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

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**Key words**

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Dothideomycetes  
fungal pathogen  
*Mycoleptodiscus*  
mycoses  
near taxa  
Sordariomycetes

**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 *Muyocopronales* (*Dothideomycetes*), together with *Arxilla*, *Leptodiscella*, *Muyocopron*, *Neochelarnomyces*, and *Paramycoleptodiscus*. *Mycoleptodiscus* terestris, the type species, and *M. sphaericus* are reduced to synonyms, and one new species is introduced, *M. suttonii*. *Mycoleptodiscus* atromaticans, *M. coloratus*, *M. freycinetiae*, *M. geniculatus*, *M. indicus*, *M. lateralis* (including *M. unilateralis* and *M. variabilis* as its synonyms) and *M. taiwanensis* belong to *Muyocopron* (*Muyocopronales*, *Dothideomycetes*), and *M. affinis* and *M. lunatus* to *Omnidemptus* (*Magnaporthales*, *Sordariomycetes*). Based on phylogenetic analyses we propose *Muyocopron* alcornii sp. nov., a fungus associated with leaf spots on *Epandrum* sp. (*Ochidaceae*) in Australia, *Muyocopron* zamiace 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 venezuelensis* gen. & sp. nov. is introduced for a genus similar to *Mycoleptodiscus in Muyocopronaceae*.

**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, cym- 
drical-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 *Ophiocер- aceae* 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 *Muyocopronales*, 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 *Muyocopron* (*Muyocopronales*). *Muyocopron* was proposed by Spegazzini (1881), re-described by Saccardo (1883), and its taxonomi- cal placement treated initially in *Microthyriaceae* (Von Arx & Müller 1975, Lumbsch & Huhndorf 2007) and later in *Muyocopronaceae* (Hyde et al. 2013, Pang et al. 2013, Mapook et al. 2016a). *Muyocopron* is characterised by pseudo-thyriothelial, superficial, flattened, carbonaceous, brittle ascomata, with pseudoparaphyses that are longer than the asc and ellipsoid to ovate, unicellular ascospores (Hyde et al. 2013, Mapook et al. 2016a).
| Species | Old names | Strains | Other collections | GenBank accession numbers | References |
|---------|-----------|---------|-------------------|--------------------------|------------|
| *Acroserpum compressum* | | | | | |
| *A. marmoreum* | M151‡ | EU940161 | – | – | – | Stenroos et al. (2010) |
| | M152‡ | EU940162 | – | – | – | Stenroos et al. (2010) |
| *Anxienella dolichandrae* | CBS 138857 | CPC 22951 | NR_137930 | KP000477 | – | MK492710 MK495954 Crous et al. (2014), this study |
| | A. terrestris | CBS 268.65 | MH685856 | MH670201 | – | – | Vu et al. (2019) |
| *Asterodiscus tamariscis* | CBS 136918 | L113 | KU234100 | KU234110 | KU234132 | Voglmayr et al. (2016) |
| *Conyrespa cassiolaea* | CBS 100822 | – | GU301808 | GU301742 | GU301802 | Schoch et al. (2009) |
| *Dothidea sambuci* | DAOM 231.303 | AF10-ID 274 | NR_111220 | AY154861 | – | DQ522854 DQ847606 Schoch et al. (2014) |
| *Dylobalomyces citeriosmesis* | NTOU 3636‡ | – | KEC692156 | KEC692156 | – | KC82157 Pang et al. (2013) |
| *Jahrunia australis* | R88_1‡ | JN942334 | EF175655 | – | – | Campbell et al. (2007) |
| | A. sargentiflorae | A402_1B‡ | JN942349 | EF175661 | – | – | Campbell et al. (2007) |
| | A. seychelensis | SS2113‡ | – | EF175655 | – | – | Campbell et al. (2007) |
| | J. siamensis | SS81.02‡ | – | EF175666 | – | – | Campbell et al. (2007) |
| *Leptodiscella africana* | CBS 400.65 | NR_145369 | MH670275 | – | – | MK492711 MK495955 Madid et al. (2012), Vu et al. (2019), this study |
| | *L. melli* | CBS 144927 | LR025180 | LR025181 | – | – | Crous et al. (2018) |
| *Mycoleptodiscus alcornii* | BRIP 43897 | CBS 141314 | MK487735 | MK487708 | – | MK492712 MK495956 This study |
| *Mu. atroaculans* | Mycoleptodiscus atroaculans | MFLUCC 14-1108 | KU726965 | – | – | Ky225778 Mapook et al. (2016a, b) |
| *Mu. castanopsis* | MFLUCC 14-1109 | – | NR_160197 | – | – | MK492710 MK495958 This study |
| *Mu. coloratum* | Mycoleptodiscus coloratus | CBS 720.95 | – | – | – | MK492714 MK495958 This study |
| *Mu. diptercarpici* | MFLUCC 14-1103 | – | KU726966 | – | – | MK492719 MK495963 Mapook et al. (2016a, b) |
| | Mycoleptodiscus diptercarpici | – | – | – | – | – |
| | Mycoleptodiscus geniculatus | CBS 721.95 | MK487737 | MK487711 | – | MK492715 MK495959 This study |
| *Mu. laterale* | Mycoleptodiscus lateralis | CBS 141029 | BRIP 16247, ATCC 200213 | MK487738 | MK487712 | – | MK492716 MK495960 This study |
| | Mycoleptodiscus unilateralis | IMI 324533 | MK487740 | MK487713 | – | MK492717 MK495961 This study |
| | Mycoleptodiscus variabilis | CBS 719.95 | BRIP 16983, ATCC 96451 | MK487740 | MK487714 | – | MK492718 MK495962 This study |
| | Mycoleptodiscus sp. | CBS 141033 | BRIP 20066 | MK487741 | MK487715 | – | MK492719 MK495963 This study |
| | Mycoleptodiscus sp. | URM7802 | – | MK487742 | MK487716 | – | MK492720 MK495964 This study |
| | Mycoleptodiscus sp. | URM7801 | – | MK487743 | MK487717 | – | MK492721 This study |
| | Mycoleptodiscus indicus | CBS 127677 | UAMH 10746 | MK487744 | MK487718 | – | MK492722 MK495965 This study |
| | Mycoleptodiscus sp. | CBS 145310 | UTHSC D1-17-18 | MK487745 | MK487719 | – | MK492723 MK495966 This study |
| | Mycoleptodiscus sp. | CBS 145315 | UTHSC D1-17-23 | MK487746 | MK487720 | – | MK492724 MK495967 This study |
| | Mycoleptodiscus sp. | CBS 145313 | UTHSC D1-17-21 | MK487747 | MK487721 | – | MK492725 MK495968 This study |
| | Mycoleptodiscus sp. | CBS 145309 | UTHSC D1-17 | MK487748 | MK487722 | – | MK492726 MK495969 This study |
| | Mycoleptodiscus sp. | CBS 145314 | UTHSC D1-17-22 | MK487749 | MK487723 | – | MK492727 MK495970 This study |
| | Mycoleptodiscus sp. | CBS 145311 | UTHSC D1-17-19 | MK487750 | MK487724 | – | MK492728 This study |
| | Mycoleptodiscus sp. | CBS 145312 | UTHSC D1-17-20 | MK487751 | MK487725 | – | MK492729 MK495971 This study |
| | Mycoleptodiscus sp. | CBS 145316 | UTHSC D1-17-24 | MK487752 | MK487726 | – | MK492730 MK495972 This study |
| | Mycoleptodiscus sp. | FMR13797 | MK874615 | MK874616 | – | MK875802 MK875803 This study |
| *Mu. lithocarpi* | MFLUCC 10-0041 | – | – | – | – | Wu et al. (2011) |
| | MFLUCC 14-1106 | – | – | – | – | Mapook et al. (2016a, b) |
| *Mu. zamiae* | Mycoleptodiscus sp. | CBS 203.71 | – | – | – | MK492727 This study |
| ‘*Mycoleptodiscus endophytics*’ | Mycoleptodiscus sp. | MFLUCC 17-0545 | NR_158860 | MG649496 | – | MG649495 Tibbromma et al. (2018) |
| *Mycoleptodiscus suttonii* | Mycoleptodiscus terrestris | CBS 276.72 | MK487753 | MK487728 | – | MK492732 MK495974 This study |
| | Mycoleptodiscus terrestris | CBS 141030 | BRIP 16943, ATCC 200215 | – | – | MK492729 This study |

**Table 1** GenBank accession numbers included in the alignments of Dothideomycetes and Sordariomycetes.
| Species† | Old names | Strains‡ | Other collections | GenBank accession numbers§ | References |
|----------|-----------|----------|-------------------|---------------------------|------------|
| M. terrestris | Leptodiscus terrestris | CBS 231.53† | IMI 159038 | MK487754 – MK487770 – MK492734 – MK495976 | This study |
| Neocamarosporium betae | Mycoleptodiscus sphaericus | CBS 109410 | IMI 159038 | MK487755 – MK487771 – MK492735 – MK495977 | This study |
| Neomycoleptodiscus venezuelense | Mycoleptodiscus terrestris | CBS 100519 | IMI 159038 | MK487756 – MK487772 – MK492736 – MK495978 | This study |
| Paramycoleptodiscus albizziae | Mycoleptodiscus terrestris | CBS 141320 | CPC 27552 | MK487757 – MK487773 – MK492737 – MK495979 | This study |
| Saccobella rhizophora | Mycoleptodiscus sphaericus | CBS 109410 | KY940790 | GU754178 – GU349075 | De Gruyter et al. (2009), Schoch et al. (2009), Woudenberg et al. (2017) |
| Stigmatodiscus enigmaticus | Mycoleptodiscus terrestris | CBS 116.29 | CPC 27552 | MK487758 – MK487774 – MK492738 – MK495980 | Schoch et al. (2006) |
| Sydowiella polyspora | Mycoleptodiscus terrestris | CBS 100519 | IMI 159038 | MK487759 – MK487775 – MK492739 – MK495981 | Schoch et al. (2006) |

Sordariomycetes

| Species† | Old names | Strains‡ | Other collections | GenBank accession numbers§ | References |
|----------|-----------|----------|-------------------|---------------------------|------------|
| Buergenerula spartinae | Bussabanomyces longisporus | CBS 125232† | CPC 27552 | MK487755 – MK487771 – MK492737 – MK495979 | This study |
| Falcorhiella oryzae | F. solani terrestrial | CBS 117.83† | IMI 353435 | MK487756 – MK487772 – MK492736 – MK495978 | This study |
| Gaeumannomyces graminis | G. graminis | CBS 116.29 | CPC 26033 | MK487757 – MK487773 – MK492737 – MK495979 | This study |
| G. medullaris | G. medullaris | CBS 117849† | JK5528S | MK484852 – MK484968 – MK485058 – – | Klaubauf et al. (2014) |
| Magnaporthe oryzae | Magnaporthe oryzae | CBS 117.83† | IMI 353435 | MK487756 – MK487772 – MK492736 – MK495978 | This study |
| Ma. oryzae | Ma. oryzae | CBS 117.83† | IMI 353435 | MK487756 – MK487772 – MK492736 – MK495978 | This study |
| Neogaeumannomyces tambusica | Neogaeumannomyces tambusica | CBS 117.83† | IMI 353435 | MK487756 – MK487772 – MK492736 – MK495978 | This study |
| Omnidemptus affinis | Mycoleptodiscus affinis | BRIP 17195a† | CPC 26033 | MK487757 – MK487773 – MK492737 – MK495979 | This study |
| O. graminis | O. graminis | CBS 138107† | IMI 353435 | MK487757 – MK487773 – MK492737 – MK495979 | This study |
| Pseudophialophora eragrostis | P. eragrostis | CM12m9 | CPC 26033 | MK487757 – MK487773 – MK492737 – MK495979 | This study |
| Pyricularia oryzae | P. oryzae | BRIP 17195b† | CPC 26033 | MK487757 – MK487773 – MK492737 – MK495979 | This study |
| Slopeiomyces cylindrosporus | Slopeiomyces cylindrosporus | CBS 60.75† | IMI 353435 | MK487757 – MK487773 – MK492737 – MK495979 | This study |

1. New species are in **bold italic**.
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, DAFM: 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: Mycothèque 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 nrRNA 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**.
Gerdemann (1953), when introducing Mycoleptodiscus (as Leptodiscus), demonstrated M. terestris to be a pathogen of herbaceous Fabaceae with economic interest, such as Glycine, Lespedeza, Lotus, Medicago, Mellilotus, Pismum, and Trifolium in the USA. Other Mycoleptodiscus species have also been reported to cause diseases of economically important plants, such as Alternaria, Carpotroctus, Cattleya, Dianella, Panicum, and Stypandra 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 (Martínez-Luis 1993), Arecaeus in Taiwan (Matsushima 1987), Fabaceae (including Lotus) and Zamia in the USA (Ostazeski 1967, Sutton 1973, Vaney 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 Freycinetia 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 Chamaeyparis thyoides (Bills & Poliakheh 1992a, b), the aquatic Myxophyta epiphytum in the USA (Shearer 2001), Desmotes incomparrabalis in Panama (Martínez-Luis et al. 2011, Ortega et al. 2013), Aeroc trunctum and Cinnamoomum camphora in China (Sun et al. 2011, He et al. 2012), Borriarea verticillata and Opunita ficus-indica in Brazil (Andrioli et al. 2012, Bezerra et al. 2012), and Freycinetia sp. in Thailand (Tibpromma et al. 2018). Mycoleptodiscus terestris has also been isolated as an endophyte from aquatic submerged 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) (Padyke 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 a 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. terestris 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 egugenit, 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 grammineous 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 N1 compound microscope, using a DS-R12 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 ± 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 (Katoh & 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, and rpb2, and tef1. Another phylogenetic analysis for Magnaporthes (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) ≥ 70 % from a ML search with 1 000 replicates and posterior probabilities (PP) ≥ 0.95. The sequences generated during this study and the alignments

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 ≥ 70 % and Bayesian posterior probability (PP) scores ≥ 0.95 are shown at the nodes. GenBank accession numbers are indicated in Table 1. 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 *Muyocopronales* (Dothideomycetes). While *M. affinis* and the strain CBS 138107, were similar to *Magnaporthales* (*Sordariomycetes*).

The first concatenated matrix contained a total of 3 364 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 *Muyocopronales*. 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. 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 *Neomycocleptodiscus venezuelense* gen. & sp. nov. A second clade (100/0.97), including *M. atomaculans*, *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 *Muyocron*. 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 *Muyocron* 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 2 882 characters (589 for ITS, 752 for LSU, 618 for *rpb2* and 127677 and the ex-type strains of *M. terrestris*, *M. variabilis*, and *M. lateralis* represented (100/0.99 PP) includes the ex-type sequences of *M. terrestris*, *M. variabilis*, and *M. lateralis*. 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* and the strain CBS 138107, were placed in *Magnaporthaceae*. *M. affinis* 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 ≥ 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.](image)
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 Muyocopronaceae (Muyocopronales, Dothideomycetes; Fig. 1), confirming previous results (Crous et al. 2018). Since the relationship of Muyocopron with all of these genera within the Muyocopronales 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 conidal 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. tawanensis, including mycoleptodiscus-like asexual morphs in Muyocopron.

Omnidemptus, 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

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

Type family. Muyocopronaceae K.D. Hyde.

Ascomata pseudo-thyrothecial, 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, ellipsoidal or broadly-ellipsoidal, curved to geniculate, usually with terminal and/or lateral appendages, hyaline. Conidia one-celled or septate, lunate, falcate, fusiform or fusoid-ellipsoidal, curved to geniculate, usually with terminal and/or lateral appendages, hyaline. Conidiomata 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 black-brown pseudoparenchymatous cells of textura epidermoidea, an inner layer comprised of pale brown cells of textura angularis; hamathecium of cylindrical to filiform, septate pseudoparaphyses. Ascospores aseptate, irregularly arranged, oval to obovoid with obtuse ends, brown. 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 comentinum 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 black-brown pseudoparenchymatous cells of textura epidermoidea, an inner layer comprised of pale brown cells of textura angularis; hamathecium of dense, septate pseudoparaphyses, longer than the ascii, immersed in mucilage and inclined towards the centre. Asci 8-spored, bitunicate/fissitunicate, pedicellate, with a small ocellar chamber. Ascospores aseptate, ellipsoidal to oblong-oval or obovoid, narrowly clavate or subcylindrical, sometimes uncinate, 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.

Notes — Muyocopron is an old name, based on M. corrientinum described from leaves of Oncidium in Argentina (Spegazzini 1881). Lutterl (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 Muyocopronaceae 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 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 ascii, immersed in mucilage and inclined towards the centre. Asci 8-spored, bitunicate/fissitunicate, pedicellate, with a small ocellar chamber. Ascospores aseptate, ellipsoidal to oblong-oval or obovoid, narrowly clavate or subcylindrical, sometimes uncinate, occasionally sigmoid or bluntly bifurcate, straight or curved.
| Species               | Strains and/or fungarium materials | Sporodochia (µm) | Conidiogenous cells | Conidia | Appressoria* (size in µm) | References |
|-----------------------|-----------------------------------|-----------------|---------------------|---------|---------------------------|------------|
| **Muyocopron alcornii** | BRIP 43879                         | 36–89 x 38–60   | 12.5–18 x 12–18.5   | 3–6 x 4.5–8 | Lunate, fusiform; 17.5–20 x 8–9 | 0–1 (–2) Apical and basal 3–5.5 | This study |
|                       | MUCL 34983                         | –               | 9.5–14.5 diam       | 2.5–4 x 2–7.5 | Broadly falcate or lunate; 15.5–23 x 6.5–8.5 | 0 Apical and basal 1–3 | Bills & Polishook (1992a) |
| **Muyocopron coloratum** | CBS 720.95                         | 25–165 x 16–125 | 17–25 x 13–19 (–21) | 3–10 x 5–8 | Broadly lunate to inequilateral oval-ellipsoidal; 16–27 x 8–13 (–16) | 0 Apical 2–8; basal 1–6 | Alcorn (1994) |
|                       | CBS 720.95                         | –               | 17–29 x 16.5–26     | 3.5–6 x 4–6 | Broadly lunate; 22–34 x 8–15 | 0 Apical 2–7; basal 0–5 | This study |
| **Muyocopron freycineticola** | IFRD 8995                         | 32–55 diam      | 9–18 x 6–12         | 2–2.5 x 1.5–3 | Broadly falcate to lunate; 11–15 x 4–4.5 | 0 Apical and basal 2–3 | Whitton et al. (2012) |
| **Muyocopron geniculatum** | CBS 721.95                         | Up to 126 diam  | 10–15 diam          | 3–12 x 3.5–6.5 | Lunate to fusiform or fusoid-ellipsoidal; 14–20 x 5.5–7.5 | 0 Apical 4–12.5; basal 1–10 | Alcorn (1994) |
|                       | CBS 719.95                         | –               | 10–24 x 10–15       | 1–2 x 3–5 | Lunate, fusiform; 16.5–22 x 8–9.5 | 0 Apical and basal 2–17; lateral 9–20 | This study |
| **Muyocopron laterale** | BRIP 16247                         | 25–160 x 20–150 | 9–16 diam           | 4–6 diam | Lunate, fusiform; 15–18 x 6–8 | 0 Apical (9–)15–24; basal 5–22.5; lateral 12–26 | Sutton & Alcorn (1990) |
|                       | Type Mu. lateralis                 |                 |                     |          |                           |            |
|                       | IMI 324533                         | 27–45 x 13–32   | 9–12.5 diam         | 3–4.5 diam | Lunate, fusiform; 15–20 x 6–8 | 0 Apical 7.5–12.5; basal 5–11; lateral 7–9 | This study |
|                       | Type Mu. unilateralis              |                 |                     |          |                           |            |
|                       | CBS 719.95                         | 125–370 x 100–225 | 14–24 x 9–16       | 4–6.5 diam | Lunate, fusiform; 15–25 x 5.5–8 | 0 Apical 3–21; basal 4–15; lateral 11–22 | Alcorn (1994) |
|                       | Type Mu. variabilis                |                 |                     |          |                           |            |
|                       | CBS 719.95                         | –               | 12–16 x 10–15       | 1–2 x 3–5 | Lunate, fusiform; 16.5–22 x 8–9.5 | 0 Apical and basal 2–17; lateral 9–20 | This study |
|                       | Type Mu. variabilis                |                 |                     |          |                           |            |
|                       | CBS 145315                         | –               | 12–19 x 7.5–11      | 3–4.5 diam | Lunate, fusiform; 16.5–21 x 5.5–7 | 0 Apical, basal and lateral 8–15.5 | This study |
| **Muyocopron sahnii** | IMI 108220                         | 200–300 diam    | –                   | –       | Lunate, fusiform; 4–10 x 1.7–3.3 | 0 One at each end | Sahni (1968) |
|                       | IMI 108220                         | 54–71 diam, 56–135 x 53–256 | 4.5–10.5 diam | –         | Lunate, fusiform; 13.5–14.5 x 5–6 | 0 Basal 3 | This study |
|                       | Several isolates                   | 30–100 diam     | 7–13 x 3.5–7        | Up to 3 long | Lunate, fusiform; 11–18.5 x 4.5–7.5 | 0 Apical 1–10; basal 0–6 | Sutton (1973) |
| 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) |                                      |
| **Muyocopron taiwanense**            | MFC-6T720                          | –                | 6–12 x 7–14         | Broadly falcate  | 0   | Apical and basal 1–3   | Matsushima (1987)                    |
|                                      |                                    |                  |                     | 12–21 x 5.5–7   |      |                        |                                      |
| **Muyocopron zamiiae**               | CBS 203.71                         | –                | 7.5–14 x 8.5–12     | Lunate, fusiform; | 0   | Apical 2.5–6; basal 0.75–5 | This study                           |
|                                     |                                    |                  | 1 x 2.5–3           | 16–20 x 5.5–6.5 |      |                        |                                      |
| *Mycoleptodiscus brasiliensis*       | IMI 196481e                        | 30–45 diam       | 11–17.5 x 5–11.5    | Cylindrical;    | 1   | Apical 19–27           | Sutton & Hodges (1976)               |
|                                     |                                    |                  | 3 x 6               | 17–19 x 4–4.5   |      |                        |                                      |
| *Mycoleptodiscus disciformis*        | MFC-1P143                          | 85–430 diam      | 4–7 x 3–5           | Cylindrical;    | 1   | Apical and basal 5–8   | Matsushima (1993)                    |
|                                     |                                    |                  |                     | 17.5–25 x 4–5   |      |                        |                                      |
| *Mycoleptodiscus minimus*            | Holotype Discosia minima           | 40–85 diam       | 5–8.5 x 3.5–7       | Cylindrical;    | 0   | Apical and basal, up to 8 | Vaneev (1983)                        |
|                                     | 5113 Herb. Berk.                   |                  |                     | 20–25(–29) x 3.5–4 |      |                        |                                      |
| **Mycoleptodiscus terrestris**       | BPI 403851                         | 200–800 diam     | Evanscent           | Cylindrical;    | 1   | Apical and basal 8.7–18 | Gerdemann (1953)                     |
|                                     | (ILL31238)                         |                  |                     | 20–34.8 x 4.4–7 |      |                        |                                      |
|                                      | ATCC 18104                         | 110–187 x 86–144 | Obsolete            | Cylindrical;    | 1(–2) | Apical 0–14           | Ostazeski (1967)                     |
|                                     | Type of M. sphaericus               |                  |                     | 28.8–43.2 x 5–9 |      |                        |                                      |
|                                      |                                     |                  |                     | 24.3–34         |      |                        |                                      |
| **Neomycoleptodiscus venezuelensis** | CBS 100519                         | 24–125 x 17–104  | 5–11 x 4–6.5        | Cylindrical;    | 1   | Apical and basal 6.5–13 | This study                           |
|                                     |                                     |                  |                     | 18–27 x 3–5     |      |                        |                                      |
| **Omnidemptus affinis**              | BRIP 17195b                        | 50–160 diam      | 7–12 diam [ampulliform]; 11–22 x 6–10 [elongated] | Falcate; 21–30 x 3–4 | 1–2(–3) | –                      | Cannon & Alcorn (1994)               |
|                                      | Type Mycoleptodiscus affinis       |                  | 3–4 x 2–3           |                        |      |                        |                                      |
| **Omnidemptus graminis**             | CBS 138107                         | –                | 10–14 diam          | Falcate; 11–23 x 3–4 | 1   | –                      | This study                           |
|                                     |                                     |                  | 1 x 3               |                        |      |                        |                                      |
| **Omnidemptus lunatus**              | IMI 271703                         | 10.5–13 x 6.5–11 | 3–4.5 diam          | Falcate; 24.5–32 x 3.5–4.5 | 1   | –                      | Sutton & Alcorn (1985)               |
|                                     |                                     |                  | 1.5–2 diam          |                        |      |                        |                                      |

* 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 Mycocordoticpus, 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 (Ostaszek 1967, Sutton & Hodges 1976, Sutton & Alcorn 1990, Matsushima 1993, Alcorn 1994). No sexual morph is currently known for Mycocordoticpus 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 Mycocondoticpus.

**Typus.** AUSTRALIA, Queensland, Logan (Greenbank), leaf spot (blight) of Epidendrum sp., 2004, L.I Forsberg 9R324 (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 2 wk at 25 °C, slightly elevated, cottony to hispid, buff to ochreous, margin effuse, diffusible pigment apricot; reverse dark amber 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.** Mycoleptodiscus 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, sub-globose 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-
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, Biboohra, 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 collarate 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 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 collarette, 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

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**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 Whittet al. 2012). Sexual morph unknown.

Habitat — Decaying leaves of Freycinetia sp. and F. scadens (Whittet al. 2012).

Distribution — Australia, Philippines.

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

**Myuco**

The annotations and figures are omitted for brevity. The text continues with descriptions of various species and their characteristics, including their conidiomata, conidiogenous cells, conidia, and habitat preferences. The text also includes notes and additional materials examined. The final paragraphs discuss the distribution, habitat, and notes on the species, concluding with the introduction of M. unilateralis 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. unilateralis 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. unilateralis, M. unilateralis, and M. variabilis grouped in a highly supported subclade (89/0.99) in Myuco**copron**}
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](image-url)  
*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.* <i>Amerodiscoscellia indica</i> V.P. Sahni, Mycopathol. Mycol. Appl. 36: 277. 1968.

*Synonyms.* <i>Mycotexcibis indicus</i> (V.P. Sahni) B. Sutton, Trans. Brit. Mycol. Soc. 69: 528. 1973.

*Pucciniopsis guarantitica* Speeg., Anales Soc. Ci. Argent. 26: 74. 1888. pro parte.

**Etymology.** Name after the Indian mycologist V.P. Sahni.

**Typus.** India, Jabalpur, on <i>Ixora parviflora</i>, 1964, V.P. Sahni (IMI 108220 holotype of <i>Amerodiscoscellia indica</i> V.P. Sahni).

**Hyphae** septate, pale brown to brown, smooth. *Conidiomata* sporodochial-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 collarette, 3 × 1.5–2.5 µm, brown. *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 <i>Passiflora edulis</i> var. <i>flavicarpa</i> and <i>P. edulis</i> (Sutton & Hodges 1976).

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

**Notes.** *Amerodiscoscellia indica* was first described from India causing leaf spots on <i>Ixora parviflora</i>. It was characterised by pycnidial, ostiolate conidiomata, and conidia with appendages at each end (Sahni 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 (<i>Cocos yatay</i>, <i>Cordyline</i>, <i>Chlorophyrum comosum</i>, <i>Grewia asiatica</i>, <i>Hippaeastrum</i>, <i>Hymenocallis arenicola</i>, <i>Roupellia grata</i>, and <i>Zamia</i>) and transferred this species to *Mycoleptodiscus*. 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* (Sahni 1968). During the present study, we re-examined the holotype of *A. indica* and confirmed that the conidiomata were sporodochial-like and the few conidia observed were larger than the measurements provided in the protologue (Sahni 1968) but smaller than those from Sutton (1973), with reduced conidal 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 *M. sahnii* are not completely known.

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

*Basionym.* <i>Mycoleptodiscus taiwanensis</i> Matsush., Matsushima Mycol. Mem. 5: 21. 1987.

**Typus.** Taiwan, Nan-Jen-Shan, on rotten leaf rachis of <i>Areca catechu</i>, 1986 (holotype MFC 67720, not seen).

**Illustration.** See Matsushima (1987).

**Hyphae** branched, septate, hyaline to pale brown, 1.5–4 µm wide. *Conidiomata* sporodochial-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 *Mycoleptodiscus* (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 fischeri*, date unknown, isol. S.A. Alferri Jr., No. 070-2273 (holotype CBS H-23882, culture ex-type CBS 203.71).

**Hyphae** septate, brown dark near the conidiomata, pale brown to hyaline when distant, smooth, 1.5–4 µm wide. *Conidiomata* sporodochial-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 collarette, 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.

**Cultural 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.

![Image 7](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. Affler 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 doliiform, brown, walled phialides. **Sclerotia** that are often produced both on the natural substrate and in culture (Ostazesky 1967). 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).

**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 (Ostazesky 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.

![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.](image)
(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 20 mm diam after 2 wk at 25 °C, aerial mycelium scarce, cottony, white, glabrous in the centre, greyish yellow green, with a circular aperture situated in the upper side, 1–2 µm, dark brown, smooth, with a filamentous appendage at each end, produced in a mucous pale yellow to brown mass. *Sclerotia* not observed. *Appressoria* not observed.

Neomycoleptodiscus Hern.-Restr., J.D.P. Bezerra & Crous, gen. nov. — MycoBank MB828929.

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 *Gyranthera 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 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.
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. discomiformis*, 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, biseriate, fusiform, centrally swollen, hyaline. *Conidiomata* absent or sporodochial-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 colarette. *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 ascocyst 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 *Magnaportheaceae* (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*. *Mycopropodium affinis* P.F. Cannon & Alcorn, *Mycotaxon* 51: 483. 1994 — Fig. 10

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

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**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 deliquescent at maturity, periphyses 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 collarette 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, 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 171995 = 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 Orgil, 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 collarette, 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

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

Typus. Australia, Queensland, Perenbah Beach, on leaf spot of Carpobrotus glaucescens, 1982, J.L. Alcorn 8231b (holotype IMI 271703, not seen; culture ex-type IMI 271703 = BRIP 13892).

Illustration — See Sutton & Alcorn (1985).

Conidiomata sporodochium-like, flat, effuse, irregular and variable in shape, sometimes linear, consisting of a few to 30 grouped conidigenous cells, pale to medium brown. Conidiogenous cells ampulliform to doliform 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 collarette, 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 collarette. 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 doliform 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 collarette 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 collarette 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.
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 *tsf1* sequences (Tibbomma 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) Vaney, 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 Vaney (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 Vaney 1983). Sexual morph unknown.

Habitat — On leaves of *Ilex opaca* and *Ilex sp.* (Vaney 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 distinguishable 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 ‘stellatiosporus’, 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 doliform, cylindrical or doliiform, 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 apexes, 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 *Muyocopronales* (*Dothideomycetes*), confirming that *Mycoleptodiscus* and *Omnidemptus* are unrelated genera as suggested by Luo & Zhang (2013).

Among *Muyocopronaceae*, 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 Arb & 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. genitalicum*, *Mu. laterale*, and *Mu. taiwanense*) including two with new names (*Mu. freycineticola* and *Mu. sahnii*), and two new species (*Mu. alcorni* and *Mu. zamiae*). Furthermore, *Muyocopronaceae* and *Muyocopronales* are emended to include the asexual genera: *Arxiella*, *Leptodiscella*, *Neocochlearomyces*, *Muyocopron*, *Mycoleptodiscus*, *Paramycoleptodiscus*, and *Omnidemptus*.

Our study shows that conidial morphology, conidiomatal development, and conidiogenous cells are important features in delimiting *Mycoleptodiscus* and related genera in *Muyocopronales*. 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 *Omnidemptus* 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 *Omnidemptus*. *Omnidemptus* 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-latiosporus, 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 Mycrocopron 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 Mycrocopron, 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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