013)
<i>Jahnula aquatica</i>		R68_1†		JN942354	EF175655	–	–	Campbell et al. (2007)
<i>J. sangamonensis</i>		A402_1B†		JN942349	EF175661	–	–	Campbell et al. (2007)
<i>J. seychellensis</i>		SS2113†		–	EF175665	–	–	Campbell et al. (2007)
<i>J. siamensis</i>		SS81.02†		–	EF175666	–	–	Campbell et al. (2007)
<i>Leptodiscella africana</i>		CBS 400.65 ^T		NR_145359	MH870275	–	MK492711	MK495955 Madrid et al. (2012), Vu et al. (2019), this study
<i>L. rintellii</i>		CBS 144927 ^T		LR025180	LR025181	–	–	Crous et al. (2018)
<i>Muyocopropon alcornii</i>		BRIP 43897 ^T	CBS 141314	MK487735	MK487708	–	MK492712	MK495956 This study
<i>Mu. atromaculans</i>	<i>Mycoleptodiscus atromaculans</i>	MUCL 34983 ^T	BPI GB1369	MK487736	MK487709	–	MK492713	MK495957 This study
<i>Mu. castanopsis</i>		MFLUCC 14-1108 ^T		–	KUJ726965	–	KY225778	– Mapook et al. (2016a, b)
<i>Mu. coloratum</i>	<i>Mycoleptodiscus coloratus</i>	CBS 720.95 ^T		NR_160197	MK487710	–	MK492714	MK495958 This study
<i>Mu. dipterocarpi</i>		MFLUCC 14-1103 ^T		–	KUJ726966	–	KY225779	– Mapook et al. (2016a, b)
<i>Mu. garethjonesii</i>		MFLUCC 16-1370 ^T		–	KY070274	–	–	Tibpromma et al. (2016)
<i>Mu. geniculatum</i>	<i>Mycoleptodiscus geniculatus</i>	CBS 721.95 ^T		MK487737	MK487711	–	MK492715	MK495959 This study
<i>Mu. laterale</i>	<i>Mycoleptodiscus lateralis</i>	CBS 141029 ^T	BRIP 16247, ATCC 200213	MK487738	MK487712	–	MK492716	MK495960 This study
	<i>Mycoleptodiscus unilaterialis</i>	IMI 324533 ^T		MK487739	MK487713	–	MK492717	MK495961 This study
	<i>Mycoleptodiscus variabilis</i>	CBS 719.95 ^T	BRIP 16983, ATCC 96451	MK487740	MK487714	–	MK492718	MK495962 This study
	<i>Mycoleptodiscus</i> sp.	CBS 141033	BRIP 20066	MK487741	MK487715	–	MK492719	MK495963 This study
	<i>Mycoleptodiscus</i> sp.	URM 7802		MK487742	MK487716	–	MK492720	MK495964 This study
	<i>Mycoleptodiscus</i> sp.	URM 7801		MK487743	MK487717	–	MK492721	– This study
	<i>Mycoleptodiscus indicus</i>	CBS 127677	UAMH 10746	MK487744	MK487718	–	MK492722	MK495965 This study
	<i>Mycoleptodiscus</i> sp.	CBS 145310	UTHSC DI17-18	MK487745	MK487719	–	MK492723	MK495966 This study
	<i>Mycoleptodiscus</i> sp.	CBS 145315	UTHSC DI 17-23	MK487746	MK487720	–	MK492724	MK495967 This study
	<i>Mycoleptodiscus</i> sp.	CBS 145313	UTHSC DI 17-21	MK487747	MK487721	–	MK492725	MK495968 This study
	<i>Mycoleptodiscus</i> sp.	CBS 145309	UTHSC DI 17-17	MK487748	MK487722	–	MK492726	MK495969 This study
	<i>Mycoleptodiscus</i> sp.	CBS 145314	UTHSC DI 17-22	MK487749	MK487723	–	MK492727	MK495970 This study
	<i>Mycoleptodiscus</i> sp.	CBS 145311	UTHSC DI 17-19	MK487750	MK487724	–	MK492728	– This study
	<i>Mycoleptodiscus</i> sp.	CBS 145312	UTHSC DI 17-20	MK487751	MK487725	–	MK492729	MK495971 This study
	<i>Mycoleptodiscus</i> sp.	CBS 145316	UTHSC DI 17-24	MK487752	MK487726	–	MK492730	MK495972 This study
	<i>Mycoleptodiscus</i> sp.	FMR 13797		MK874615	MK874616	–	MK875802	MK875803 This study
<i>Mu. lithocarpi</i>		MFLUCC 10-0041		–	JQ036230	–	–	Wu et al. (2011)
		MFLUCC 14-1106 ^T		–	KUJ726967	–	KY225780	– Mapook et al. (2016a, b)
<i>Mu. zamiae</i>	<i>Mycoleptodiscus</i> sp.	CBS 203.71 ^T		–	MK487727	–	MK492731	MK495973 This study
'Mycoleptodiscus endophyticus'		MFLUCC 17-0545		NR_158860	MG646946	–	–	Tibpromma et al. (2018)
<i>Mycoleptodiscus terrestris</i>	<i>Mycoleptodiscus terrestris</i>	CBS 276.72 ^T		MK487753	MK487728	–	MK492732	MK495974 This study
<i>Mycoleptodiscus suttonii</i>	<i>Mycoleptodiscus terrestris</i>	CBS 141030	BRIP 16943, ATCC 200215	–	MK487729	–	MK492733	MK495975 This study

Table 1 (cont.)

Species ¹	Old names	Strains ²	Other collections	GenBank accession numbers ³				References
				ITS	LSU	rpb1	rpb2	
<i>M. terrestris</i>	<i>Leptodiscus terrestris</i>	CBS 231.53 ^T	ATCC 18104	MK487754	MK487730	–	MK492734	This study
	<i>Mycocleptodiscus sphaericus</i>	IMI 159038 ^T		MK487755	MK487731	–	MK492735	This study
<i>Neocamarosporium betae</i>		CBS 109410		KY940790	EU754178	–	GU371774	De Gruyter et al. (2009), Schoch et al. (2009), Woudenberg et al. (2017)
<i>Neomycocleptodiscus venezuelense</i>	<i>Mycocleptodiscus terrestris</i>	CBS 100519 ^T		MK487756	MK487732	–	MK492736	This study
	<i>Paramycocleptodiscus albizziae</i>	CBS 141320 ^T	CPC 27552	KX228279	KX228330	–	MK492737	Crous et al. (2016), this study
<i>Saccardoella rhizophorae</i>		JK 5456A		GU479799	GU479799	–	GU479860	Suetrong et al. (2009)
<i>Stemphylium botryosum</i>		CBS 714.68	AFTOL-ID 934	AF071345	DQ678049	–	DQ677943	Berbee et al. (1999), Schoch et al. (2006)
<i>Stigmatodiscus enigmaticus</i>		L82‡		KU234112	KU234112	–	KU234125	Voglmayr et al. (2016)
<i>Sydowia polyspora</i>		CBS 116.29	AFTOL-ID 1300	–	DQ678058	–	DQ677953	Schoch et al. (2006)
Sordariomycetes								
<i>Buergenerula spartinae</i>		ATCC 22848		JX134666	DQ341492	JX134720	–	Thongkantha et al. (2009), Luo & Zhang (2013)
<i>Bussabanomyces longisporus</i>		CBS 125232 ^T		KM009166	KM484951	KM485046	–	Klaubauf et al. (2014)
<i>Falciphothiella oryzae</i>		CBS 125863 ^T	R-5-6-1	FJ752606	KJ026705	KJ026706	–	Yuan et al. (2010), Su et al. (2013), Xu et al. (2015)
<i>F. solaniterrestris</i>		CBS 117.83 ^T		KM484842	KM484959	KM485058	–	Klaubauf et al. (2014)
<i>Gaeumannomyces graminis</i>		CBS 141385	CPC 26033	KX306501	KX306571	KX306636	–	Hernández-Restrepo et al. (2016a)
		CPC 26045		KX306505	KX306575	KX306640	–	Hernández-Restrepo et al. (2016a)
<i>Kohlmeyeriopsis medullaris</i>		CBS 117849 ^T	JK5528S	KM484852	KM484968	KM485068	–	Klaubauf et al. (2014)
<i>Magnaportheiopsis incrustans</i>		M35‡		JF414843	JF414892	JF710437	–	Zhang et al. (2011)
<i>Ma. poae</i>		M48‡		JF414837	–	JF710434	–	Zhang et al. (2011)
<i>Ma. rhizophila</i>		M23‡		JF414834	JF414846	JF710432	–	Zhang et al. (2011)
<i>Nakataea oryzae</i>		CBS 252.34		KM484862	KM484976	KM485078	–	Klaubauf et al. (2014)
<i>Neogaeumannomyces bambusicola</i>				KP744449	KP744492	–	–	Liu et al. (2015)
<i>Omnideniptus affinis</i>		MFLUCC 11 0390 ^T	ATCC 200212, IMI 353435, CBS 141031	JX134674	JX134686	JX134728	–	Luo & Zhang (2013)
		BRIP 17195a ^T						
		BRIP 17195b ^T	CBS 141032	MK487757	MK487733	–	–	This study
<i>O. graminis</i>		CBS 138107 ^T	FMR 12415	MK487758	MK487734	–	–	This study
<i>Pseudophialophora eragrostis</i>		CM12m9 ^T		KF689648	KF689638	KF689618	–	Luo et al. (2014)
<i>Pyricularia grisea</i>		BR0029‡		KM484880	KM484995	KM485100	–	Klaubauf et al. (2014)
		CR0024‡		KM484882	KM484997	KM485102	–	Klaubauf et al. (2014)
<i>Slopeiomyces cylindrosporus</i>		CBS 609.75 ^T		KM484944	KM485040	KM485158	–	Klaubauf et al. (2014)

¹ New species are in **bolditalic**.
² ATCC: American Type Culture Collection, Virginia, USA; BRIP: Queensland Plant Pathology Herbarium, Brisbane, Australia; CBS: Westerdijk Fungal Biodiversity Institute, Utrecht, The Netherlands; CPC: Culture collection of Pedro Crous, housed at Westerdijk Fungal Biodiversity Institute; DAOI: National Mycological Herbarium, Department of Agriculture, Ottawa, Ontario, Canada; IMI: International Mycological Institute, Kew, UK; MFLUCC: Mae Fah Luang University Culture Collection, Chiang Rai, Thailand; MUCL: Mycologue de l'Université catholique de Louvain, Louvain-la-Neuve, Belgium; URM: Culture collection Prof. Maria Auxiliadora Cavalcanti, Recife, Brazil; UTHSC: Fungus Testing Laboratory of the University of Texas Health Science Center at San Antonio, USA; ‡ for other codes (A, BR, CR, JK, L, M, NTOU, R, SS) see References. † indicate ex-type strains.
³ ITS: internal transcribed spacers and intervening 5.8S nrDNA; LSU: partial large subunit (28S) of the nrDNA gene operon; *rpb1* & *rpb2*: partial RNA polymerase II largest subunit gene; *tef1*: partial translation elongation factor 1-alpha gene. Newly generated sequences are in **bold**.

2016a). No asexual morph has ever been described for any *Muyocopron* species (Spegazzini 1881, Wu et al. 2011, Mapook et al. 2016a).

Gerdemann (1953), when introducing *Mycoleptodiscus* (as *Leptodiscus*), demonstrated *M. terrestris* to be a pathogen of herbaceous *Fabaceae* with economic interest, such as *Glycine*, *Lespedeza*, *Lotus*, *Medicago*, *Melilotus*, *Pisum*, and *Trifolium* in the USA. Other *Mycoleptodiscus* species have also been reported to cause diseases of economically important plants, such as *Alloteropsis*, *Carpobrotus*, *Cattleya*, *Dianella*, *Panicum*, and *Stypantra* in Australia (Sutton & Alcorn 1985, 1990, Alcorn 1994, Cannon & Alcorn 1994), *Eucalyptus*, *Garcinia*, and *Vanilla* in Brazil (Sutton & Hodges 1976, Bezerra & Ram 1986, Paim et al. 2012), *Piper* in the Dominican Republic (Watanabe et al. 1997), *Ficus* in Peru (Matsushima 1993), *Arecaceae* in Taiwan (Matsushima 1987), *Fabaceae* (including *Lotus*) and *Zamia* in the USA (Ostazeski 1967, Sutton 1973, Vanev 1983). They have also occurred on several plant species in Brunei, Cuba, India, New Zealand, and Nigeria (Sutton & Hodges 1976, Sutton & Alcorn 1990). *Mycoleptodiscus* species also recorded as putative pathogens of symptomatic tropical forest seedlings in Panama (Spear 2017), and reported on dead leaves of *Freyinetia* in Australia and the Philippines (Whitton et al. 2012).

Although *Mycoleptodiscus* species have been widely reported as plant pathogens, some have been isolated as endophytes from *Chamaecyparis thyoides* (Bills & Polishook 1992a, b), the aquatic *Myriophyllum spicatum* in the USA (Shearer 2001), *Desmotes incomparabilis* in Panama (Martínez-Luis et al. 2011, Ortega et al. 2013), *Acer truncatum* and *Cinnamomum camphora* in China (Sun et al. 2011, He et al. 2012), *Borreria verticillata* and *Opuntia ficus-indica* in Brazil (Andrioli et al. 2012, Bezerra et al. 2012), and *Freyinetia* sp. in Thailand (Tibpromma et al. 2018). *Mycoleptodiscus terrestris* has also been isolated as an endophyte from aquatic submersed macrophytes in New Zealand (Hofstra et al. 2009, 2012).

The clinical importance of *Mycoleptodiscus* was first associated with a subcutaneous infection (phaeohyphomycosis) in the knee of a male with Wegener's granulomatosis and immunodeficiency in South Carolina (USA) (Padhye et al. 1995) and in a liver transplant patient with human immunodeficiency virus and hepatitis C co-infection (Garrison et al. 2008). The infection caused by *Mycoleptodiscus* was also reported from a mycotic arthritis of the knee in a healthy Canadian male (Dewar & Sigler 2010). In New Zealand, Koo et al. (2012) reported an association with *Mycoleptodiscus* from progressive necrotizing fungal cellulitis and myositis in the leg of a patient with glioblastoma multiforme. Domesticated animals were also reported with infections associated with *Mycoleptodiscus* species, such as a subcutaneous infection in a cat in Australia (Hull et al. 1997), and in an immunosuppressed dog in the USA (Metry et al. 2010). The clinical importance of *Mycoleptodiscus* species, mainly *M. indicus*, was discussed by De Hoog et al. (2000).

As scientific research has focused on the discovery of novel microorganisms for biotechnology purposes, some studies have outlined the potential of *Mycoleptodiscus*. Martínez-Luis et al. (2011) demonstrated the anti-parasitic ability of a *Mycoleptodiscus* sp. isolated as an endophyte from the leaves of *D. incomparabilis*. Other studies have established the ability of *M. terrestris* as a biological control of aquatic plants (Verma & Charudattan 1993, Shearer & Jackson 2006, Nelson & Shearer 2008). Ortega et al. (2013) showed compounds produced by *Mycoleptodiscus* strains could inhibit the growth of cancer cells *in vitro*. Furthermore, interesting compounds were identified and isolated from *M. indicus*, namely eugenitin, four known polyketides, and three new azaphilones, named mycoleptones A–C (Andrioli et al. 2012, 2014). Grandi & Silva (2010) studied

the impact of *M. disciformis* in nutrient cycling in the leaf litter decomposition in Brazil.

The aim of the present study is to clarify the taxonomy and phylogeny of *Mycoleptodiscus* species within *Ascomycota*. For this purpose, we used a set of strains of *Mycoleptodiscus* species isolated from clinical and plant specimens, including the available ex-type strains, and performed the multi-locus analyses of ITS rDNA, LSU, *rpb1*, *rpb2* and *tef1* sequences.

MATERIALS AND METHODS

Strains and morphological analysis

A total of 30 strains were examined (Table 1). Specimens of *Mycoleptodiscus* species, including holotypes and ex-type strains, were obtained from the Westerdijk Fungal Biodiversity Institute (CBS, The Netherlands), the Fungus Testing Laboratory of the University of Texas Health Science Center at San Antonio (UTHSCSA, USA), the Queensland Plant Pathology Herbarium (BRIP, Australia), the Kew Royal Botanic Gardens (IMI, England), and the Mycothèque of the UCL (BCCM/MUCL, Belgium).

Fresh specimens were collected in Brazil and Spain. The Brazilian specimens were isolated as endophytes from *Opuntia ficus-indica* and *Poincianella pyramidalis* growing in a tropical dry forest. The Spanish specimen was collected in Navarra, Robledal de Orgi natural area, growing on a gramineous plant close to a stream. Pure cultures were obtained from the conidia of the fungi transferred onto water agar (WA; Difco agar 5 g, 1 L tap water, pH 6).

Strains were sub-cultured on malt extract agar (MEA; 40 g malt extract, 15 g agar, 1 L distilled water) and oatmeal agar (OA, filtered oat flakes, 20 g agar, 1 L distilled water), and incubated at 25 °C under daylight conditions for 1–3 wk; UV light conditions were used for some isolates to induce sporulation. After 1–2 wk of incubation, the colony diameters were measured and the colony morphologies described. Colony colours on the surface and reverse of inoculated media were assessed according to the colour charts of Rayner (1970). Micro-morphological descriptions and measurements of relevant features were carried out from fungal structures and herbarium specimens mounted in clear lactic acid 90 % v/v. Observations and photomicrographs were made with a Nikon SMZ1500 dissecting microscope and with a Nikon eclipse Ni compound microscope, using a DS-Ri2 digital camera (Nikon, Tokyo, Japan) and NIS-Elements imaging software v. 4.20. Strains and fungarium materials were deposited at the CBS, BRIP, or at the culture collection of Prof. Maria Auxiliadora Cavalcanti from the Federal University of Pernambuco (URM, Recife, Brazil). Taxonomic information and nomenclature for new species were deposited in MycoBank (www.Mycobank.org).

DNA isolation, amplification, sequence alignment and phylogenetic analysis

Genomic DNA was extracted from fungal colonies growing on MEA using the Wizard® Genomic DNA purification kit (Promega, Madison, USA), according to the manufacturer's protocols. Procedures for amplifying and sequencing the nuclear rDNA, ITS1-5.8S-ITS2 (ITS) and $\pm$ 900 bp of the large subunit (LSU), was performed as described in Hernández-Restrepo et al. (2016b). Part of the largest and second largest subunit of the RNA polymerase II gene (*rpb1* and *rpb2*) was amplified and sequenced as described in Hernández-Restrepo et al. (2016b) and Klaubauf et al. (2014), respectively. Translation elongation factor 1- α gene (*tef1*), corresponding to section 983–1567 bp, was amplified and sequenced as described in Rehner & Buckley (2005). Consensus sequences were assembled in SeqMan Pro

(DNASTAR, Madison, WI, USA). The dataset for each gene was aligned using MAFFT v. 7 (Kato & Standley 2013), using the defaults settings and adjusted by hand in MEGA v. 6.06 (Tamura et al. 2013).

BLASTn searches using ITS and LSU sequences were carried out and sequences of related species, belonging to *Dothideomycetes* and *Sordariomycetes*, were obtained from GenBank and listed in Table 1. Two multi-locus phylogenetic analyses were carried out. The first one for *Dothideomycetes* was based on a concatenated alignment of ITS, LSU, *rpb2*, and *tef1*. Another phylogenetic analysis for *Magnaporthales* (*Sordariomycetes*) was based on a concatenated alignment of ITS, LSU, *rpb1*, and *tef1*. Individual alignment of each locus and the concatenated

four-loci dataset were analysed by Maximum Likelihood (ML) using the RAXML HPC BlackBox v. 8.2.10 (Stamatakis 2014) online server of the Cipres Science gateway portal (Miller et al. 2012). The multi-locus datasets were combined using Sequence Matrix v. 1.8 (Vaidya et al. 2011). A Markov Chain Monte Carlo (MCMC) algorithm was used to generate phylogenetic trees with Bayesian probabilities from the concatenated four-locus dataset using MrBayes v. 3.2.6 (Ronquist et al. 2012). The best model of nucleotide substitution for each locus was determined using MrModeltest v. 2.3 (Nylander 2004). Confident branch support was defined as bootstrap values (BS) $\geq 70\%$ from a ML search with 1000 replicates and posterior probabilities (PP) ≥ 0.95 . The sequences generated during this study and the alignments

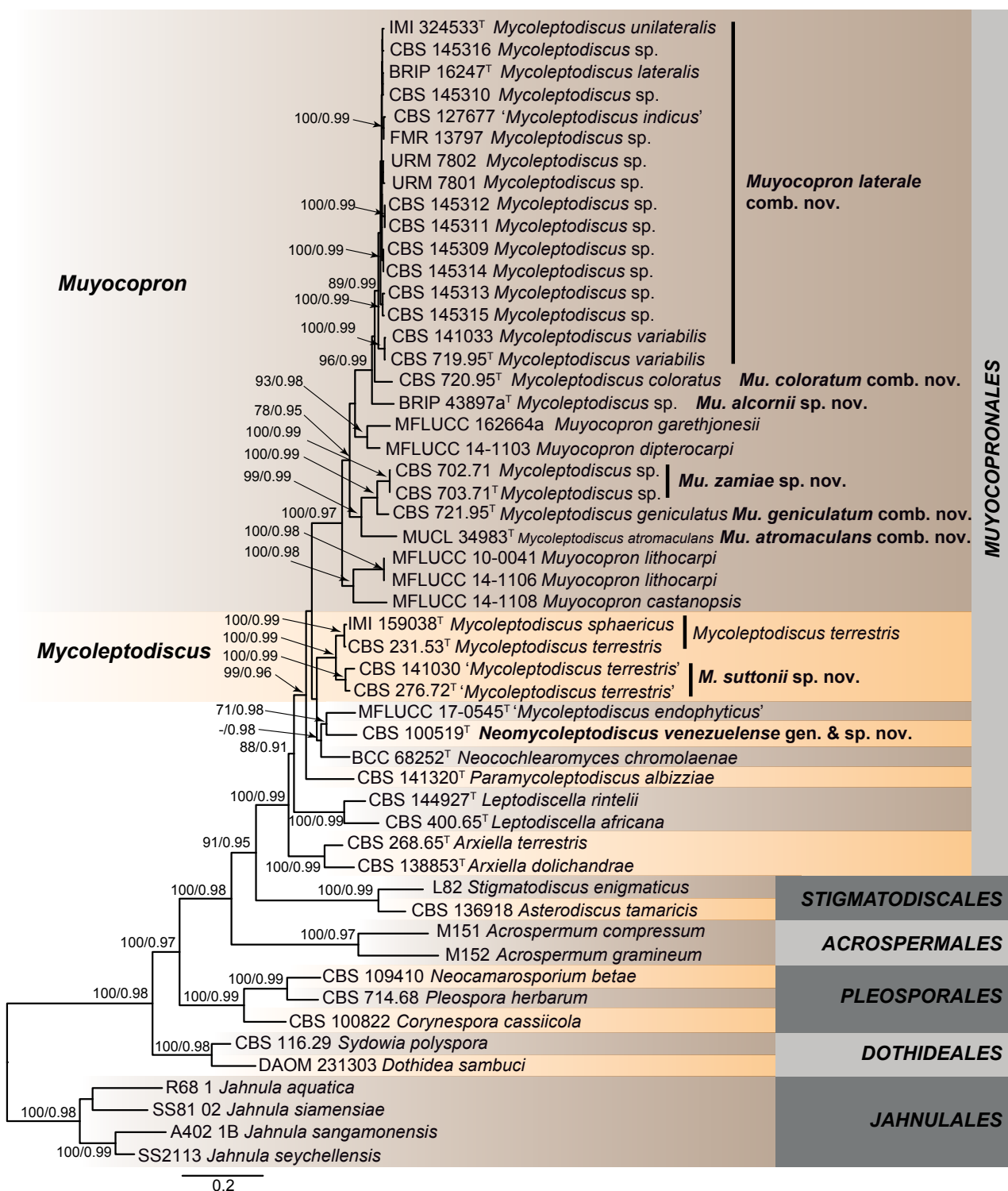


Fig. 1 RAxML phylogram obtained from the combined ITS, LSU, *rpb2*, and *tef1* sequences of *Dothideomycetes* members. The tree was rooted to *Jahnulales*. Taxonomic novelties described in this study are shown in **bold**. RAxML bootstrap support (BS) values $\geq 70\%$ and Bayesian posterior probability (PP) scores ≥ 0.95 are shown at the nodes. GenBank accession numbers are indicated in Table 1. [†] indicates ex-type.

used in the phylogenetic analyses were deposited in GenBank (Table 1) and TreeBASE (submission number 23523), respectively.

RESULTS

DNA phylogeny

BLASTn searches revealed that the ITS and LSU sequences of *M. atromaculans*, *M. coloratus*, *M. geniculatus*, '*M. indicus*', *M. lateralis*, *M. sphaericus*, *M. terrestris*, *M. unilateralis*, and *M. variabilis* were similar to sequences of members of *Muyocoprionales* (*Dothideomycetes*). While *M. affinis* and the strain CBS 138107, were similar to *Magnaporthales* (*Sordariomycetes*).

The first concatenated matrix contained a total of 3364 characters (761 for ITS, 846 for LSU, 819 for *rpb2*, and 938 for *tef1*). For Bayesian analysis, MrModel test proposed a GTR+I+G model for all the loci. The consensus tree obtained from the Bayesian analysis agreed with the topology of the best scoring ML tree (Fig. 1). In the phylogenetic tree, *Mycoleptodiscus* species were scattered into two well-supported clades in *Muyocoprionales*. The *Mycoleptodiscus* clade (100 ML BS/0.99 PP) includes the ex-type sequences of *M. sphaericus* and *M. terrestris*. The analysis also revealed the existence of a cryptic species in the current concept of *M. terrestris*, represented by two strains, CBS 276.72 and CBS 141030, and for which *M. suttonii* sp. nov. is proposed as a new species in the taxonomy section. The strain CBS 100519, formerly identified as

'*M. terrestris*', was phylogenetically distant and morphologically different from *M. terrestris* s.str. and formed a subclade with '*M. endophyticus*' (71/0.98) and *Neocochlearomyces chromolaenae* (56/0.98), and is therefore proposed here as *Neomycoleptodiscus venezuelense* gen. & sp. nov. A second clade (100/0.97), including *M. atromaculans*, *M. coloratus*, *M. geniculatus*, '*M. indicus*', *M. lateralis*, *M. unilateralis*, *M. variabilis*, and numerous unidentified *Mycoleptodiscus* strains, was placed in a monophyletic lineage together with species of *Muyocoprion*. Furthermore, it is of note that a strain of '*M. indicus*' CBS 127677 and the ex-type strains of *M. lateralis*, *M. unilateralis*, and *M. variabilis* were grouped in the same clade (89/0.99). Our analysis revealed two undescribed *Muyocoprion* species among the specimens studied, proposed here as *Mu. alcornii* sp. nov. (BRIP 43897) and *Mu. zamiae* sp. nov. (CBS 702.71, CBS 703.71).

The *Magnaporthales* concatenated matrix contained a total of 2882 characters (589 for ITS, 752 for LSU, 618 for *rpb1*, and 923 for *tef1*). For Bayesian analysis, the MrModel test proposed a GTR+I+G model for ITS and LSU and a GTR+G for *rpb1* and *tef1*. The consensus tree obtained from that analysis agreed with the topology of the best scoring ML tree (Fig. 2). In the phylogenetic tree, *M. affinis* CBS 141031, *O. affinis* ATCC 200212 and CBS 138107 formed an independent clade (100/1.0) in the *Magnaporthaceae*. *Omnidemptus* is circumscribed and *M. affinis* is formally synonymised under *O. affinis*, and the strain CBS 138107 is introduced as *Omnidemptus graminis* sp. nov. based on its phylogenetic and morphological differences.

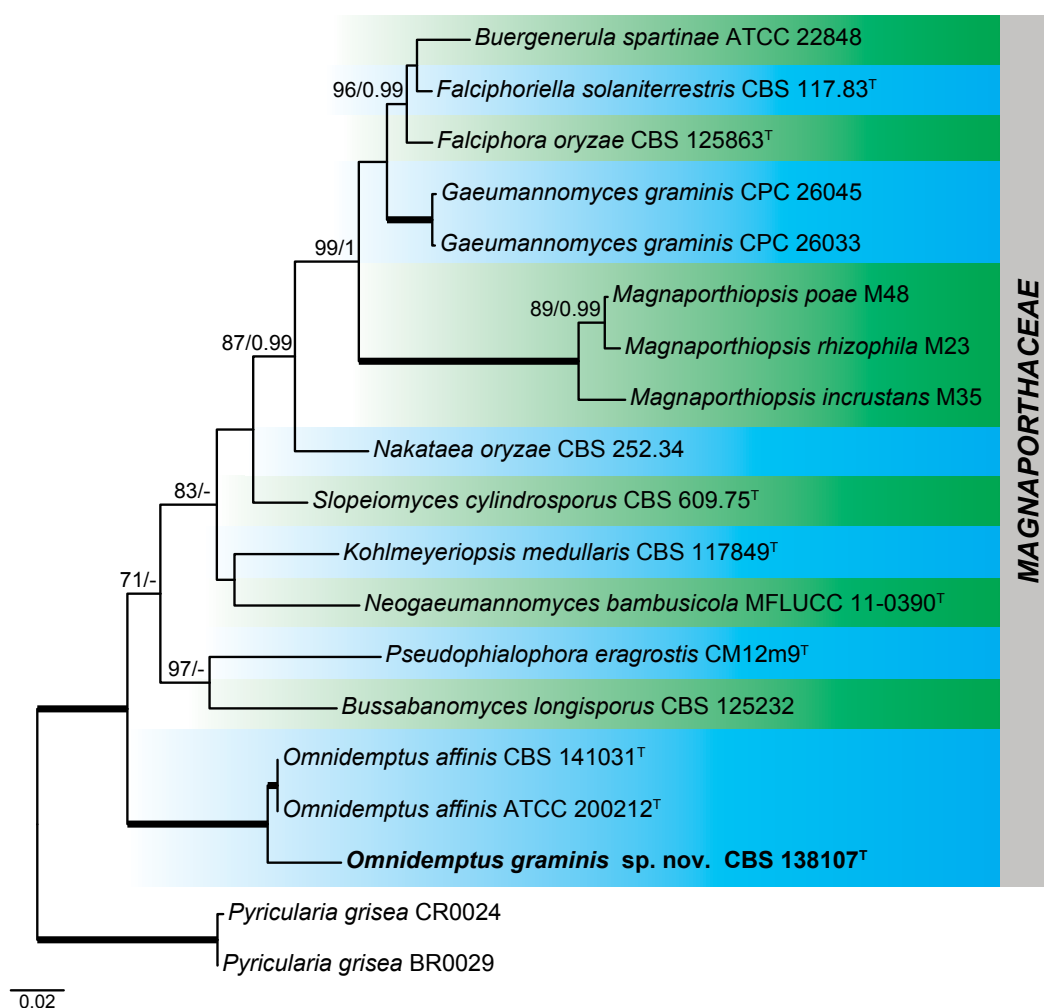


Fig. 2 RAxML phylogram obtained from the combined ITS, LSU, *rpb1*, and *tef1* sequences of *Magnaporthales* members. The tree was rooted to *Pyricularia grisea*. The new species described in this study is shown in **bold**. RAxML bootstrap support (BS) values $\geq 70\%$ and Bayesian posterior probability (PP) scores ≥ 0.95 are shown at the nodes and thickened lines represent nodes with BS = 100% and PP = 1.00. GenBank accession numbers are indicated in Table 1. ^T indicates ex-type.

Taxonomy

According to our phylogenetic analyses using DNA sequences from four loci (ITS, LSU, *rpb2*, and *tef1*), *Mycoleptodiscus* and *Muyocopron*, together with the genera *Arxiella*, *Leptodiscella*, *Neocochlearomyces*, *Neomycoleptodiscus*, and *Paramycoleptodiscus*, belong to the *Muyocoproneae* (*Muyocoproneales*, *Dothideomycetes*; Fig. 1), confirming previous results (Crous et al. 2018). Since the relationship of *Muyocopron* with all of these genera within the *Muyocoproneales* is reported for the first time, the circumscription of the order and family is emended below. *Mycoleptodiscus* s.str. is restricted to species characterised by cylindrical conidia with appendages at one or both ends. However, one new genus, *Neomycoleptodiscus*, very similar to *Mycoleptodiscus*, is recognised based on phylogenetic inferences and subtle morphological differences. Morphological and molecular data revealed that several species with broadly lunate conidia and with variable production of conidial appendages, previously included in *Mycoleptodiscus*, are part of what we interpret as the core clade of *Muyocopron*. Following the single-name nomenclature (Hawksworth et al. 2011), new combinations are proposed for *M. atromaculans*, *M. coloratus*, *M. freycinetiae*, *M. geniculatus*, *M. indicus*, *M. lateralis*, and *M. taiwanensis*, including mycoleptodiscus-like asexual morphs in *Muyocopron*.

Omnidemtus, which was previously placed in *Magnaporthales* (Cannon & Alcorn 1994, Luo & Zhang 2013, Klaubauf et al. 2014), is restricted to *O. affinis* and mycoleptodiscus-like species with falcate conidia lacking appendages.

Dothideomycetes

Muyocoproneales Mapook et al., Phytotaxa 265: 230. 2016; emend.

Type family. *Muyocoproneae* K.D. Hyde.

Ascomata pseudo-thyriothecial, superficial, coriaceous, appearing as circular, flattened, with a central ostiole, brown to dark brown, without subiculum, with a poorly developed basal layer; peridium comprising two layers, an outer layer composed of black-brown pseudoparenchymatous cells of *textura epidermoidea* and an inner layer composed of pale brown cells of *textura angularis*; hamathecium of pseudoparaphyses. *Asci* 8-spored, bitunicate, cylindrical to pyriform. *Ascospores* aseptate, oval to obovoid with obtuse ends, hyaline. *Conidiomata* if present, sporodochium-like. *Conidiophores* often reduced to conidiogenous cells. *Conidiogenous cells* solitary or aggregated, mono- or polyblastic, sympodial and often denticulate (*Arxiella*, *Leptodiscella*), or phialidic, globose to ampulliform (*Mycoleptodiscus*, *Neocochlearomyces*, *Neomycoleptodiscus*, *Paramycoleptodiscus*). *Conidia* one-celled or septate, lunate, falcate, fusiform or fusoid-ellipsoid, curved to geniculate, usually with terminal and/or lateral appendages, mostly hyaline. *Appressoria*, if present, ellipsoid to oblong-oval or obovoid, narrowly clavate or subcylindrical, sometimes uncinatate, occasionally sigmoid or bluntly bifurcate, straight or curved, brown. *Sclerotia* often present in culture, black. Pathogenic on plants and opportunistic pathogen on animals, lignicolous, foliicolous and soil-borne.

Muyocoproneae K.D. Hyde, Fung. Diversity 63: 164. 2013; emend.

Type genus. *Muyocopron* Speg.

Ascomata pseudo-thyriothecial, superficial, circular, flattened, lenticular in section, scattered, rarely coalescing, carbonaceous and brittle, black, basal layer slightly developed, with a central ostiole; upper wall comprising irregularly arranged radiating

cells; peridium comprising two strata, an outer layer composed of black-brown pseudoparenchymatous cells of compact thick-walled *textura epidermoidea*, an inner layer comprised of pale brown cells of *textura angularis*; hamathecium of dense, septate pseudoparaphyses, longer than the asci, immersed in mucilage and inclined towards the centre. *Asci* 8-spored, bitunicate/fissitunicate, pedicellate, with a small ocular chamber. *Ascospores* aseptate, ellipsoidal to ovate with obtuse ends, hyaline, with a granular appearance. *Conidiomata*, if present, sporodochium-like. *Conidiogenous cells* solitary or aggregated, mono- or polyblastic, sympodial, often denticulate (*Arxiella*, *Leptodiscella*), or phialidic, globose or ampulliform (*Mycoleptodiscus*, *Neocochlearomyces*, *Neomycoleptodiscus*, *Paramycoleptodiscus*), smooth. *Conidia* one-celled or septate, lunate, falcate, fusiform or fusoid-ellipsoid, curved to geniculate, usually with terminal and/or lateral appendages, hyaline. *Appressoria* if present ellipsoid to oblong-oval or obovoid, narrowly clavate or subcylindrical, sometimes uncinatate, occasionally sigmoid or bluntly bifurcate, straight or curved. *Sclerotia* often present in culture, black. Pathogenic on plants and opportunistic pathogen on animals, lignicolous, foliicolous, and soil-borne.

Other included genera — *Arxiella*, *Leptodiscella*, *Mycoleptodiscus*, *Neocochlearomyces*, *Neomycoleptodiscus*, and *Paramycoleptodiscus*.

Muyocopron Speg., Anales Soc. Ci. Argent. 12: 113. 1881; emend.

Type species. *Muyocopron corrientinum* Speg.

Ascomata superficial, solitary or scattered, coriaceous, appearing as circular, flattened, brown to dark brown, without subiculum, with a poorly developed basal layer and an irregular margin, with a central ostiole; peridium comprising two strata, an outer layer composed of dark brown to black pseudoparenchymatous cells of *textura epidermoidea*, an inner layer comprised of pale brown cells of *textura angularis*; hamathecium of cylindrical to filiform, septate pseudoparaphyses. *Asci* 8-spored, bitunicate, saccate or broadly obpyriform, pedicellate, straight or slightly curved, with small ocular chamber. *Ascospores* aseptate, irregularly arranged, oval to obovoid with obtuse ends, with a granular appearance, hyaline. *Conidiomata* sporodochium-like, highly irregular. *Conidiogenous cells* solitary or aggregated, enteroblastic, monophialidic, globose, broadly ellipsoidal to ampulliform, the conidiogenous locus often bordered with a collarette, brown, smooth. *Conidia* aseptate to septate, falcate, lunate, curved to geniculate, fusiform or fusoid-ellipsoid, with terminal and/or lateral appendages, hyaline, smooth. *Appressoria* ellipsoid to oblong-oval or obovoid, narrowly clavate or subcylindrical, sometimes uncinatate, occasionally sigmoid or bluntly bifurcate, straight or curved, 1–2 inconspicuous or invisible pores, brown, smooth. Saprobic and pathogenic on plants, opportunistic pathogen on animals.

Notes — *Muyocopron* is an old name, based on *M. corrientinum* described from leaves of *Oncidium* in Argentina (Spegazzini 1881). Luttrell (1951) was the first to include *Muyocopron* in its own family. However, the family was invalidly published, lacking a Latin diagnosis, and other authors have recognised this genus as a member of the *Microthyriaceae* (Hawksworth et al. 1995, Lumbsch & Huhndorf 2007). Hyde et al. (2013) provided an English diagnosis and accepted *Muyocoproneae* in *Dothideomycetes* based on molecular data of *Mu. castanopsis*, *Mu. dipterocarpi*, and *Mu. lithocarpi*.

The present study is the first description of an asexual morph for *Muyocopron*, which is mycoleptodiscus-like. Morphologically, the asexual morph of *Muyocopron* is distinguished from *Mycoleptodiscus* by conidiogenous cells with conspicuous flared

Table 2 Morphological features of *Muyocopron*, *Mycleptodiscus* and *Omniemptus* species treated in this paper.

Species	Strains and/or fungarium materials	Sporodochia (µm)	Conidiogenous cells		Conidia		Appressoria* (size in µm)	References
			Size (µm)	Collarette (µm)	Shape & size (µm)	Septa	Appendages length (µm)	
<i>Muyocopron alcornii</i>	BRIP 43879	36–89 × 38–60	12.5–18 × 12–18.5	3–6 × 4.5–8	Lunate, fusiform; 17.5–20 × 8–9	0–1(–2)	Apical and basal 3–5.5	This study
<i>Muyocopron atromaculans</i>	MUCL 34983	–	9.5–14.5 diam	2.5–4 × 2–7.5	Broadly falcate or lunate; 15.5–23 × 6.5–8.5	0	Apical and basal 1–3	Bills & Polishhook (1992a)
<i>Muyocopron coloratum</i>	CBS 720.95	25–165 × 16–125	17–25 × 13–19(–21)	3–10 × 5–8	Broadly lunate to inaequilateral oval-ellipsoidal; 16–27 × 8–13(–16)	0	Apical 2–8; basal 1–6	Alcorn (1994)
	CBS 720.95	–	17–29 × 16.5–26	3.5–6 × 4–6	Broadly lunate; 22–34 × 8–15	0	Apical 2–7; basal 0–5	This study
<i>Muyocopron freycineticola</i>	IFRD 8995	32–55 diam	9–18 × 6–12	2–2.5 × 1.5–3	Broadly falcate to lunate; 11–15 × 4–4.5	0	Apical and basal 2–3	Whitton et al. (2012)
<i>Muyocopron geniculatum</i>	CBS 721.95	Up to 125 diam	10–15 diam	3–12 × 3.5–6.5	Lunate to fusiform or fusoid-ellipsoidal; 14–20 × 5.5–7.5	0	Apical 4–12.5; basal 1–10	Alcorn (1994)
<i>Muyocopron laterale</i>	BRIP 16247 Type <i>Mu. lateralis</i>	25–160 × 20–150	9–16 diam	4–6 diam	Lunate, fusiform; 15–18 × 6–8	0	Apical (9–)15–24; basal 5–22.5; lateral 12–26	Sutton & Alcorn (1990)
	IMI 324533 Type <i>Mu. unilateralis</i>	27–45 × 13–32	9–12.5 diam	3–4.5 diam	Lunate, fusiform; 15–20 × 6–8	0	Apical 7.5–12.5; basal 5–11; lateral 7–9	Sutton & Alcorn (1990)
	CBS 719.95 Type <i>Mu. variabilis</i>	125–370 × 100–225	14–24 × 9–16	4–6.5 diam	Lunate, fusiform; 15–25 × 5.5–8	0	Apical 3–21; basal 4–15; lateral 11–22	Alcorn (1994)
	CBS 719.95 Type <i>Mu. variabilis</i>	–	12–16 × 10–15	1–2 × 3–5	Lunate, fusiform; 16.5–22 × 8–9.5	0	Apical and basal 2–17; lateral 9–20	This study
	CBS 145315	–	12–19 × 7.5–11	3–4.5 diam	Lunate, fusiform; 16.5–21 × 5.5–7	0	Apical, basal and lateral 8–15.5	This study
<i>Muyocopron sahnii</i>	IMI 108220	200–300 diam	–	–	Lunate, fusiform; 4–10 × 1.7–3.3	0	One at each end	Sahní (1968)
	IMI 108220	54–71 diam, 56–135 × 53–256	4.5–10.5 diam	–	Lunate, fusiform; 13.5–14.5 × 5–6	0	Basal 3	This study
	Several isolates	30–100 diam	7–13 × 3.5–7	Up to 3 long	Lunate, fusiform; 11–18.5 × 4.5–7.5	0	Apical 1–10; basal 0–6	Sutton (1973)

Table 2 (cont.)

Species	Strains and/or fungarium materials	Sporodochia (µm)	Conidiogenous cells		Conidia		Appressoria* (size in µm)	References
			Size (µm)	Collarette (µm)	Shape & size (µm)	Septa	Appendages length (µm)	
<i>Muyocopron taiwanense</i>	MFC-6T720	–	6–12 × 7–14	–	Broadly falcate 12–21 × 5.5–7	0	Apical and basal 1–3	Matsushima (1987)
<i>Muyocopron zamaiae</i>	CBS 203.71	–	7.5–14 × 8.5–12	1 × 2.5–3	Lunate, fusiform; 16–20 × 5.5–6.5	0	Apical 2.5–6; basal 0.75–5	This study
' <i>Mycoleptodiscus brasiliensis</i> '	IMI 196481e	30–45 diam	11–17.5 × 5–11.5	3 × 6	Cylindrical; 17–19 × 4–4.5	1	Apical 19–27	Sutton & Hodges (1976)
' <i>Mycoleptodiscus disciformis</i> '	MFC-1P143	85–430 diam	4–7 × 3–5	–	Cylindrical; 17.5–25 × 4–5	1	Apical and basal 5–8	Matsushima (1993)
' <i>Mycoleptodiscus minimus</i> '	Holotype <i>Discosia minima</i> 5113 Herb. Berk.	40–85 diam	5–8.5 × 3.5–7	–	Cylindrical; 20–25(–29) × 3.5–4	0	Apical and basal, up to 8	Vaney (1983)
<i>Mycoleptodiscus terrestris</i>	BPI 403851 (ILL31238)	200–800 diam	Evanescant	–	Cylindrical; 20–34.8 × 4.4–7	1	Apical and basal 8.7–18	Gerdemann (1953)
<i>Neomycoleptodiscus venezuelense</i>	ATCC 18104 Type of <i>M. sphaericus</i>	110–187 × 86–144	Obsolete	–	Cylindrical; 28.8–43.2 × 5–9	1(–2)	Apical 0–14	Ostazeski (1967)
<i>Omnidemiptus affinis</i>	BRIP 17195b Type <i>Myco-leptodiscus affinis</i>	50–160 diam	7–12 diam [ampuli-form]; 11–22 × 6–10 [elongated]	3–4 × 2–3	Falcate; 21–30 × 3–4	1–2(–3)	–	Cannon & Alcorn (1994)
<i>Omnidemiptus graminis</i>	CBS 138107	–	10–14 diam	1 × 3	Falcate; 11–23 × 3–4	1	–	This study
<i>Omnidemiptus lunatus</i>	IMI 271703	10.5–13 × 6.5–11	3–4.5 diam	1.5–2 diam	Falcate; 24.5–32 × 3.5–4.5	1	–	Sutton & Alcorn (1985)

* Appressoria description taken from Alcorn (1994).

collarettes, wider lunate conidia, and appressoria being unlobed or rarely with two lobes, with inconspicuous or indistinct pore. In *Mycleptodiscus*, the conidiogenous cells lack a collarette, the conidia are usually cylindrical, the appressoria have a visible pore surrounded by dark radial lines, and sclerotia are often present (Ostazeski 1967, Sutton & Hodges 1976, Sutton & Alcorn 1990, Matsushima 1993, Alcorn 1994). No sexual morph is currently known for *Mycleptodiscus* as here redefined.

Muyocopron alcornii Hern.-Restr., J.D.P. Bezerra & Y.P. Tan, *sp. nov.* — MycoBank MB828980; Fig. 3

Etymology. Named after the Australian mycologist, John L. Alcorn, who described several species related to *Mycleptodiscus*.

Typus. AUSTRALIA, Queensland, Logan (Greenbank), leaf spot (blight) of *Epidendrum* sp., 2004, L.I Forsberg R9324 (holotype BRIP 43897, culture ex-type BRIP 43897 = CBS 141314).

Hyphae septate, branched, dark brown near the conidiomata, pale brown to hyaline when distant, smooth, 1.5–7 µm wide. **Conidiomata** sporodochium-like, superficial, mid- to dark brown, varying from a few combined cells to large aggregations, variable in shape and size due to confluence, 36–89 × 38–60 µm. **Conidiogenous cells** globose to ampulliform, 12.5–18 × 12–18.5 µm, often with a distinct flared collarette, 3–6 × 4.5–8 µm, medium to dark brown, smooth. **Conidia** 0–1(–2)-septate, lunate, fusiform, curved, guttulate, 17.5–20 × 8–9 µm, with a filiform, unbranched appendage at each end, 3–5.5 × 0.5–1 µm, hyaline, smooth. **Appressoria** not observed. **Sexual morph** unknown.

Culture characteristics — Colonies on OA attaining 75 mm diam after 2 wk at 25 °C; aerial mycelium scarce, zonate, centre hispid, dark brick, periphery glabrous, luteous, margin effuse, diffusible pigment luteous to pale luteous; reverse sienna in the centre, fulvous to the periphery. On MEA attaining 40 mm diam after 1 wk at 25 °C, slightly elevated, cottony to hispid, buff to ochreous, margin effuse, diffusible pigment apricot; reverse dark umber in the centre, paler to the periphery.

Habitat — *Epidendrum* sp. (Orchidaceae).

Distribution — Australia.

Notes — *Muyocopron alcornii* can be distinguished from other species by having conidia with up to two septa. *Muyocopron alcornii* is similar to *Mu. sahnii*, but differs from it by having

larger conidiogenous cells and conidia (Table 2). Phylogenetically, it is placed on an independent branch in the *Muyocopron* clade.

Muyocopron atromaculans (Bills & Polishook) Hern.-Restr., J.D.P. Bezerra & Crous, *comb. nov.* — MycoBank MB828981

Basionym. *Mycleptodiscus atromaculans* Bills & Polishook, Mycotaxon 43: 454. 1992.

Typus. USA, New Jersey, Burlington, Wading River, near State Highway 563, endophytic from leaves of *Chamaecyparis thyoides*, 1991, H. Pond (holotype BPI GB1369, not seen; culture ex-isotype MUCL 34983).

Illustration — See Bills & Polishook (1992a).

Hyphae septate, branched, hyaline to pale olive grey, 1.5–4 µm diam. **Conidiomata** sporodochium-like, highly irregular, initially consisting of small groups of conidiogenous cells, in aging irregular forming confluent masses of > 50 conidiogenous cells. **Conidiogenous cells** solitary, often aggregated, globose, subglobose or irregularly ellipsoid, compressed when aggregated, 9.5–14.5 µm diam, with a cylindrical to flared collarette having ragged margins, 2.5–4 × 2–7.5 µm, pale brown to blackish brown, usually darkest at the base of the collarette, smooth. **Conidia** aseptate, broadly falcate or lunate, narrowed at both ends to form terminal appendages, with highly refractive cytoplasm, hyaline, smooth, 15.5–22 × 6.5–8.5 µm; appendages 1–3 µm long (adapted from Bills & Polishook 1992a). **Sexual morph** unknown.

Culture characteristics — Colonies on OA attaining 60–65 mm diam after 2 wk at 25 °C, mycelium slightly raised, radially plicate, zonate, with some medium buckling and cracking beneath centre of colony, aerial mycelium moderately abundant to sparse at the margin, floccose to minutely hispid, with black conidiomata scattered beneath aerial mycelium over inner third of colony, margin entire, white to pale or medium grey, pale drab grey, pale smoke grey (adapted from Bills & Polishook 1992a).

Habitat — Endophytic fungi from leaves of *Chamaecyparis thyoides* (Bills & Polishook 1992a).

Distribution — USA.

Notes — *Muyocopron atromaculans* morphologically resembles *Mu. coloratum* and *Mu. taiwanense*. *Muyocopron atromaculans*, however, has smaller conidia and shorter appendages than *Mu. coloratum*, and slightly larger conidia than *Mu. taiwanense* (Table 2). Although, each species is repre-

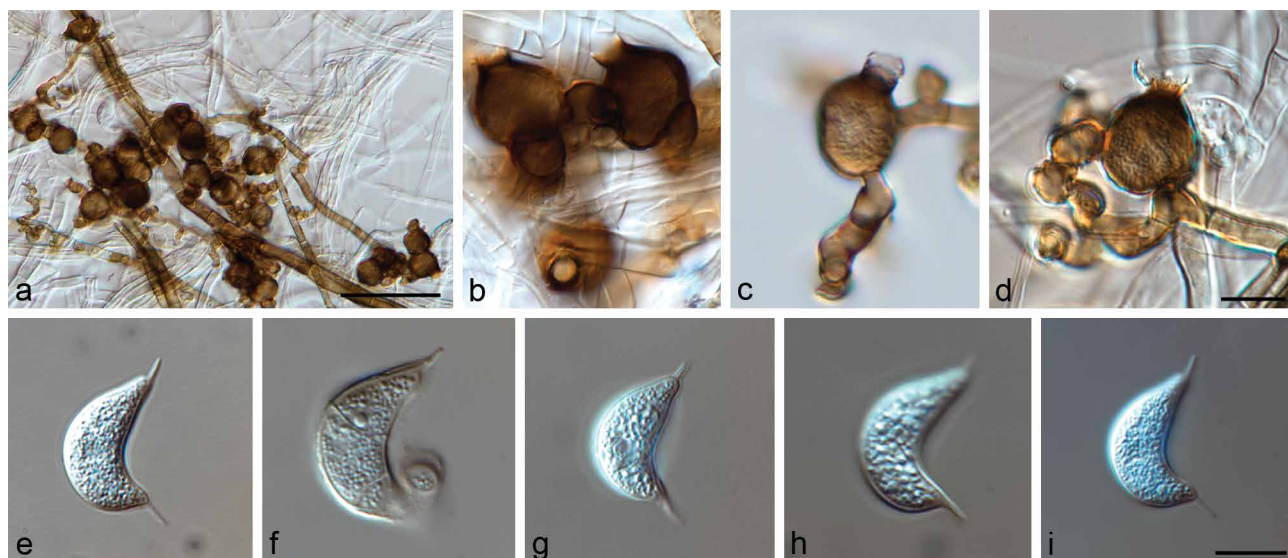


Fig. 3 *Muyocopron alcornii* sp. nov. ex-type BRIP 43897. a–d. Conidiogenous cells; e–i. conidia. — Scale bars: a = 50 µm, others = 10 µm, d applies to b–d, i applies to e–i.

sented by one strain, they differ in host affinity and geographic distribution. *Muyocopron atromaculans* was isolated as an endophyte from leaves of *Chamaecyparis* in the USA (Bills & Polishook 1992a), *Mu. coloratum* is known only from *Cattleya* in Australia (Alcorn 1994), while *Mu. taiwanense* is only known from a decaying leaf rachis of *Areca* in Taiwan (Matsushima 1987). Phylogenetically, *Mu. atromaculans* is closely related to *Mu. geniculatum* and *Mu. zamiae* (Fig. 1).

Muyocopron coloratum (Alcorn) Hern.-Restr., J.D.P. Bezerra & Crous, *comb. nov.* — MycoBank MB828982; Fig. 4

Basionym. *Mycoleptodiscus coloratus* Alcorn, Austral. Syst. Bot. 7: 596. 1994.

Typus. AUSTRALIA, Queensland, Bibbohra, on leaf spot of *Cattleya* sp., 16 Jan. 1992, J. Allen & K.R.E. Grice M6076 (holotype BRIP 19988, culture ex-type BRIP 19988 = CBS 720.95).

Hyphae septate, branched, hyaline to brown, 2–5 µm diam. *Conidiomata* sporodochium-like, varying from a few cells up to moderately large aggregations, sometimes rounded, but generally irregular in outline, dark brown. *Conidiogenous cells* ampulliform to broadly ellipsoidal, 17–29 × 13–26 µm, with a cylindrical to flared collarete having ragged margins, 3–10 × 4–8 µm, mid- to dark brown, often darker around the neck. *Conidia* aseptate, broadly lunate to inaequilateral oval-ellipsoidal, strongly convex on one side, concave to flattened to more or less convex on other side which often has a distinct median swelling varying in degree of protrusion, 16–34 × 8–16 µm, with a filiform, unbranched appendage at each end, apical 2–8 µm long, basal 1–6 µm long, 1 µm wide; the basal appendage often inserted eccentrically on the truncate base. *Sexual morph* unknown.

Culture characteristics — Colonies on OA attaining 80 mm diam after 2 wk at 25 °C, aerial mycelium cottony to hispid, apricot, margin effuse; reverse apricot. On MEA attaining 30 mm diam after 1 wk at 25 °C, aerial mycelium scarce velvety, rust,

margin effuse, diffusible pigment after 2 wk apricot; reverse sienna.

Habitat — *Cattleya* sp. (Alcorn 1994).

Distribution — Australia.

Notes — The size of the structures observed in this study differs from those described in the protologue of *Mu. coloratum*. The conidiogenous cells were slightly larger with smaller necks and conidia with reduced appendages were longer (Table 2). The LSU sequence of *M. coloratum* (DQ341499) previously deposited by Thongkantha et al. (2009) was dissimilar to the sequence generated during the present study. Newly generated sequences of the ex-type strain of *Mu. coloratum* (CBS 720.95) related it to *Muyocopron* species, and formed an independent lineage, basal to *Mu. laterale*.

Muyocopron freycineticola Hern.-Restr. & Crous, *nom. nov.* — MycoBank MB828983

Basionym. *Mycoleptodiscus freycinetiae* Whitton et al., Fungal Diversity Research Series 21: 251. 2012. Non *Muyocopron freycinetiae* (F. Stevens & R.W. Ryan) G. Arnaud, Ann. Cryptog. Exot. 4: 88. 1931.

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

Typus. PHILIPPINES, Luzon Island, Quezon Region, Barangay Llabac Real, on decaying leaves of *Freycinetia* sp., 22 Oct. 1996, S.R. Whitton HKU(M)12794 (holotype IFRD 8995, not seen).

Illustration — See Whitton et al. (2012).

Hyphae brown to pale brown, smooth, septate, branched, irregular, sparse or sometimes abundant. *Conidiomata* sporodochium-like, superficial, either solitary or aggregated, typically circular, 32–55 µm diam, brown. *Conidiogenous cells* ampulliform, 9–18 × 6–12 µm, with a distinct, sometimes thickened collarete, 2–2.5 µm long, aperture 1.5–3 µm diam, brown, smooth. *Conidia* aseptate, broadly falcate to lunate, hyaline, smooth, 11–15 × 4–4.5 µm, with a filiform, unbranched appendage at

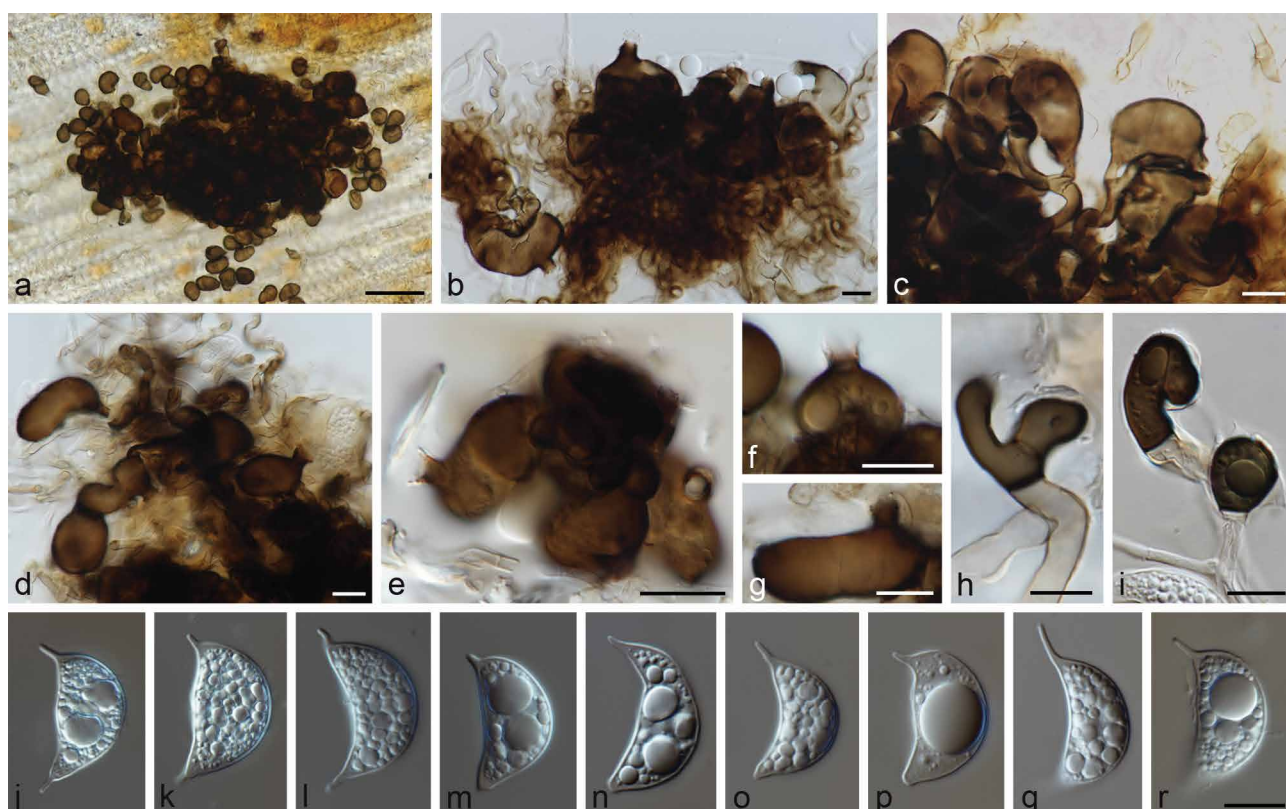


Fig. 4 *Muyocopron coloratum* ex-type CBS 720.94. a–g. Conidiogenous cells; h–i. appressoria; j–r. conidia. — Scale bars: a = 50 µm, others = 10 µm, r applies to j–r.

each end; appendages 2–3 µm long (adapted from Whitton et al. 2012). *Sexual morph* unknown.

Habitat — Decaying leaves of *Freycinetia* sp. and *F. scadens* (Whitton et al. 2012).

Distribution — Australia, Philippines.

Notes — *Muyocopron freycineticola* is similar to *Mu. sahnii*, but the former is distinguished by the spherical shape of the conidiomata and wider conidia (Whitton et al. 2012).

Muyocopron geniculatum (Alcorn) Hern.-Restr., J.D.P. Bezerra & Crous, *comb. nov.* — MycoBank MB828984

Basionym. *Mycoleptodiscus geniculatus* Alcorn, Austral. Syst. Bot. 7: 598. 1994.

Typus. AUSTRALIA, Queensland, Girraween National Park, on *Stypanandra glauca*, 13 Oct. 1990, V.P. Cooper 55 (holotype BRIP 17274, culture ex-type BRIP 17274 = CBS 721.95).

Illustration — See Alcorn (1994).

Hyphae immersed, 1.5–7 µm diam, aerial hyphae 1.5–6 µm diam. *Conidiomata* sporodochium-like, varying from a few conidiogenous cells to irregularly aggregations up to 125 µm diam, or larger by confluence, dark brown. *Conidiogenous cells* ampulliform, 10–15 µm diam, with a cylindrical to flared collarette having ragged margins, 4–6.5 µm diam, sometimes extended into a thick-walled cylindrical neck 3–12 × 3.5–6.5 µm, circular pore 2–3.5 µm diam, dark brown, smooth. *Conidia* aseptate, lunate to fusiform or fusoid-ellipsoidal, curved to geniculate with a distinct change in curvature in the upper part, hyaline, smooth, 14–20 × 5.5–7.5 µm, with a filiform, unbranched, appendage at each end, measuring 4–12.5 µm long (apical) and 1–10 µm long (basal), 0.5–1 µm wide (adapted from Alcorn 1994). *Sexual morph* unknown.

Culture characteristics — Colonies on OA attaining 90 mm diam after 2 wk at 25 °C, aerial mycelium scarce, cottony to funiculose, buff, margin effuse; reverse buff. On MEA attaining 45–50 mm diam after 1 wk at 25 °C, elevated, aerial mycelium cottony to funiculose, white, margin effuse; reverse dark brown in the centre paler to the periphery.

Habitat — *Stypanandra glauca* (Alcorn 1994).

Distribution — Australia.

Notes — *Muyocopron geniculatum* is morphologically similar to *Mu. sahnii* and *Mu. zamiae*. However, *Mu. geniculatum* has slightly larger, geniculate conidia with a distinct change in curvature in the upper part, while conidia in *Mu. sahnii* and *Mu. zamiae* are smoothly curved (Table 2).

Muyocopron laterale (Alcorn & B. Sutton) Hern.-Restr., J.D.P. Bezerra & Crous, *comb. nov.* — MycoBank MB828986; Fig. 5

Basionym. *Mycoleptodiscus lateralis* Alcorn & B. Sutton, Mycol. Res. 94: 564. 1990.

Synonyms. *Mycoleptodiscus unilateralis* B. Sutton & Alcorn, Mycol. Res. 94: 565. 1990.

Mycoleptodiscus variabilis Alcorn, Austral. Syst. Bot. 7: 599. 1994.

Typus. AUSTRALIA, Queensland, Beerwah, on leaf spot of *Alloteropsis semialata*, 19 Mar. 1988, J.L. Alcorn 8841a (holotype BRIP 16247, isotype IMI 330181, culture ex-type BRIP 16247 = CBS 141029 = ATCC 200213).

Hyphae thick-walled, septate, branched, dark brown near the conidiomata, pale brown to hyaline when distant, smooth. *Conidiomata* sporodochium-like, superficial, mid- to dark brown, varying from a few combined conidiogenous cells to large aggregations, sometimes rounded in outline but usually variable in shape and size due to confluence, 25–160(–370) × 13–150(–225) µm. *Conidiogenous cells* ampulliform, 14–24

× 9–16 µm diam, often with a distinct flared collarette, 3–6.5 µm diam, circular pore 2–3 µm diam, medium to dark brown, smooth. *Conidia* aseptate, lunate, fusiform, curved, base obtuse to truncate, often guttulate, hyaline, smooth, 15–25.5 × 5.5–8 µm, with a filiform, unbranched appendage at each end, measuring 1–24 µm long (apical), 4–22.5 µm long (basal), 0.5–1 µm wide; often with 1–2 lateral appendages originate on the convex side of the conidium in a median or slightly suprmedian position, 7–26 × 0.5–1 µm. *Sexual morph* unknown.

Culture characteristics — Colonies on OA attaining 70–90 mm diam after 2 wk at 25 °C, zonate with aerial mycelium scarce, cottony, or glabrous, in the centre buff, rosy buff to apricot, paler to the periphery, margin effuse; reverse buff, brick, apricot in the centre paler to the periphery. On MEA attaining 30–60 mm diam after 1 wk at 25 °C, elevated, aerial mycelium cottony to hispid, white, buff, pale grey, margin effuse; reverse saffron, apricot, umber, dark umber in the centre paler to the periphery.

Habitat — On leaves of monocotyledons plants such as *Alloteropsis semialata*, *Chlorophytum capense*, and *Dianella congesta* (Sutton & Alcorn 1990, Alcorn 1994), endophyte from *Banksia verticillata* (Andrioli et al. 2012, as *M. indicus*) and *Opuntia ficus-indica* (Bezerra et al. 2012), fresh water foam (Ramesh & Vijaykumar 2005), *Homo sapiens* (Padhye et al. 1995, Garrison et al. 2008, Dewar & Sigler 2010, Koo et al. 2012, as *M. indicus*), *Canis lupus* subsp. *familiaris* (Metry et al. 2010, as *M. indicus*), and *Felis catus* (Hull et al. 1997).

Distribution — America, Australia, India.

Additional materials examined. AUSTRALIA, Queensland, Peregrine beach, on leaf spot of *Dianella congesta*, 28 Jan. 1990, J.L. Alcorn 9007 (BRIP 16983 = CBS 719.95 = ATCC 96451, culture ex-type of *M. variabilis*); Queensland, Peregrine beach, on leaf spot of *Dianella congesta*, 3 May 1992, J.L. Alcorn 92/1764 (BRIP 20066 = CBS 141033). — BRAZIL, Paraíba, Santa Teresinha, Tamanduá farm (S07°1.524 W037°23.518), as endophyte from *Poincianella pyramidalis*, May 2013, J.D.P. Bezerra (URM 7802); Pernambuco, Itaíba, Curral Velho farm, as endophyte from *Opuntia ficus-indica*, May 2013, J.D.P. Bezerra (URM 7801 = isolate PF108). — CANADA, Vancouver General Hospital, R. Rennie, aspirate ex joint from *Homo sapiens*, unknown date, unknown collector (CBS 127677 = UAMH 10746, as *M. indicus*). — INDIA, Kerala, Trivandrum, on leaves of *Chlorophytum capense*, 15 Jan. 1988, K. Nayar (IMI 324533 culture ex-type of *M. unilateralis*). — USA, Alabama, H. sapiens (tissue-knee wound), Mar. 2012, D.A. Sutton (UTHSC DI17-18 = CBS 145310); Florida, H. sapiens (tissue-foot), Dec. 2013, D.A. Sutton (UTHSC DI 17-23 = CBS 145315); Florida, H. sapiens (unknown clinical specimen), Sept. 2011, D.A. Sutton (FMR 13797); Louisiana, H. sapiens (tissue toe), Mar. 2013, D.A. Sutton (UTHSC DI 17-21 = CBS 145313); Massachusetts, H. sapiens (fascial biopsy), June 2008, D.A. Sutton (UTHSC DI 17-17 = CBS 145309); South Carolina, H. sapiens (tissue-foot), May 2013, D.A. Sutton (UTHSC DI 17-22 = CBS 145314); Texas, H. sapiens (eye), Oct. 2012, D.A. Sutton (UTHSC DI 17-19 = CBS 145311); Texas, H. sapiens (eye), Oct. 2012, D.A. Sutton (UTHSC DI 17-20 = CBS 145312); Texas, H. sapiens (tissue-arm), June 2015, D.A. Sutton (UTHSC DI 17-24 = CBS 145316).

Notes — Sutton & Alcorn (1990) introduced *M. lateralis* and *M. unilateralis* for species similar to *M. indicus* (Sahni 1968) but distinguished by larger conidia with larger apical appendages and the presence of lateral appendages (Table 2). Later, Alcorn (1994) introduced *M. variabilis*, another species with lateral appendages, differing from *M. lateralis* and *M. unilateralis* mainly by the size of the conidial appendages and conidiomata characteristics. However, these morphological features are not always constant among strains and can be influenced by external factors. In our molecular analyses, the ex-type strains of *M. lateralis*, *M. unilateralis*, and *M. variabilis* grouped in a highly supported subclade (89/0.99) in *Muyocopron*, together with strains previously identified as '*M. indicus*' and several clinical isolates of '*Mycoleptodiscus* sp.' (Fig. 1), from what we concluded that they are conspecific, with *M. lateralis* having priority.

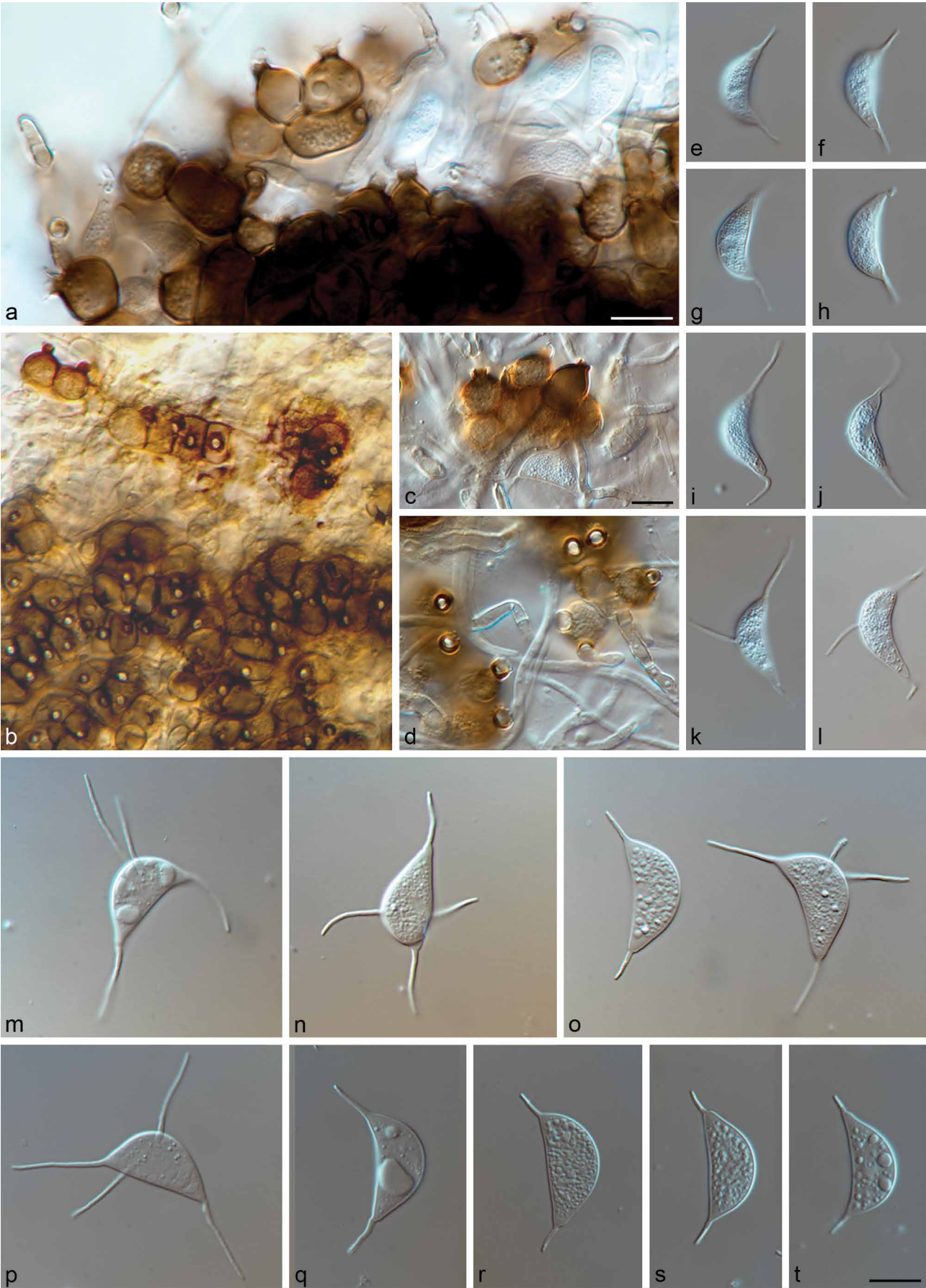


Fig. 5 *Muyocopron laterale* CBS 145315 (a, e–h); CBS 145316 (b–d, i–l), CBS 719.95 (m–t). a–d. Conidiogenous cells; e–t. conidia. — Scale bars: = 10 μm, c applies to b, c; t applies to d–t.

All the clinical isolates included in this study grouped in *Mu. laterale* clade. The first report of *Muyocopron* (as *Mycoleptodiscus*) as etiologic agent of phaeohyphomycosis was attributed to *M. indicus* (Padhye et al. 1995). Since then, several authors have reported clinical cases of *M. indicus* in human and other mammals (Garrison et al. 2008, Dewar & Sigler 2010, Metry et al. 2010). However, the LSU and ITS sequences data from those strains indicated close affinities with *Mu. laterale*.

Additionally, some of those strains showed conidia with lateral appendages (Dewar & Sigler 2010, Metry et al. 2010). Besides *M. indicus*, only one case of phaeohyphomycosis was reported as caused by *M. lateralis* in a cat (Hull et al. 1997), while Koo et al. (2012) were unable to identify at the species level one strain isolated from a man with glioblastoma multiforme, due to inconsistencies between the morphological and molecular data.



Fig. 6 *Muyocopron sahnii* holotype IMI 108220. a. Holotype details; b–c. leaf spot with sporodochia on the substrate; d–g. sporodochia; d–e. top view; f. down view; g. lateral view; h. conidiogenous cell with collarette; i–l. conidia close to sporodochial; m. conidia. — Scale bars: d = 50 µm, others = 10 µm, f applies to e, f, l applies to i–l.

Muyocopron sahnii Hern.-Restr. & Crous, *nom. nov.* — MycoBank MB828985; Fig. 6

Basionym. *Amerodiscosiella indica* V.P. Sahní, Mycopathol. Mycol. Appl. 36: 277. 1968.

Synonyms. *Mycoleptodiscus indicus* (V.P. Sahní) B. Sutton, Trans. Brit. Mycol. Soc. 60: 528. 1973.

Pucciniopsis guaranitica Speg., Anales Soc. Ci. Argent. 26: 74. 1888. pro parte.

Etymology. Name after the Indian mycologist V.P. Sahní.

Typus. INDIA, Jabalpur, on *Ixora parviflora*, 1964, V.P. Sahní (IMI 108220 holotype of *Amerodiscosiella indica* V.P. Sahní).

Hyphae septate, pale brown to brown, smooth. *Conidiomata* sporodochium-like, superficial, varying from a few combined cells to large aggregations, sometimes rounded in outline 54–71 µm diam, but usually variable in shape and size due to confluence, 56–135 × 53–256 µm, dark brown, smooth. *Conidiogenous cells* ampulliform, 4.5–10.5 µm diam, often with a distinct flared collarete, 3 × 1.5–2.5 µm, brown, smooth. *Conidia* aseptate, lunate, fusiform, curved, base obtuse to truncate, often guttulate, 13.5–14.5 × 5–6 µm, hyaline, smooth, often guttulate, with a reduced appendage. *Sexual morph* unknown.

Habitat — On leaves of several mono- and dicotyledonous plants (Sutton 1973, Sutton & Hodges 1976, Bezerra & Ram 1986), the fruit of *Passiflora edulis* var. *flavicarpa* and *P. edulis* (Sutton & Hodges 1976).

Distribution — America, India, New Zealand (Sutton 1973).

Notes — *Amerodiscosiella indica* was first described from India causing leaf spots on *Ixora parviflora*. It was characterised by pycnidial, ostiolate conidiomata, and conidia with appendages at each end (Sahní 1968, Table 2). Sutton (1973) examined the type material (IMI 108220) and additional specimens from different countries (Brunei, Cuba, India, New Zealand, Nigeria, USA, and Venezuela) and host plants (*Cocos yatay*, *Cordyline*, *Chlorophytum comosum*, *Grewia asiatica*, *Hippeastrum*, *Hymenocallis arenicola*, *Roupellia grata*, and *Zamia*) and transferred this species to *Myculeptodiscus*. However, in the emended description provided, Sutton (1973) described the conidiomata as sporodochial instead of pycnidial and larger conidia, with appendages at one or both ends (Table 2), differing considerably from the protologue of *A. indica* (Sahní 1968). During the present study, we re-examined the holotype of *A. indica* and confirmed that the conidiomata were sporodochium-like and the few conidia observed were larger than the measurements provided in the protologue (Sahní 1968) but smaller than those from Sutton (1973), with reduced conidial appendages (Fig. 6).

Since the epithet *indicum* is preoccupied in *Muyocopron*, a new name is necessary for this fungus. Unfortunately, no ex-type strain of *A. indica* was available and the phylogenetic relationships of this species with members of *Muyocopron* still needs to be assessed. Furthermore, the geographic distribution and host preferences of *Mu. sahnii* are not completely known.

Muyocopron taiwanense (Matsush.) Hern.-Restr. & Crous, *comb. nov.* — MycoBank MB828987

Basionym. *Myculeptodiscus taiwanensis* Matsush., Matsushima Mycol. Mem. 5: 21. 1987.

Typus. TAIWAN, Nan-Jen-Shan, on rotten leaf rachis of *Areca catechu*, 1986 (holotype MFC 6T720, not seen).

Illustration — See Matsushima (1987).

Hyphae branched, septate, hyaline to pale brown, 1.5–4 µm wide. *Conidiomata* sporodochium-like, irregular, brown. *Conidiogenous cells* densely aggregated, ampulliform, apex with a protruding neck, 6–12 × 7–14 µm, brown to dark brown at the neck, smooth. *Conidia* aseptate, broadly falcate, 12–21 × 5.5–7 µm long (including appendages), hyaline, smooth, with an unbranched appendage at each end; apical appendage acute, 1–3 µm long; basal appendage inserted obliquely exogenously, 1–3 µm long (adapted from Matsushima 1987). *Sexual morph* unknown.

Habitat — Rotten leaf rachis of *Areca catechu* (Matsushima 1987).

Distribution — Taiwan.

Notes — *Muyocopron taiwanense* is similar to species relocated to *Muyocopron* rather than *Myculeptodiscus* (see *Mu. atromaculans*).

Muyocopron zamiae Hern.-Restr. & Crous, *sp. nov.* — MycoBank MB828988; Fig. 7

Etymology. Name refers to *Zamia*, the plant genus from which this fungus was collected.

Typus. USA, Florida, *Zamia fisheri*, date unknown, isol. S.A. Alfieri Jr., No. 070-2273 (holotype CBS H-23882, culture ex-type CBS 203.71).

Hyphae septate, branched, dark brown near the conidiomata, pale brown to hyaline when distant, smooth, 1.5–4 µm wide. *Conidiomata* sporodochium-like, superficial, varying from a few combined cells to large aggregations, variable in shape and size due to confluence, mid- to dark brown. *Conidiogenous cells* globose to ampulliform, 7.5–14 × 8.5–12 µm, evanescent, sometimes with a flared collarete, 1 × 2.5–3 µm, medium to dark brown, smooth. *Conidia* aseptate, lunate, fusiform, curved, 16–20 × 5.5–6.5 µm, hyaline, smooth, guttulate, with a filiform, unbranched appendage at each end, apical 2.5–6 µm long, basal 0.5–5 µm long. *Appressoria* not observed. *Sexual morph* unknown.

Culture characteristics — Colonies on OA attaining 70 mm diam after 2 wk at 25 °C, aerial mycelium scarce, cottony to hispid, smoke grey in the centre greyish sepia to the periphery, margin effuse; reverse olivaceous black. On MEA attaining 65–70 mm diam after 1 wk at 25 °C, elevated, aerial mycelium cottony to hispid, buff, cinnamon close to the agar, margin effuse; reverse sienna in the centre umber to the periphery.

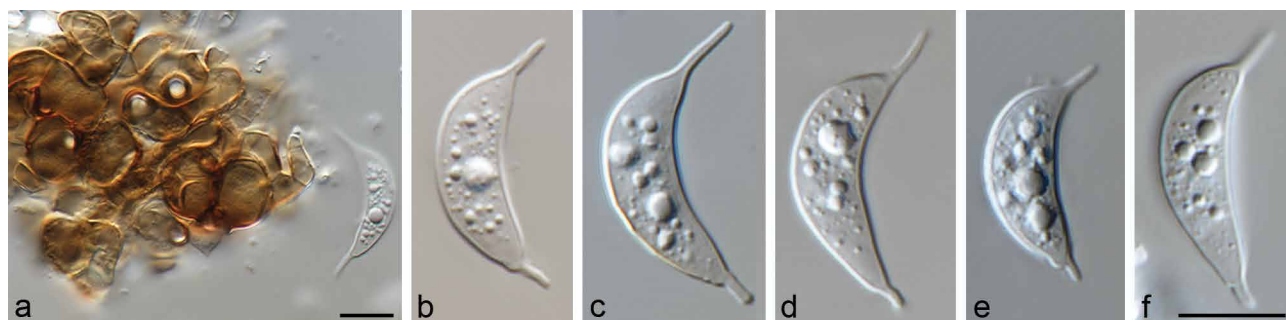


Fig. 7 *Muyocopron zamiae* sp. nov. ex-type CBS 203.71. a. Conidiogenous cells and conidia; b–f. conidia. — Scale bars: = 10 µm, f applies to b–f.

Habitat — *Zamia fisheri*, *Z. integrifolia*.

Distribution — USA.

Additional material examined. USA, Florida, leaf spot and necrotic tip on *Z. integrifolia* (= *Z. floridana*), date unknown, isol. S.A. Alfieri Jr. No. 070-2288, CBS 202.71.

Notes — *Muyocopron zamiae* is known from *Z. fisheri* and *Z. integrifolia* in the USA, causing oval leaf spots that are more evident in older leaves. Although morphologically similar to *Mu. sahnii*, conidia of *Mu. zamiae* are larger (Table 2). Phylogenetically, it formed a subclade (100/0.99) with *Mu. atromaculans* and *Mu. geniculatum* (Fig. 1). *Muyocopron zamiae* can be distinguished from *Mu. atromaculans* by having slender conidia with longer conidial appendages, and from *Mu. geniculatum*, its closest relative, by having smoothly curved conidia with shorter conidial appendages (Table 2).

Mycoleptodiscus Ostaz., Mycologia 59: 970. 1968 (1967)

Synonyms. *Leptodiscus* Gerd., Mycologia 45: 552. 1953.

Pucciniopsis Speg., Anales Soc. Ci. Argent. 26: 74. 1888. pro parte.

Type species. *Mycoleptodiscus terrestris* (Gerd.) Ostaz.

Conidiomata sporodochium-like, superficial, solitary or confluent, developing radially from central cell to form a thin stroma, circular to irregular in outline, dark brown, comprised of thick-walled phialides. *Conidiogenous cells* enteroblastic, monophialidic, ampulliform to doliform, brown, *textura globulosa* in face view, evanescent; conidiogenous locus circular, perforating the upper cell wall, without a collarette. *Conidia* 0–2-septate, cylindrical, hyaline, smooth, with an apical and sometimes a basal, unbranched, straight, appendage, base truncated, apex pointed. *Sclerotia* when present, spherical, black. *Sexual morph* unknown.

Notes — *Mycoleptodiscus* is limited to species with sporodochium-like conidiomata, that have conidiogenous cells lacking collarettes, cylindrical conidia with one or two appendages, and sclerotia that are often produced both on the natural substrate and in culture (Ostazeski 1967).

According to our phylogenetic analyses, *Mycoleptodiscus* includes two phylogenetic species morphologically indistinguishable, namely the type of the genus, *M. terrestris*, and one new species, *M. suttonii* (Fig. 1). Other species previously included in the genus, such as *M. brasiliensis*, *M. disciformis*, *M. minimus*, and *M. stellatosporus* (strictly based on morphological criteria) and *M. endophyticus* (introduced with only molecular data), are treated here as doubtful species.

Mycoleptodiscus suttonii Hern.-Restr., J.D.P. Bezerra & Crous, sp. nov. — MycoBank MB828989; Fig. 8

Etymology. Named after the British mycologist, Brian C. Sutton, who described several species related to *Mycoleptodiscus*.

Typus. BRAZIL, Itabuna, Asha Ram, Centro de Pesquisas do Cacau, on roots of *Theobroma cacao*, unknown date (dep. 2 Dec. 1971), A. Ram (holotype designated here CBS H-14851, culture ex-type CBS 276.72).

A dry sporulating culture on CMA with a twig consists of scattered, circular *conidiomata* sporodochia-like and 1-septate, cylindrical *conidia*, 33–36 × 7–7.5 µm, pale brown, with appendages at both ends, up to 19 µm, forming an orange mass. Cultures from ex-type and CBS 141030 remain sterile. *Mycoleptodiscus suttonii* (CBS 276.72) differs from its closest phylogenetic neighbour, *M. terrestris* (CBS 231.53), by unique fixed alleles in four loci based on alignments of the separate loci deposited in TreeBASE (23523): ITS positions 171 (A), 192 (T), 197 (C), 201 (T), 287 (–), 299 (T), 719 (A), and 745 (T); LSU positions 506 (T), 514 (T), 541 (T), 697 (T), 698 (T), and 740 (A); *rpb2* positions 76 (T), 88 (C), 100 (T), 124 (A), 133 (G), 163 (T), 175 (C), 190 (T), 214 (G), 223 (C), 250 (G), 253 (C), 289 (T), 301 (T), 307 (A), 313 (A), 328 (C), 349 (G), 388 (A), 391 (C), 394 (C), 397 (G), 451 (T), 457 (A), 460 (T), 508 (C), 511 (T), 526 (T), 547 (G), 556 (C), 581 (C), 589 (C), 592 (G), 595 (G), 616 (C), 634 (G), 637 (T), 667 (T), 673 (A), 682 (G), 689 (C), 690 (C), 748 (G), 790 (A), 808 (T), 811 (T), 814 (C), 844 (G), and 862 (T); *tef1* positions 44 (T), 160 (T), 214 (T), 263 (C), 264 (A), 322 (C), 344 (A), 358 (T), 369 (G), 371 (C), 411 (G), 423 (C), 426 (C), 427 (A), 428 (G), 432 (T), 438 (T), 457 (G), 463 (C), and 472 (G).

Culture characteristics — Colonies on OA attaining 80–90 mm diam after 2 wk at 25 °C, aerial mycelium, cottony to hispid, white, pale olivaceous grey to olivaceous black in the centre buff to the periphery, margin effuse; reverse olivaceous buff, to olivaceous grey in the centre paler to the periphery. On MEA attaining 90 mm diam after 1 wk at 25 °C, slightly elevated, aerial mycelium cottony, white to olivaceous buff, margin effuse; reverse cinnamon to umber.

Habitat — *Sannantha (Baeckea) virgata* and *Theobroma cacao*.

Distribution — Australia, Brazil.

Additional material examined. AUSTRALIA, Queensland, Cairns, on stem lesion of *Sannantha (Baeckea) virgata*, 6 Mar. 1990, J.L. Alcorn LF90/985, BRIP 16943a = CBS 141030 = ATCC 200215.

Notes — The conidia observed in the holotype of *M. suttonii* are very similar to those described in *M. terrestris* (Table 2). *Mycoleptodiscus suttonii* is mainly proposed based on the phylogenetic differences using sequences of four loci. The sequences generated from two cultures placed it in a highly supported clade (100/0.99), related to the *M. terrestris* clade

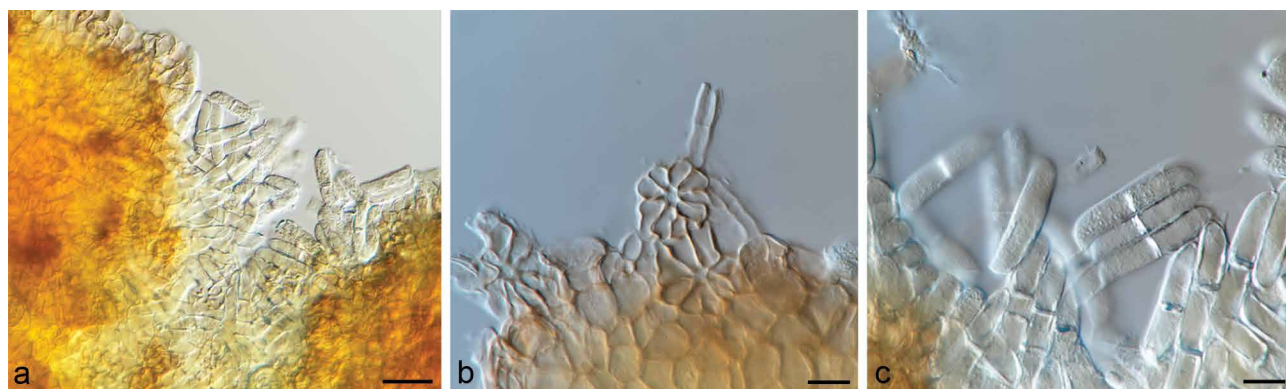


Fig. 8 *Mycoleptodiscus suttonii* sp. nov. holotype CBS H-14851. a. Sporodochia and conidia; b. sporodochia; c. conidia. — Scale bars: a = 50 µm, b–c = 10 µm.

(Fig. 1). After using several culture media, different plant tissues, and incubation conditions, no sporulation was observed in culture.

***Mycoleptodiscus terrestris* (Gerd.) Ostaz., Mycologia 59: 970. 1967**

Basionym. *Leptodiscus terrestris* Gerd., Mycologia 45: 552. 1953.

Synonym. *Mycoleptodiscus sphaericus* Ostaz., Mycologia 59: 971. 1967.

Typus. USA, Virginia, Illinois, Urbana, Agronomy South Farm of the Illinois Agricultural Experiment Station, isolated from a disease root of *Trifolium pratense*, 1951, J.W. Gerdemann (lectotype ILL31238 of *Leptodiscus terrestris*, iso-lectotype BPI 403851, not seen; culture ex-type CBS 231.53).

Illustrations — See Gerdemann 1953, Ostazeski 1967.

Conidiomata sporodochium-like, superficial, developing radially from central cell to form a thin stroma, one cell layer thick, peltate, often fusing to form irregular plates 100–200 × 86–144 µm, pale to dark brown. *Conidiogenous cells* evanescent. *Conidia* 1(–2)-septate, cylindrical, 20–43 × 4.5–9 µm, hyaline, with pale yellow contents, often becoming brown as the spores age, usually with a filamentous, unbranched appendage at each end, 8–18 µm long, or lacking one appendage, produced in a mucous, pale yellow to brown mass. *Sclerotia* spherical to fusiform, black, up to 1 mm diam (adapted from Gerdemann 1953, Ostazeski 1967).

Culture characteristics — Colonies on OA attaining 90 mm diam after 2 wk at 25 °C, aerial mycelium scarce, cottony, white, glabrous in the centre, greyish yellow green, if sclerotia are produced the colony is glabrous with olivaceous grey spots, margin effuse, diffusible pigment yellow green; reverse greyish yellow green, or pale grey olivaceous to black. On MEA attaining 90 mm diam after 1 wk at 25 °C, slightly elevated, aerial mycelium cottony, white to mouse grey, margin effuse; reverse cinnamon, umber or olivaceous grey.

Habitat — Root rot of *Trifolium pratense* (Gerdemann 1953), on decaying roots of *Lotus corniculatus* (Ostazeski 1967), black pepper roots (Watanabe et al. 1997), endophytic in *Myrangium spicatum* (Shearer 2001), *M. propinquum* and *Potamogeton cheesemanii* (Hofstra et al. 2012).

Distribution — Dominican Republic, New Zealand, USA.

Additional material examined. USA, on decaying roots of *Lotus corniculatus*, 1967, S.A. Ostazeski (culture ex-type of *Mycoleptodiscus sphaericus* IMI 159038 = ATCC 18104).

Notes — *Mycoleptodiscus terrestris* was first introduced as *L. terrestris* for a fungus causing root rot in red clover and other *Fabaceae* in the USA (Gerdemann 1953). The genus, however, was invalid because the name had been previously used for

a flagellate alga, and Ostazeski (1967) proposed *Mycoleptodiscus*, to accommodate *L. terrestris*, and introduced a new species, *M. sphaericus*. *Mycoleptodiscus sphaericus* differed from *M. terrestris* only in its sclerotial size, being larger in *M. terrestris*, and the presence of only apical conidial appendages in *M. sphaericus* (Table 2). Phylogenetically, the ex-type strains of both species are grouped in the same clade, suggesting that those subtle morphological differences are intraspecific variations. In our study, both strains remained sterile in culture and the production of sclerotia was only observed in IMI 159038.

***Neomycoleptodiscus* Hern.-Restr., J.D.P. Bezerra & Crous, gen. nov.** — MycoBank MB829829.

Etymology. Name reflects a morphological similarity with the genus *Mycoleptodiscus*.

Type species. *Neomycoleptodiscus venezuelense* Hern.-Restr., J.D.P. Bezerra & Crous.

Hyphae smooth, hyaline to pale brown. *Conidiomata* sporodochium-like, superficial, often fusing to form irregular plates, brown. *Conidiogenous cells* ampulliform to doliiform, angular in face view, dark brown, smooth, with a circular aperture situated in the upper side. *Conidia* 1-septate, cylindrical, hyaline, guttulate, with a filamentous appendage at each end, produced in a mucous pale yellow to brown mass. *Sclerotia* not observed. *Appressoria* not observed.

***Neomycoleptodiscus venezuelense* Hern.-Restr., J.D.P.**

Bezerra & Crous, *sp. nov.* — MycoBank MB828990; Fig. 9

Etymology. Named after the country, Venezuela, where it was found.

Typus. VENEZUELA, on leaf litter of *Gynerthera caribensis*, 25 Nov. 1997, R.F. Castañeda-Ruiz (holotype designated here CBS H-23881, culture ex-type CBS 100519).

Hyphae septate, smooth, hyaline to pale brown. *Conidiomata* superficial, often fusing to form irregular plates, 24–125 × 17–104 µm, brown. *Conidiogenous cells* ampulliform to doliiform, *textura angularis* in face view, 5–11 × 4–6.5 µm, dark brown, smooth, with a circular aperture situated in the upper side, 1–2 µm. *Conidia* 1-septate, cylindrical, 18–27 × 3–5 µm, hyaline, guttulate, with a filamentous appendage at each end, straight, 6.5–13 µm long, produced in a mucous pale yellow to brown mass. *Sclerotia* not observed. *Appressoria* not observed.

Culture characteristics — Colonies on OA attaining 20 mm diam after 1 wk at 25 °C, aerial mycelium scarce, cottony, zonate centre pale mouse grey, orange, pale luteous to buff to the periphery, margin effuse; reverse orange in the centre, pale luteous to buff to the periphery. On MEA attaining 24–27 mm

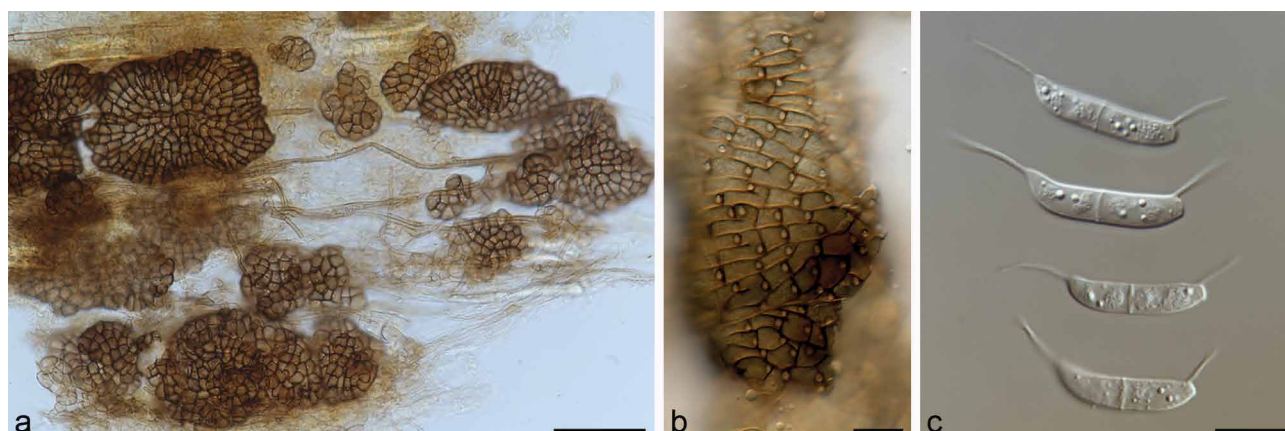


Fig. 9 *Neomycoleptodiscus venezuelense* gen. & sp. nov. ex-type CBS 100519. a–b. Sporodochia and conidiogenous cells; c. conidia. — Scale bars: a = 50 µm, others = 10 µm.

diam after 1 wk at 25 °C elevated, aerial mycelium velvety, mouse grey in the centre, darker to the periphery, margin effuse; reverse iron grey.

Habitat — Leaf litter of *Gyranthera caribensis*.

Distribution — Venezuela.

Notes — Based on phylogenetic inference in this study, a strain previously identified as *M. terrestris*, formed a single lineage, close to '*M. endophyticus*' and *Neocochlearomyces chromolaenae*, and distant to the *Mycoleptodiscus* s.str. clade (Fig. 1). Therefore, the monotypic genus *Neomycoleptodiscus* is hereby introduced. *Neocochlearomyces* can be distinguished from *Neomycoleptodiscus* by the presence of a setiform conidiophore bearing an apical fan-like conidiogenous region with inconspicuous loci and aseptate conidia (Crous et al. 2018). *Neomycoleptodiscus* is distinguished from *Mycoleptodiscus* by subtle morphological differences. In *Mycoleptodiscus*, conidiogenous cells are brown, with *textura globulosa* in face view with conidia with recurved ends (Hofstra et al. 2012), while in *Neomycoleptodiscus* conidiogenous cells are dark brown, and conidia are curved at the apex, and truncate at the base. *Neomycoleptodiscus venezuelense* is similar to *M. disciformis*, but it has smaller conidial appendages (Table 2).

Sordariomycetes, Magnaporthales, Magnaporthaceae

Omnidemptus P.F. Cannon & Alcorn, Mycotaxon 51: 483. 1994

Type species. Omnidemptus affinis P.F. Cannon & Alcorn.

Hyphae hyaline to pale brown, smooth, septate. *Ascomata* superficial, perithecial, ostiolate, pyriform, with a long neck; peridium of *textura angularis* composed of dark brown cells; hamathecium composed of thin-walled, septate paraphyses. *Asci* bitunicate, 8-spored, cylindric-clavate, short-stalked, with an obtuse apex, apical pore. *Ascospores* 1–3-septate, biseri-ate, fusiform, centrally swollen, hyaline. *Conidiomata* absent or sporodochium-like, irregularly shaped, aggregations, pale to dark brown. *Conidiogenous cells* phialidic, ampulliform or elongated, cylindrical, clavate or ellipsoid, dark brown, smooth, with a circular aperture enclosed by a cylindrical to flared col-

larette. *Conidia* dry, 1–2(–3)-septate, commonly asymmetrically 2-septate, falcate, hyaline, guttulate. *Appressoria* entire or lobed, mid-olivaceous brown, smooth (adapted from Cannon & Alcorn 1994).

Notes — Cannon & Alcorn (1994) introduced *Omnidemptus* as the sexual morph of *Mycoleptodiscus*, and described the asexual morph of *M. affinis*. Based on similarities of the ascomata and ascus features, the presence of appressoria, and the affinity for monocotyledons host, the authors suggested that *Omnidemptus* was related to *Buergenerula*, *Gaeumannomyces*, and *Magnaporthe* (Cannon & Alcorn 1994). After the multi-locus phylogenetic analyses, *Omnidemptus* was shown to belong to the *Magnaporthaceae* (Luo & Zhang 2013, Klaubauf et al. 2014). Subsequently, many authors assumed that *Mycoleptodiscus* was also phylogenetically positioned in *Magnaporthaceae*, because of the connection with *Omnidemptus*.

In our study phylogenetic inferences clearly showed that *Omnidemptus* is different from *Mycoleptodiscus*, the latter is placed in the *Muyocopronaceae* (*Dothideomycetes*). The phylogenetic inference using representative sequences of genera in *Magnaporthaceae* (Fig. 2), resolved *Omnidemptus* as a fully supported independent lineage. *Omnidemptus* has ascospores narrowly fusoid and its asexual morph is mycoleptodiscus-like. *Omnidemptus* is hereby formally separated from *Mycoleptodiscus*, and *M. lunatus* is transferred to *Omnidemptus*.

Omnidemptus affinis P.F. Cannon & Alcorn, Mycotaxon 51: 483. 1994 — Fig. 10

Synonym. Mycoleptodiscus affinis P.F. Cannon & Alcorn, Mycotaxon 51: 485. 1994.

Typus. AUSTRALIA, Queensland, Wooford, Stony Creek State Forest, on leaf spot of *Panicum effusum*, 19 May 1990, V.P. Cooper (holotype BRIP 17195a, isotype IMI 353435, culture ex-type BRIP 17195a = CBS 141031 = ATCC 200212).

Illustration — See Cannon & Alcorn (1994).

Hyphae hyaline to pale brown, smooth, septate, 2–5.5 µm diam. *Ascomata* superficial perithecial, ostiolate, pyriform, body

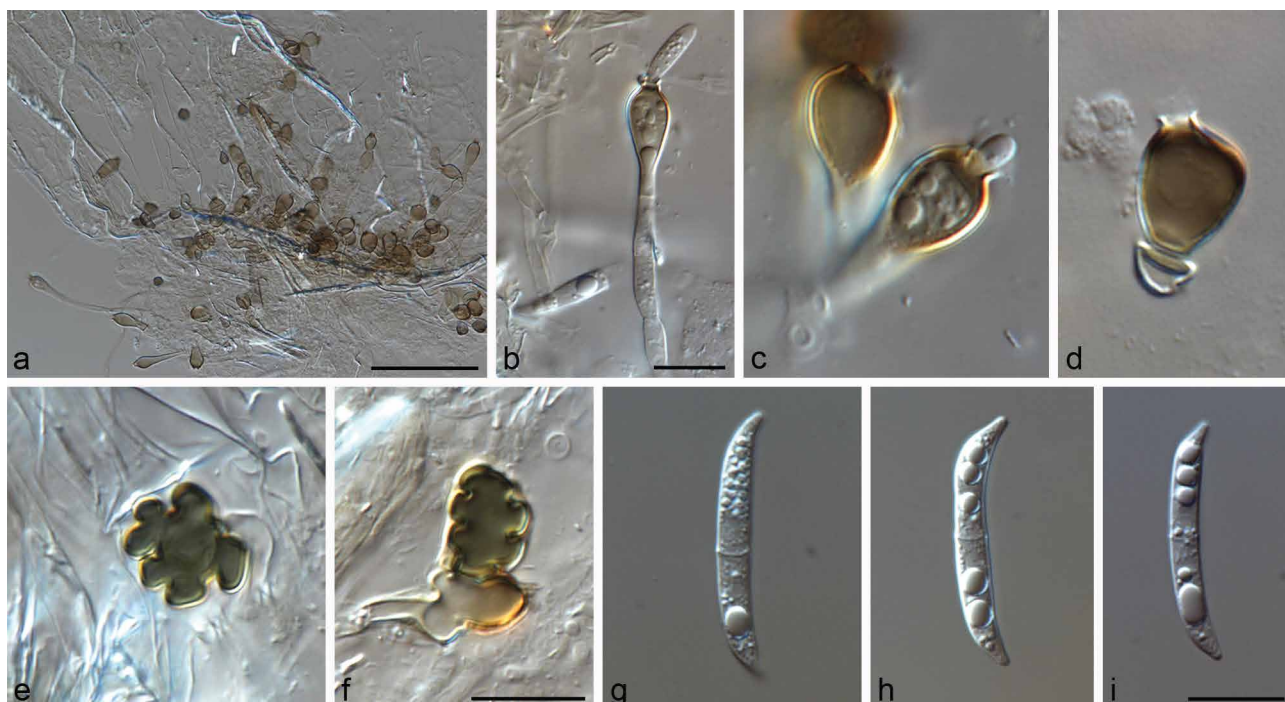


Fig. 10 *Omnidemptus affinis* ex-type CBS 141031. a–d. Conidiogenous cells; e–f. appressoria; g–i. conidia. — Scale bars: a = 50 µm, others = 10 µm, f applies to c–f, i applies to g–i.

145–205 µm diam, dark brown and glabrous, neck 100–250 µm long, 80–110 µm wide at the base and tapering gradually to 40–60 µm wide at the apex, dark brown and densely hairy, with hairs up to 60 × 2 µm; peridium composed of several layers of dark brown fairly thick-walled, angular cells, 6–10 µm diam; hamathecium with paraphyses 3–6 µm diam, very thin-walled, septate, sometimes deliquescing at maturity, paraphyses not observed. *Asci* cylindric-clavate, short-stalked, sometimes evanescent at the base, fairly thick-walled but without discernible layers, the apex obtuse, with an apical pore 2–3 µm diam and c. 4 µm deep, with a small ring at the base which stains dark blue in Melzer's reagent, usually 8-spored but not infrequently 4-spored, 54–68 × 10–13 µm. *Ascospores* usually 1–3-septate, the medium septum usually placed slightly below the widest point, biseriate, at first narrowly fusiform, sometimes with the end slightly swollen, the central portion usually swelling into an ellipsoidal central bulge, thin-walled, hyaline, without gelatinous sheaths or appendages. *Conidiomata* absent or sporodochium-like, irregularly shaped, 50–160 µm diam. *Conidiogenous cells* ampulliform, 7–12 µm diam, or elongated, cylindrical, clavate or ellipsoid, 11–22 × 6–10 µm, rounded to somewhat angular in face view, dark brown, smooth, with a circular aperture 2–3 µm diam enclosed by a cylindrical to flared collarete 3–4 µm diam. *Conidia* 1–2(–3)-septate, commonly asymmetrically 2-septate, with the first septum median and the second in the upper half, occasionally in the lower half, falcate, thin-walled, bluntly pointed at the extremities, the base sometimes with an abrupt change in contour to short pedicel-like extension, lacking polar or lateral appendages, 21–30 × 3–4 µm, hyaline, guttulate, smooth. *Appressoria* developed by germinating conidia, with outline entire or usually moderately to deeply lobed, 7.5–14 × 5–8.5(–11) µm and with germ pore 1.8–2 µm diam, mid-olivaceous brown, smooth (adapted from Cannon & Alcorn 1994).

Habitat — On *Panicum effusum* (Cannon & Alcorn 1994).

Distribution — Australia.

Additional material examined. AUSTRALIA, Queensland, Woodford, Stony Creek State Forest, on leaf spot of *Panicum effusum*, 19 May 1990, V.P. Cooper (culture ex-type of *Mycoleptodiscus affinis* BRIP 17195b = CBS 141032).

Notes — *Omnidemptus affinis* resembles *O. lunatus* in having septate conidia without appendages. Nevertheless, *O. lunatus* has conidia with a middle septum, which generally taper gradually towards the base (Sutton & Alcorn 1985), whereas in *O. affinis* conidia are narrowed more or less abruptly at the extremities and commonly 2-septate (Table 2). Furthermore, they are slightly narrower than those of *O. lunatus*.

Omnidemptus graminis Hern.-Restr., Gené & Guarro, *sp. nov.* — MycoBank MB828991; Fig. 11

Etymology. Name refers to the host family, *Gramineae* (= *Poaceae*), from which this species was collected.

Typus. SPAIN, Navarra, Robledal de Orgi, leaf of unidentified grass, Mar. 2012, M. Hernández-Restrepo & J. Capilla (holotype designated here CBS H-21887, culture ex-type CBS 138107 = FMR 12415).

Hyphae septate, hyaline to pale brown, smooth, 1–3 µm wide. *Conidiomata* absent or sporodochium-like, irregularly shaped, effuse, punctiform, dark brown to black. *Conidiogenous cells* ampulliform, subglobose, angular in face view, 10–14 µm diam, brown, smooth, with a cylindrical collarete, 1 × 3 µm. *Conidia* (0–)1-septate, falcate, bluntly pointed at the ends, 11–23 × 3–4 µm, hyaline, guttulate. *Appressoria* brown, smooth, multi-lobed, 10–15 × 7.5–10 µm, with 1–2 germ pores, 1–3 µm diam. *Sexual morph* unknown.

Culture characteristics — Colonies on OA attaining 30–40 mm diam after 1 wk at 25 °C, zonate, centre cottony, pale mouse grey, periphery glabrous, mouse grey, margin effuse;

reverse mouse grey. On MEA attaining 18–20 mm diam after 1 wk at 25 °C, elevated, cottony, vinaceous buff, margin rhizoid; reverse black in the centre, white to the periphery.

Habitat — On grass leaves.

Distribution — Spain.

Notes — *Omnidemptus graminis* is distinguished from *O. affinis* and *O. lunatus* by its smaller conidia (Table 2).

Omnidemptus lunatus (B. Sutton & Alcorn) Hern.-Restr., J.D.P. Bezerra & Crous, *comb. nov.* — MycoBank MB828992

Basionym. *Mycoleptodiscus lunatus* B. Sutton & Alcorn, Trans. Brit. Mycol. Soc. 84: 441. 1985.

Typus. AUSTRALIA, Queensland, Peregian Beach, on leaf spot of *Carpobrotus glaucescens*, 1982, J.L. Alcorn 8231b (holotype IMI 271703, not seen; culture ex-type IMI 271703 = BRIP 13852).

Illustration — See Sutton & Alcorn (1985).

Conidiomata sporodochium-like, flat, effuse, irregular and variable in shape, sometimes linear, consisting of a few to 30 grouped conidiogenous cells, pale to medium brown. *Conidiogenous cells* ampulliform to doliiform or sometimes lageniform, 10.5–13 × 6.5–11 µm, pale brown, smooth, the circular aperture 1.5–2 µm diam, surrounded by a distinct, ragged collarete, 3–4.5 µm diam. *Conidia* medially 1-septate, falcate, 24.5–32 × 3.5–4.5 µm, tapered gradually to the obtuse to truncate base, apex slightly prolonged but not constituting an appendage, hyaline, often guttulate (adapted from Sutton & Alcorn 1985). *Sexual morph* unknown.

Habitat — On leaves of *Carpobrotus glaucescens* (Sutton & Alcorn 1985).

Distribution — Australia.

Notes — *Omnidemptus lunatus* is morphologically similar to asexual morphs of *Omnidemptus* in having conidia lacking appendages, and conidiogenous cells with a distinct collarete. The phylogenetic relationship of *O. lunatus* will require assessment in the future.

EXCLUDED OR DOUBTFUL SPECIES

Mycoleptodiscus brasiliensis B. Sutton & Hodges, Nova Hedwigia 27: 694. 1976

Typus. BRAZIL, Maranhão, São Luís, on dead leaves of *Eucalyptus* sp., 24 June 1975, C.S. Hodges (holotype IMI 196481e, not seen).

Illustration — See Sutton & Hodges (1976).

Hyphae intracellular, septate, hyaline to pale brown, branched. *Conidiomata* sporodochium-like, superficial, 30–45 µm diam, dark brown. *Conidiogenous cells* ampulliform to doliiform or cylindrical, 11–17.5 × 5–11.5 µm, dark brown, smooth, each with a single distinct circular aperture in the upper wall and a flared or recurved collarete up to 3 µm long, 6 µm wide. *Conidia* medially 1-septate, cylindrical, straight, base obtuse, apex rounded, 17–19 × 4–4.5 µm, hyaline, guttulate, with a subapical, unbranched and recurved appendage, 19–27 µm long. *Sexual morph* unknown (adapted from Sutton & Hodges 1976).

Habitat — On dead leaves of *Eucalyptus saligna* and *Eucalyptus* sp. (Sutton & Hodges 1976) and *Quercus xalapensis* (Abarca et al. 2006).

Distribution — Brazil, Mexico, USA.

Notes — *Mycoleptodiscus brasiliensis* might belong to a different genus since the conidiogenous cells have a flared collarete and conidia are cylindrical tapering to an obtuse base with only one subapical recurved appendage. These morphological characters do not fit with the *Mycoleptodiscus* concept.

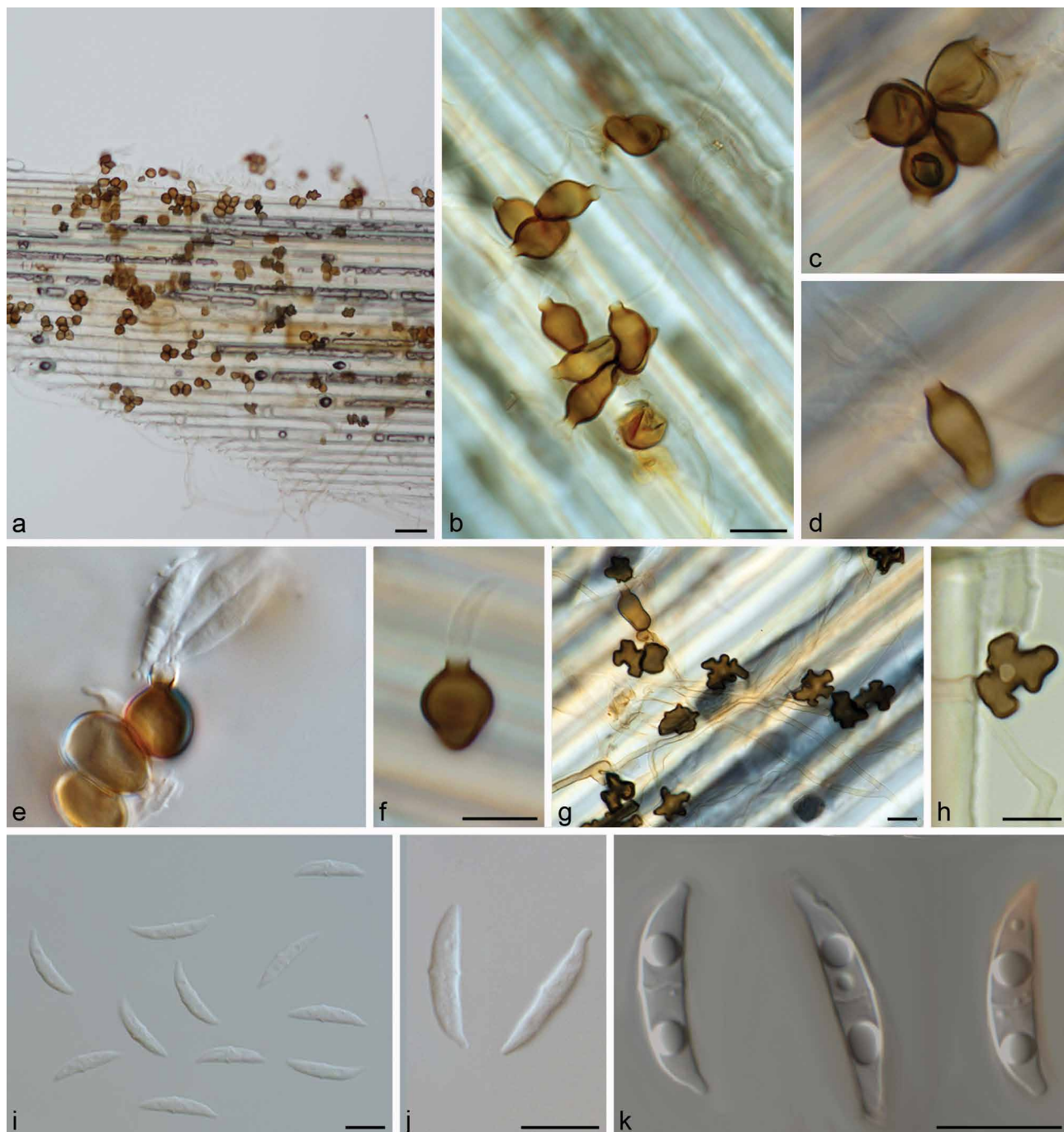


Fig. 11 *Omnidemptus graminis* sp. nov., holotype CBS H-21887. a. Conidiogenous cells and appressoria in natural substrate; b–f. conidiogenous cells; g–h. appressoria; i–k. conidia. — Scale bars: a = 50 µm, others = 10 µm, f applies to c–f.

***Mycoleptodiscus disciformis* Matsush., Matsushima Mycol. Mem. 7: 58. 1993**

Typus. PERU, Loreto, 'Rio Monanti', decaying leaf of 'Oje' (folk name of *Ficus* sp.) (*Moraceae*), 1991 (holotype MFC-1P143, not seen).

Illustration — See Matsushima (1993).

Hyphae smooth, hyaline to pale brown. *Conidiomata* sporodochium-like, discoid, more or less circular, (85–)100–250(–430) µm diam, solitary, later confluent, composed of two layers, a lower layer of rectangular sterile cells, pale olive, and an upper stratum with rectangular or quadratic, conidiogenous cells, 4–7 × 3–5 µm wide, dark brown. *Conidia* medially 1-septate, cylindrical, slightly asymmetrical, 17.5–25 × 4–5 µm, apex acute, base truncate, hyaline, smooth, with appendages at both ends, unbranched, 5–8 µm long, aggregating in a white mass in the top of the conidiomata (adapted from Matsushima 1993). *Sexual morph* unknown.

Habitat — Decaying leaves of *Moraceae* species (Matsushima 1993) and leaf litter (Schoenlein-Crusius et al. 2006, Grandi & Silva 2010).

Distribution — Brazil and Peru.

Notes — *Mycoleptodiscus disciformis* is comparable with *N. venezuelense*, in having more or less discoid conidiomata, cylindrical, 1-septate conidia, and conidial appendages at both ends. They can be distinguished by the size of their conidial appendages, which are smaller in *M. disciformis* (Table 2).

***Mycoleptodiscus endophyticus* Tibpromma & K.D. Hyde, MycoKeys 33: 49. 2018**

Typus. THAILAND, Ranong, Muang, on healthy leaves of *Freycinetia* sp. (*Pandanaceae*), 3 Dec. 2016, S. Tibpromma FE101 (holotype MFLU 18-0001, not seen).

Notes — *Mycoleptodiscus endophyticus* was introduced based on molecular data of LSU, SSU, and *tef1* sequences (Tibpromma et al. 2018). Our phylogenetic analysis demonstrates that this taxon does not belong to *Mycoleptodiscus* s.str. It nested in a subclade (71/0.98) related to CBS 100519, which is described here as a new genus. Given the absence of morphological characters, however, we prefer not to introduce any taxonomic changes until a more accurate study of the available reference material can be carried out.

Mycoleptodiscus minimus (Berk. & M.A. Curtis) Vanev, Proc. Kon. Ned. Akad. Wetensch. C 86: 433. 1983

Basionym. *Discosia minima* Berk. & M.A. Curtis, Grevillea 25: 7. 1874.

Typus. USA, Alabama, Beaumont, on leaves of *Ilex*, 1897 (holotype of *Discosia minima* 5113 Herb. Berk., not seen).

Illustration — See Vanev (1983).

Hyphae immersed, intracellular, brown. **Conidiomata** sporodochium-like, superficial, generally rounded in outline, 40–85 µm diam, dark brown. **Conidiogenous cells** radially arranged from the centre towards the periphery, angular (rectangular to irregular), 5–8.5 × 3.5–7 µm, brown, conidiogenous locus circular, 1–1.5 µm diam, without collarette. **Conidia** aseptate, cylindrical, tapered at both ends, straight or slightly curved at the ends, 20–25(–29) × 3.5–4 µm, hyaline, often guttulate, with appendages at both ends, unbranched, straight, up to 8 µm long (adapted from Vanev 1983). **Sexual morph** unknown.

Habitat — On leaves of *Ilex opaca* and *Ilex* sp. (Vanev 1983). **Distribution** — USA.

Notes — *Mycoleptodiscus minimus* is similar to *M. disciformis* and *M. terrestris* in having cylindrical conidia with apical appendages at both ends. Nevertheless, *M. minimus* is distinguished from both species by its aseptate conidia (Table 2).

Mycoleptodiscus stellatisporus K. Ando, Czech Mycol. 49: 3. 1996

Typus. AUSTRALIA, Queensland, Kuranda, isolated from soil, 1989, K. Ando (holotype TNS-F-180375 as '*stellatosporus*', not seen).

Illustration — See Ando (1996).

Hyphae septate, dark brown near the conidiomata, pale brown to hyaline when distant, 1.5–4.5 µm diam. **Conidiomata** sporodochium-like, varying from a few combined conidiogenous cells to large aggregations, sometimes rounded in outline but usually variable in shape and size due to the confluence, mid to dark brown. **Conidiogenous cells** ampulliform to doliiform, cylindrical or deltoid, 4–9.5 × 2.5–5.5 µm, dark brown, smooth, with a single distinct circular aperture in the upper wall surrounded by a flared collarette 0.5–1.5(–2.5) µm diam. **Conidia** aseptate, pentagonal, long isosceles triangular, rhomboid or of irregular shape, with rounded apices, 4.5–7.5 × 4–5.5 µm, with a truncate base (c. 1 µm wide), hyaline, smooth, with single appendages at each distal apex, up to 11 µm long, c. 0.5 µm wide (adapted from Ando 1996). **Sexual morph** unknown.

Habitat — Soil (Ando 1996).

Distribution — Australia.

Notes — The conidial shape of *M. stellatisporus* is triangular to pentagonal with 3–4 appendages, differing notably from all the species described in *Mycoleptodiscus* and related genera. The stellate conidia and phialidic conidiogenous cells arranged in conidiomata resembles those of *Nawawia malaysiana* which is placed in *Chaetosphaeriales* (Crous et al. 2009).

DISCUSSION

This study provides morphological and molecular data to facilitate the circumscription of *Mycoleptodiscus*. Phylogenetic analyses confirmed that taxa with mycoleptodiscus-like fungi do not constitute a monophyletic lineage in the *Magnaporthales* (*Sordariomycetes*), as previously suggested (Thongkantha et al. 2009, Klaubauf et al. 2014). The core of *Mycoleptodiscus* resides within *Muyocoprionales* (*Dothideomycetes*), confirming that *Mycoleptodiscus* and *Omniemptus* are unrelated genera as suggested by Luo & Zhang (2013).

Among *Muyocoprionaceae*, the majority of species previously included in *Mycoleptodiscus* grouped in a well-supported lineage that we recognise as *Muyocopron*. This is distinct from the *Mycoleptodiscus* lineage, which includes the type species of the genus, *M. terrestris*. *Muyocopron*, for which the previous description was based only on the sexual morph (Spegazzini 1881, Saccardo 1883, Von Arx & Müller 1975, Lumbsch & Huhndorf 2007, Hyde et al. 2013, Pang et al. 2013), has been redefined in accordance with the one fungus one name principles to accommodate also asexually reproducing species. Therefore, seven new combinations are proposed (*Mu. atromaculans*, *Mu. coloratum*, *Mu. geniculatum*, *Mu. laterale*, and *Mu. taiwanense*) including two with new names (*Mu. freycineticola* and *Mu. sahnii*), and two new species (*Mu. alcornii* and *Mu. zamiae*). Furthermore, *Muyocoprionaceae* and *Muyocoprionales* are emended to include the asexual genera: *Arxiella*, *Leptodiscella*, *Neocochlearomyces*, *Muyocopron*, *Mycoleptodiscus*, *Paramycoleptodiscus*, and *Neomycoleptodiscus*.

Our study shows that conidial morphology, conidiomatal development, and conidiogenous cells are important features in delimiting *Mycoleptodiscus* and related genera in *Muyocoprionales*. The newly defined *Mycoleptodiscus* comprises *M. suttonii* and *M. terrestris*. Morphologically, *Mycoleptodiscus* s.str. is characterised by having sporodochium-like conidiomata, conidiogenous cells without or with inconspicuous collarette, and 0–2-septate, cylindrical conidia with appendages at one or both ends. Some species also develop sclerotia in both natural substrate and in culture and appressoria with a pore surrounded by radial lines (Gerdemann 1953, Ostazeski 1967, Alcorn 1994). Species of this genus has been isolated mainly from roots and leaves of plants collected in Australia, Brazil, and the USA (Gerdemann 1953, Ostazeski 1967, this study). The new genus *Neomycoleptodiscus* is practically indistinguishable from *Mycoleptodiscus*, however, phylogenetically it was located in a distant lineage.

Species relocated in *Muyocopron* are characterised by sporodochium-like conidiomata, conidiogenous cells with a flared collarette, and lunate to broadly lunate conidia with appendages at both ends, while in some species lateral appendages are also present, and appressoria entire or with a few lobes and inconspicuous pore. *Muyocopron* asexual morphs have been isolated mainly from leaf spots, as endophytes or saprobes on plant material, mainly from Australia and the USA (Sutton & Alcorn 1985, 1990, Alcorn 1994, Cannon & Alcorn 1994). Interestingly, clinical isolates causing mycosis in humans were placed in *Mu. laterale*, suggesting that previous identifications of '*Mycoleptodiscus indicus*' as the etiological agent of mycosis in cats, dogs, and humans were incorrect (Padhye et al. 1995, Hull et al. 1997, Garrison et al. 2008, Dewar & Sigler 2010, Metry et al. 2010, Koo et al. 2012).

Species that are excluded from *Mycoleptodiscus* are *M. affinis* and *M. lunatus*, which were relocated in *Omniemptus*. *Omniemptus* retains mycoleptodiscus-like asexual morphs, but they differ from *Mycoleptodiscus* and *Muyocopron* in having sporodochium-like conidiomata that are usually less compacted, falcate conidia lacking appendages, and phylogenetically

related to *Magnaporthaceae* (Luo & Zhang 2013, Klaubauf et al. 2014).

Since the original cultures or ex-type strains are not available for *M. brasiliensis*, *M. disciformis*, *M. minimus*, and *M. stel-latisporus*, and since they are morphologically different from the concept of *Mycoleptodiscus* as here redefined, we prefer to treat them as excluded or doubtful species. Although the generic placement could not be resolved for all *Mycoleptodiscus* species in this study, the separation of *Mycoleptodiscus* from *Muyocopron* and *Omnidemptus* represents an important step in resolving the taxonomy of these genera. The newly defined mycoleptodiscus-like morphology sheds new light in the evolution of species in these genera. To identify species of *Muyocopron*, *Mycoleptodiscus*, and related genera, molecular identification is highly recommended because of the overlapping morphological characters, or poor sporulation with inconsistencies in the production of conidial appendages.

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REFERENCES

- Abarca GH, Mota RMA, Mena-Portales J, et al. 2006. Adiciones al conocimiento de la diversidad de los hongos conidiales del bosque mesófilo de montaña del estado de Veracruz. II. Acta Botanica Mexicana 77: 15–30.
- Alcorn JL. 1994. Appressoria in Mycoleptodiscus species. Australian Systematic Botany 7: 591–603.
- Ando K. 1996. A new species of Mycoleptodiscus from Australia. Czech Mycology 49: 1–5.
- Andrioli WJ, Conti R, Araújo MJ, et al. 2014. Mycoleptones A–C and polyketides from the endophyte Mycoleptodiscus indicus. Journal of Natural Products 77: 70–78.
- Andrioli WJ, Silva TM, Silva VB, et al. 2012. The fungal metabolite eugenitin as additive for Aspergillus niveus glucoamylase activation. Journal of Molecular Catalysis B: Enzymatic 74: 156–161.
- 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.
- Bezerra JDP, Santos MGS, Svedese VM, et al. 2012. Richness of endophytic fungi isolated from Opuntia ficus-indica Mill. (Cactaceae) and preliminary screening for enzyme production. World Journal of Microbiology and Biotechnology 28: 1989–1995.
- Bezerra JL, Ram A. 1986. A crosta-negra da baunilha (Vanilla fragrans) causada por Mycoleptodiscus indicus (Moniliales, Hyphomycetes). Fitopatologia Brasileira 11: 717–724.
- Bills GF, Polishook JD. 1992a. A new species of Mycoleptodiscus from living foliage of Chamaecyparis thyoides. Mycotaxon 43: 453–460.
- Bills GF, Polishook JD. 1992b. Recovery of endophytic fungi from Chamaecyparis thyoides. Sydowia 44: 1–12.
- Campbell J, Ferrer A, Raja HA, et al. 2007. Phylogenetic relationships among taxa in the Jahnuales inferred from 18S and 28S nuclear ribosomal DNA sequences. Canadian Journal of Botany 85: 873–882.
- Cannon PF, Alcorn JL. 1994. Omnidemptus affinis gen. et. sp. nov., teleomorph of Mycoleptodiscus affinis sp. nov. Mycotaxon 51: 483–487.
- Crous PW, Groenewald JZ, Lee SS. 2009. Fungal Planet 41 Nawawia malaysiana. Persoonia 23: 194–195.
- Crous PW, Luangsa-ard JJ, Wingfield MJ, et al. 2018. Fungal Planet description sheets: 785–867. Persoonia 41: 238–417.
- Crous PW, Wingfield MJ, Richardson DM. 2014. Fungal Planet description sheets: 281–319. Persoonia 33: 212–289.
- Crous PW, Wingfield MJ, Richardson DM. 2016. Fungal Planet description sheets: 400–468. Persoonia 36: 316–458.
- De Gruyter J, Aveskamp MM, Woudenberg JH, et al. 2009. Molecular phylogeny of Phoma and allied anamorph genera: towards a reclassification of the Phoma complex. Mycological Research 113: 508–519.
- De Hoog GS, Guarro J, Gené J, et al. 2000. Atlas of Clinical Fungi. 2nd ed. Centraalbureau voor Schimmelcultures, Utrecht.
- Dewar CL, Sigler L. 2010. Fungal arthritis of the knee caused by Mycoleptodiscus indicus. Clinical Rheumatology 29: 1061–1065.
- Garrison AP, Procop GW, Vincek V, et al. 2008. A case of subcutaneous Mycoleptodiscus indicus infection in a liver transplant recipient successfully treated with antifungal therapy. Transplant Infectious Disease 10: 218–220.
- Gerdemann JW. 1953. An undescribed fungus causing a root rot of red clover and other Leguminosae. Mycologia 45: 548–554.
- Grandi RAP, Silva P. 2010. Caracterização morfológica de fungos conidiais decompositores de folheto provenientes de Cubatão, SP, Brasil. Hoehnea 37: 769–775.
- Hawksworth DL, Crous PW, Redhead SA, et al. 2011. The Amsterdam declaration on fungal nomenclature. IMA Fungus 2: 105–112.
- Hawksworth DL, Kirk PM, Sutton BC, et al. 1995. Ainsworth & Bisby's dictionary of the fungi. CABI, Wallingford, England.
- He X, Han G, Lin Y, et al. 2012. Diversity and decomposition potential of endophytes in leaves of a Cinnamomum camphora plantation in China. Ecological Research 27: 273–284.
- Hernández-Restrepo M, Groenewald JZ, Elliott ML, et al. 2016a. Take-all or nothing. Studies in Mycology 83: 19–48.
- Hernández-Restrepo M, Schumacher RK, Wingfield MJ, et al. 2016b. Fungal Systematics and Evolution: FUSE 2. Sydowia 68: 193–230.
- Hofstra D, Rendle D, Clayton J. 2012. First record of the fungus Mycoleptodiscus terrestris from native milfoil and pondweed in New Zealand. Australasian Mycologist 30: 1–4.
- Hofstra DE, Edwards T, Clayton JS, et al. 2009. New record of Mycoleptodiscus terrestris from New Zealand. New Zealand Journal of Botany 47: 411–415.
- Hull W, McNamara T, Ireland G. 1997. Subcutaneous phaeohyphomycosis due to Mycoleptodiscus lateralis in a cat. In: Anais do XXV Congresso Brasileiro de Medicina Veterinária, XIII Congresso Estadual de Medicina Veterinária, II Congresso de Medicina Veterinária do Cone Sul. Gramado, Rio Grande do Sul, Brasil.
- Hyde KD, Jones EBG, Liu JK, et al. 2013. Families of Dothideomycetes. Fungal Diversity 63: 1–313.
- Katoh K, Standley DM. 2013. MAFFT: multiple sequence alignment software version 7: improvements in performance and usability. Molecular Biology and Evolution 30: 772–780.
- Klaubauf S, Tharreau D, Fournier E, et al. 2014. Resolving the polyphyletic nature of Pyricularia (Pyriculariaceae). Studies in Mycology 79: 85–120.
- Koo S, Sutton DA, Yeh WW, et al. 2012. Invasive Mycoleptodiscus fungal cellulitis and myositis. Medical Mycology 50: 740–745.
- Liu JK, Hyde KD, Jones EBG, et al. 2015. Fungal diversity notes 1–110: taxonomic and phylogenetic contributions to fungal species. Fungal Diversity 72: 1–197.
- Lumbsch HT, Huhndorf SM. 2007. Outline of Ascomycota – 2007. Myconet 13: 1–58.
- Luo J, Walsh E, Zhang N. 2014. Four new species in Magnaporthaceae from grass roots in New Jersey Pine Barrens. Mycologia 106: 580–588.
- Luo J, Zhang N. 2013. Magnaporthiopsis, a new genus in Magnaporthaceae (Ascomycota). Mycologia 105: 1019–1029.
- Luttrell ES. 1951. Taxonomy of Pyrenomycetes. University of Missouri Studies 24: 1–120.
- Madrid H, Gene J, Cano J, et al. 2012. A new species of Leptodiscella from Spanish soil. Mycological Progress 11: 535–541.
- Mapook A, Hyde KD, Dai D-Q, et al. 2016a. Muyocopronales, ord. nov., (Dothideomycetes, Ascomycota) and a reappraisal of Muyocopron species from northern Thailand. Phytotaxa 265: 225–237.
- Mapook A, Hyde KD, Hongsanan S, et al. 2016b. Palawaniaceae fam. nov., a new family (Dothideomycetes, Ascomycota) to accommodate Palawania species and their evolutionary time estimates. Mycosphere 7: 1732–1745.
- Martínez-Luis S, Cherigo L, Higginbotham S, et al. 2011. Screening and evaluation of antiparasitic and in vitro anticancer activities of Panamanian endophytic fungi. International Microbiology 14: 95–102.
- Matsushima T. 1987. Matsushima Mycological Memoirs 7. Kobe, Japan. Published by the author.
- Matsushima T. 1993. Matsushima Mycological Memoirs 5. Kobe, Japan. Published by the author.
- Metry CA, Hoiem-Dalen PS, Maddox CW, et al. 2010. Subcutaneous Mycoleptodiscus indicus infection in an immunosuppressed dog. Journal of Clinical Microbiology 48: 3008–3011.

- Miller MA, Pfeiffer W, Schwartz T. 2012. The CIPRES science gateway: enabling high-impact science for phylogenetics researchers with limited resources. In: Proceedings of the 1st Conference of the Extreme Science and Engineering Discovery Environment: Bridging from the extreme to the campus and beyond: 1–8. Association for Computing Machinery, USA.
- Nelson LS, Shearer JF. 2008. Evaluation of triclopyr and *Mycoleptodiscus terrestris* for control of Eurasian watermilfoil (*Myriophyllum spicatum*). *Invasive Plant Science and Management* 1: 337–342.
- Nylander J. 2004. MrModeltest v2. Program distributed by the author. Evolutionary Biology Centre, Uppsala University.
- Ortega HE, Graupner PR, Asai Y, et al. 2013. *Mycoleptodiscus* A and B, cytotoxic alkaloids from the endophytic fungus *Mycoleptodiscus* sp. F0194. *Journal of Natural Products* 76: 741–744.
- Ostazeski SA. 1967. An undescribed fungus associated with a root and crown rot of birdsfoot trefoil (*Lotus corniculatus*). *Mycologia* 10: 970–975.
- Padhye AA, Davis MS, Reddick A, et al. 1995. *Mycoleptodiscus indicus*: a new etiologic agent of phaeohyphomycosis. *Journal of Clinical Microbiology* 33: 2796–2797.
- Paim ECA, Silveira AJ, Bezerra JL, et al. 2012. Etiologia do declínio de mangostanzeiros no sul da Bahia. *Revista Brasileira de Fruticultura* 34: 1074–1083.
- Pang K-L, Hyde KH, Alias SA, et al. 2013. Dyrolomycetaceae, a new family in the Dothideomycetes, Ascomycota. *Cryptogamie, Mycologie* 34: 223–232.
- Ramesh CH, Vijaykumar S. 2005. Studies of fresh water foam fungi of Uttara Kannada, Karnataka. *Indian Phytopathology* 58: 89–95.
- Rayner RW. 1970. A mycological colour chart. Commonwealth Mycological Institute, London, UK.
- Rehner SA, Buckley E. 2005. A *Beauveria* phylogeny inferred from nuclear ITS and EF1- α sequences: evidence for cryptic diversification and links to *Cordyceps* teleomorphs. *Mycologia* 97: 84–89.
- 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.
- Saccardo PA. 1883. *Sylloge Fungorum. Omnium hucusque cognitorum* 2: 658–661.
- Sahni VP. 1968. Deuteromycetes from Jabalpur III. *Mycopathologia Mycologia Applicata* 36: 267–288.
- Schoch CL, Crous PW, Groenewald JZ, et al. 2009. A class-wide phylogenetic assessment of Dothideomycetes. *Studies in Mycology* 64: 1–15.
- Schoch CL, Robbertse B, Robert V, et al. 2014. Finding needles in haystacks: linking scientific names, reference specimens and molecular data for Fungi. *Database (Oxford)* 2014: bau061.
- Schoch CL, Shoemaker RA, Seifert KA, et al. 2006. A multigene phylogeny of the Dothideomycetes using four nuclear loci. *Mycologia* 98: 1041–1052.
- Schoenlein-Crusius IH, Milanez AI, Trufem SFB, et al. 2006. Microscopic fungi in the Atlantic rainforest in Cubatão, São Paulo, Brazil. *Brazilian Journal of Microbiology* 37: 267–275.
- Shearer JF. 2001. Recovery of endophytic fungi from *Myriophyllum spicatum*. ERDC TN-APCRP-BC-03: 1–11.
- Shearer JF, Jackson MA. 2006. Liquid culturing of microsclerotia of *Mycoleptodiscus terrestris*, a potential biological control agent for the management of hydrilla. *Biological Control* 38: 298–306.
- Spear ER. 2017. Phylogenetic relationships and spatial distributions of putative fungal pathogens of seedlings across a rainfall gradient in Panama. *Fungal Ecology* 26: 65–73.
- Spegazzini C. 1881. Fungi argentini additis nonnullis brasiliensibus montevidensibusque. *Pugillus quartus (Continuacion)*. *Anales de la Sociedad Científica Argentina* 12: 97–117.
- Stamatakis A. 2014. RAxML version 8: a tool for phylogenetic analysis and post-analysis of large phylogenies. *Bioinformatics* 30: 1312–1313.
- Stenroos S, Laukka T, Huhtinen S, et al. 2010. Multiple origins of symbioses between ascomycetes and bryophytes suggested by a five gene phylogeny. *Cladistics* 26: 281–300.
- Su ZZ, Mao LJ, Li N, et al. 2013. Evidence for biotrophic lifestyle and biocontrol potential of dark septate endophyte *Harpophora oryzae* to rice blast disease. *PLoS One* 8: e61332.
- Suetrong S, Schoch CL, Spatafora JW, et al. 2009. Molecular systematics of the marine Dothideomycetes. *Studies in Mycology* 64: 155–173.
- Sun X, Guo LD, Hyde KD. 2011. Community composition of endophytic fungi in *Acer truncatum* and their role in decomposition. *Fungal Diversity* 47: 85–95.
- Sutton BC. 1973. Pucciniopsis, *Mycoleptodiscus* and *Amerodiscosiella*. *Transactions of the British Mycological Society* 60: 525–536.
- Sutton BC, Alcorn JL. 1985. Undescribed species of *Crinitospora* gen. nov., *Massariothea*, *Mycoleptodiscus* and *Neottiosporina* from Australia. *Transactions of the British Mycological Society* 84: 437–445.
- Sutton BC, Alcorn JL. 1990. New species of *Mycoleptodiscus* (Hyphomycetes). *Mycological Research* 94: 564–566.
- Sutton BC, Hodges CS. 1976. *Eucalyptus* microfungi: *Mycoleptodiscus* species and *Pseudotrachyella* gen. nov. *Nova Hedwigia* 27: 693–700.
- Tamura K, Stecher G, Peterson D, et al. 2013. MEGA 6: Molecular Evolutionary Genetics Analysis. Version 6.0. *Molecular Biology and Evolution* 30: 2725–2729.
- Thongkantha S, Jeewon R, Vijaykrishna D, et al. 2009. Molecular phylogeny of Magnaporthaceae (Sordariomycetes) with a new species, *Ophioceras Chiangdaoense* from *Dracaena loureioides* in Thailand. *Fungal Diversity* 34: 157–173.
- Tibpromma S, Hyde KD, Bhat JD, et al. 2018. Identification of endophytic fungi from leaves of Pandanaceae based on their morphotypes and DNA sequence data from southern Thailand. *Mycosphaerella* 33: 25–67.
- Tibpromma S, McKenzie EHC, Karunaratna SC, et al. 2016. *Muyocoprion garethjonesii* sp. nov. (Muyocoprionales, Dothideomycetes) on *Pandanus* sp. *Mycosphere* 7: 1480–1489.
- Vaidya G, Lohman DJ, Meier R. 2011. SequenceMatrix: concatenation software for the fast assembly of multigene datasets with character set and codon information. *Cladistics* 27: 171–180.
- Vanev SG. 1983. *Mycoleptodiscus minimus* (Berk. & Curt.) Vanev, comb. nov. Koninklijke Nederlandse Academie van Wetenschappen, Proceedings C 86: 433–435.
- Verma U, Charudattan R. 1993. Host range of *Mycoleptodiscus terrestris*, a microbial herbicide candidate for Eurasian watermilfoil, *Myriophyllum spicatum*. *Biological Control* 3: 271–280.
- Voglmaier H, Gardienet A, Jaklitsch WM. 2016. *Asterodiscus* and *Stigmatodiscus*, two new apothecial dothideomycete genera and the new order Stigmatodiscales. *Fungal Diversity* 80: 271–284.
- Von Arx JA, Müller E. 1975. A re-evaluation of the bitunicate ascomycetes with keys to families and genera. *Studies in Mycology* 9: 1–159.
- Vu D, Groenewald M, De Vries M, et al. 2019. Large-scale generation and analysis of filamentous fungal DNA barcodes boosts coverage for kingdom fungi and reveals thresholds for fungal species and higher taxon delimitation. *Studies in Mycology* 92: 135–154.
- Watanabe T, Moya JD, González JL, et al. 1997. *Mycoleptodiscus terrestris* from black pepper roots in the Dominican Republic. *Mycoscience* 38: 91–94.
- Whitton SR, McKenzie EHC, Hyde KD. 2012. Anamorphic fungi associated with Pandanaceae. In: Whitton SR, McKenzie EHC, Hyde KD (eds), *Fungi associated with Pandanaceae*. *Fungal Diversity Research Series* vol. 21: 125–353. Springer, Dordrecht.
- Woudenberg JHC, Hanse B, Van Leeuwen GCM, et al. 2017. *Stemphylium* revisited. *Studies in Mycology* 87: 77–103.
- Wu HX, Schoch CL, Boonmee S, et al. 2011. A reappraisal of Microthyriaceae. *Fungal Diversity* 51: 189–248.
- Xu X-H, Su Z-Z, Wang C, et al. 2015. The rice endophyte *Harpophora oryzae* genome reveals evolution from a pathogen to a mutualistic endophyte. *Scientific Reports* 4: 5783.
- Yuan ZL, Zhang CL, Lin FC, et al. 2010. Identity, diversity, and molecular phylogeny of the endophytic mycobiota in the roots of rare wild rice (*Oryza granulata*) from a nature reserve in Yunnan, China. *Applied and Environmental Microbiology* 76: 1642–1652.
- Zhang N, Zhao S, Shen Q. 2011. A six-gene phylogeny reveals the evolution of mode of infection in the rice blast fungus and allied species. *Mycologia* 103: 1267–1276.