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Pseudocercospora and allied genera associated with leaf spots of banana (*Musa* spp.)

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Abstract: The Sigatoka leaf spot complex on *Musa* spp. includes three major pathogens: *Pseudocercospora*, namely *P. musae* (Sigatoka leaf spot or yellow Sigatoka), *P. eumusae* (eumusae leaf spot disease), and *P. fijiensis* (black leaf streak disease or black Sigatoka). However, more than 30 species of *Mycosphaerellaceae* have been associated with Sigatoka leaf spots of banana, and previous reports of *P. musae* and *P. eumusae* need to be re-evaluated in light of recently described species. The aim of the present study was thus to investigate a global set of 228 isolates of *P. musae, P. eumusae* and close relatives on banana using multigene DNA sequence data [internal transcribed spacer regions with intervening 5.8S nrRNA gene (ITS), RNA polymerase II second largest subunit gene (*rpb2*), translation elongation factor 1-alpha gene (*tef1*), beta-tubulin gene (*tub2*), and the actin gene (*act*)] to confirm if these isolates represent *P. musae*, or a closely allied species. Based on these data one new species is described, namely *P. pseudomusae*, which is associated with leaf spot symptoms resembling those of *P. musae* on *Musa* in Indonesia. Furthermore, *P. eumusae, P. musae* and *P. fijiensis* are shown to be well defined taxa, with some isolates also representing *P. longispora.* Other genera encountered in the dataset are species of *Zasmidium* (Taiwan leaf speckle), *Metulocladosporiella* (Cladosporium leaf speckle) and Scolecobasidium leaf speckle.

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INTRODUCTION

Bananas (*Musa* spp.) originated from Indochina and South East Asia (Simmonds 1962), from where they spread across tropical and sub-tropical regions of the world, presently representing the fourth most economically important food crop after rice, wheat and maize (www.fao.org).

Bananas and plantains are, however, susceptible to several diseases that have been of serious concern to the industry, namely Fusarium wilt (Panama disease) caused by *Fusarium odoratissimum* (formerly *F. oxysporum* f. sp. *cubense* tropical race 4) (Maryani *et al.* 2019), Banana bunchy top virus (Stainton *et al.* 2015), and the Sigatoka leaf spot complex, which include the most serious leaf spot diseases of banana (Churchill 2011).

Species of the Sigatoka leaf spot complex have a confused taxonomic history, and were formerly treated in the genus *Mycosphaerella*, which was shown to be polyphyletic, representing numerous genera in the *Mycosphaerellaceae* (Crous *et al*. 2007, 2009, Videira *et al*. 2017), and in other families (Quaedvlieg *et al*. 2014). Species of the Sigatoka leaf spot complex are members of the genus *Pseudocercospora* (Arzanlou et al. 2008, Crous *et al*. 2013, Nakashima *et al*. 2016). Taxonomically, *Pseudocercospora* was formerly placed in the order *Capnodiales* in the class *Dothideomycetes*, which is the largest and most diverse class of ascomycetous fungi (Haridas *et al.* 2020). However, the *Capnodiales* represent sooty moulds that grow superficially on plant surfaces, and are associated with honeydew produced by insects, whereas the genera of plant pathogenic fungi formerly placed in *Capnodiales*, were shown to be members of the order *Mycosphaerellales* (Abdollahzadeh *et al*. 2020).

More than 30 mycosphaerella-like species have in the past been associated with leaf spot diseases of banana (see list below). The primary agents of the Sigatoka leaf spot complex found on banana include *P. musae* (previously: *Mycosphaerella musicola*) causal agent of Sigatoka leaf spot or yellow Sigatoka; *P. eumusae* (previously: *M. eumusae*) causal agent of the eumusae leaf spot disease, and *P. fijiensis* (previously: *M. fijiensis*) causal agent of black Sigatoka or black leaf streak disease, which is the most aggressive and predominant member of the Sigatoka lead spot complex worldwide. Phylogenetic reconstruction based on a set of 46 conserved single-copy genes strongly supported an earlier evolutionary radiation of *P. fijiensis* from *P. musae* and *P. eumusae* (between 15 to 40 MYA, Chang *et al*. 2016). Although

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these species can be distinguished based on differences in morphology and symptomatology, considerable overlap exists among them, making definite identification only possible by means of additional markers such as DNA sequence data (Arzanlou *et al*. 2008). Furthermore, several previous records of *P. musae* might in fact belong to the recently described *P. longispora*, while the variation within *P. eumusae* (Crous & Mourichon 2002, Arzanlou *et al.* 2008) also requires further analysis. Because the distribution and relative importance of the latter taxa remain insufficiently known, the aim of the present study was to investigate a global set of isolates to better elucidate the distribution of *Pseudocercospora* spp. associated with leaf spot diseases of banana.

MATERIALS AND METHODS

Isolates

The set of isolates studied is presented in Table 1. Isolates were sourced from the CBS and CIRAD collections and were collected from various countries. The isolates from the CIRAD collection were derived either from single conidia or ascospores as described in Zapater *et al*. (2008). They were assumed to belong to *P. musae*, *P. eumusae* or other species based on morphological observations in culture media or sequencing of the internal transcribed spacer regions with intervening 5.8S nrRNA gene (ITS) of the nrDNA operon. The isolates from CBS collection were also derived either from single conidia or ascospore as described by Crous *et al.* (1991) and Crous (1998). In the present study, colonies were sub-cultured on 2 % potato-dextrose agar (PDA), oatmeal agar (OA), MEA (Crous *et al*. 2019), autoclaved banana leaf on 2 % tap water agar (BLA), and incubated at 25 °C under continuous near-ultraviolet light to promote sporulation. Reference strains and specimens of the studied fungi are all maintained from now in the CBS culture collection (CBS) of the Westerdijk Fungal Biodiversity Institute (WI), Utrecht, the Netherlands.

DNA extraction, amplification (PCR) and phylogeny

Fungal mycelium (Table 1) was scraped from the agar surface of cultures with a sterile scalpel and genomic DNA was isolated using the Wizard® Genomic DNA Purification Kit (Promega Corporation, WI, USA) following the manufacturers' protocols. Eight loci were amplified following previously published protocols. First, the partial ITS region was sequenced for all isolates included in this study (for amplification conditions, see Fan *et al*. 2018). Amplification of the partial DNA-directed RNA polymerase II second largest subunit gene (*rpb2*), the partial translation elongation factor 1-alpha gene (*tef1*) and the partial beta-tubulin gene (*tub2*) followed Braun *et al.* (2018), while the amplification of the partial actin gene (*act*) followed Videira *et al*. (2016). The resulting fragments were sequenced in both directions using the respective PCR primers and the BigDye Terminator Cycle Sequencing Kit v. 3.1 (Applied Biosystems Life Technologies, Carlsbad, CA, USA); DNA sequencing amplicons were purified through Sephadex G-50 Superfine columns (Sigma-Aldrich, St. Louis, MO) in MultiScreen HV plates (Millipore, Billerica, MA). Purified sequence reactions were analysed on an Applied Biosystems 3730xl DNA Analyzer (Life Technologies, Carlsbad, CA, USA). The DNA sequences were analysed and consensus sequences were computed using SeqMan Pro v. 13 (DNASTAR, Madison, WI, USA).

The sequences for each gene region were subjected to megablast searches (Zhang *et al*. 2000) to identify closely related sequences in the NCBI's GenBank nucleotide database. Sequences of the individual loci were aligned using MAFFT v. 7 (http://mafft.cbrc.jp/alignment/server/index.html) (Katoh & Standley 2013), and the alignments were then manually edited in MEGA v. 7.0.21. Sequence Matrix v. 1.8 (http://www.ggvaidya.com/taxondna/) was used to concatenate the individual loci in various combinations. Phylogenetic trees on the combined datasets were generated using Bayesian analyses performed with MrBayes v. 3.2.7 (Ronquist *et al*. 2012) as explained in Braun *et al*. (2018) and *Pseudocercospora* individual gene trees were evaluated using distance and parsimony analyses with PAUP v. 4.0b10 (Swofford 2003). All resulting trees were printed with Geneious v. 11.1.5 3 (http://www.geneious.com, Kearse *et al.* 2012) and the layout of the trees was done in Adobe Illustrator v. CC 2017.

Morphology

Slide preparations were mounted in clear lactic acid or Shear's mounting fluid. Observations were made with a Nikon SMZ25 dissection microscope, and with a Zeiss Axio Imager 2 light microscope using differential interference contrast (DIC) illumination and images recorded on a Nikon DS-Ri2 camera with associated software. Colony characters and pigment production were noted after 2–4 wk of growth on MEA, PDA and OA (Crous *et al*. 2019) incubated at 25 °C. Colony colours (surface and reverse) were scored using the colour charts of Rayner (1970). Sequences derived in this study were deposited in GenBank (Table 1), the alignment in TreeBASE (www.treebase.org; study number 27043), and taxonomic novelties in MycoBank (www.MycoBank.org; Crous *et al*. 2004).

RESULTS

Phylogeny

Based on the blast results, the majority of strains belonged to *Pseudocercospora musae* (104 strains) and *Pseudocercospora eumusae* (48 strains), while other *Pseudocercospora* species included *Pseudocercospora fijiensis* (two strains), *Pseudocercospora longispora* (two strains) and five strains representing a novel *Pseudocercospora* species related to *Pseudocercospora musae* (Fig. 1). The remainder of the strains tentatively identified as *Mycosphaerella musae* based on symptomatology (seven strains), *Zasmidium musae* (five strains), *Scolecobasidium musicola* (= *Ochroconis musicola*) (four strains, Fig. 2), *Parapallidocercospora thailandica* (three strains), while one strain was identical to *Pantospora guazumae* and the last strain represented a *Penicillium* infection and was discarded from further analyses (Table 1).

Two Bayesian analyses were performed (Table 2); the first on a concatenated ITS/*act*/*tef1*/*rpb2* alignment of *Pseudocercospora* sequences (Fig. 1) and the second on a concatenated ITS/*act*/*tef1*/*tub2* alignment of *Scolecobasidium* sequences (Fig. 2). The *Pseudocercospora* phylogeny (Fig. 1) delimits four known species clades, namely *Pseudocercospora eumusae*, *Pseudocercospora fijiensis*, *Pseudocercospora longispora* and *Pseudocercospora musae*, with five strains from *Musa* (Indonesia) clustering in a

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Table 1. Collection information and GenBank accession numbers of strains included in this study. Taxonomic novelties and sequences generated in this study are shown in bold. n/a: not applicable.

Species	Collection number(s)[1]	Substrate including host, origin and collection year	GenBank accession number[2]		
			ITS	*act*	*tef1*; *rpb2*; *tub2*
Pseudocercospora eumusae	CBS 114824 = STE-U 4579 = CIRAD 1156, ex-type	*Musa*; France: Réunion; 2001	EU514238.1	LFZN01000053.1	LFZN01000037.1; LFZN01000034.1; –
	CBS 121378	*Musa*; Malaysia; –	EU514242.1	EU514305.1	–; –; –
	CBS 121380	*Musa*; Sri Lanka; –	EU514243.1	EU514306.1	–; –; –
	CIRAD 535	*Musa*; India; –	AY923759.1	–	–; –; –
	CPC 37315 = CIRAD-VNM 003	*Musa*; Vietnam; 1995	**MW063266.1**	**MW070615.1**	**MW070937.1**; **MW070796.1**; –
	CPC 37316 = CIRAD-VNM 004	*Musa*; Vietnam; 1995	**MW063267.1**	**MW070616.1**	**MW070938.1**; **MW070797.1**; –
	CPC 37318 = CIRAD-MYS 002	*Musa*; Malaysia; 2001	**MW063268.1**	**MW070617.1**	**MW070939.1**; **MW070798.1**; –
	CPC 37319 = CIRAD-MYS 003	*Musa*; Malaysia; 2001	**MW063269.1**	**MW070618.1**	**MW070940.1**; **MW070799.1**; –
	CPC 37321 = CIRAD-MYS 057	*Musa*; Malaysia; 1993	**MW063270.1**	**MW070619.1**	**MW070941.1**; **MW070800.1**; –
	CPC 37322 = CIRAD-MYS 058	*Musa*; Malaysia; 1993	**MW063271.1**	**MW070620.1**	**MW070942.1**; **MW070801.1**; –
	CPC 37323 = CIRAD-NGA 052	*Musa*; Nigeria; 1999	**MW063272.1**	**MW070621.1**	**MW070943.1**; **MW070802.1**; –
	CPC 37324 = CIRAD-NGA 053	*Musa*; Nigeria; 1999	**MW063273.1**	**MW070622.1**	**MW070944.1**; **MW070803.1**; –
	CPC 37325 = CIRAD-NGA 057	*Musa*; Nigeria; 1989	**MW063274.1**	**MW070623.1**	**MW070945.1**; **MW070804.1**; –
	CPC 37326 = CIRAD-NGA 058	*Musa*; Nigeria; 1989	**MW063275.1**	**MW070624.1**	**MW070946.1**; **MW070805.1**; –
	CPC 37327 = CIRAD-NGA 066	*Musa*; Nigeria; 1990	**MW063276.1**	**MW070625.1**	**MW070947.1**; **MW070806.1**; –
	CPC 37330 = CIRAD-REU 002	*Musa*; France: Réunion; 1999	**MW063277.1**	**MW070626.1**	–; **MW070807.1**; –
	CPC 37331 = CIRAD-REU 003	*Musa*; France: Réunion; 1999	**MW063278.1**	**MW070627.1**	**MW070948.1**; **MW070808.1**; –
	CPC 37332 = CIRAD-REU 010	*Musa*; France: Réunion; 2001	**MW063279.1**	**MW070628.1**	**MW070949.1**; **MW070809.1**; –
	CPC 37333 = CIRAD-REU 011	*Musa*; France: Réunion; 2001	**MW063280.1**	**MW070629.1**	**MW070950.1**; **MW070810.1**; –
	CPC 37334 = CIRAD-REU 012	*Musa*; France: Réunion; 2001	**MW063281.1**	**MW070630.1**	**MW070951.1**; **MW070811.1**; –
	CPC 37335 = CIRAD-REU 013	*Musa*; France: Réunion; 2001	**MW063282.1**	**MW070631.1**	**MW070952.1**; **MW070812.1**; –
	CPC 37336 = CIRAD-REU 035	*Musa*; France: Réunion; 2002	**MW063283.1**	**MW070632.1**	**MW070953.1**; **MW070813.1**; –
	CPC 37337 = CIRAD-REU 036	*Musa*; France: Réunion; 2002	**MW063284.1**	**MW070633.1**	**MW070954.1**; **MW070814.1**; –
	CPC 37338 = CIRAD-MUS 001	*Musa*; Île Maurice (Mauritius); 2003	**MW063285.1**	**MW070634.1**	**MW070955.1**; **MW070815.1**; –
	CPC 37339 = CIRAD-MUS 002	*Musa*; Île Maurice (Mauritius); 2003	**MW063286.1**	**MW070635.1**	**MW070956.1**; **MW070816.1**; –
	CPC 37340 = CIRAD-MUS 009	*Musa*; Île Maurice (Mauritius); 2003	**MW063287.1**	**MW070636.1**	**MW070957.1**; **MW070817.1**; –
	CPC 37341 = CIRAD-MUS 010	*Musa*; Île Maurice (Mauritius); 2003	**MW063288.1**	**MW070637.1**	**MW070958.1**; **MW070818.1**; –
	CPC 37342 = CIRAD-MUS 011	*Musa*; Île Maurice (Mauritius); 1996	**MW063289.1**	**MW070638.1**	**MW070959.1**; **MW070819.1**; –
	CPC 37343 = CIRAD-MUS 012	*Musa*; Île Maurice (Mauritius); 1996	**MW063290.1**	**MW070639.1**	**MW070960.1**; **MW070820.1**; –
	CPC 37344 = CIRAD-MUS 015	*Musa*; Île Maurice (Mauritius); 1996	**MW063291.1**	**MW070640.1**	**MW070961.1**; **MW070821.1**; –
	CPC 37345 = CIRAD-MUS 016	*Musa*; Île Maurice (Mauritius); 1996	**MW063292.1**	**MW070641.1**	**MW070962.1**; **MW070822.1**; –

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Table 1. (Continued).

Species	Collection number(s)[1]	Substrate including host, origin and collection year	GenBank accession number[2]		
			ITS	*act*	*tef1*; *rpb2*; *tub2*
	CPC 37346 = CIRAD-IND 001	*Musa*; India; 1999	**MW063293.1**	**MW070642.1**	**MW070963.1**; **MW070823.1**; –
	CPC 37347 = CIRAD-IND 002	*Musa*; India; 1999	**MW063294.1**	**MW070643.1**	**MW070964.1**; **MW070824.1**; –
	CPC 37349 = CIRAD-IND 009	*Musa*; India; –	**MW063295.1**	**MW070644.1**	**MW070965.1**; **MW070825.1**; –
	CPC 37350 = CIRAD-IND 010	*Musa*; India; 1998	**MW063296.1**	**MW070645.1**	**MW070966.1**; **MW070826.1**; –
	CPC 37351 = CIRAD-IND 011	*Musa*; India; 1995	**MW063297.1**	**MW070646.1**	**MW070967.1**; **MW070827.1**; –
	CPC 37352 = CIRAD-IND 031	*Musa*; India; 1992	**MW063298.1**	**MW070647.1**	**MW070968.1**; **MW070828.1**; –
	CPC 37353 = CIRAD-IND 032	*Musa*; India; 1992	**MW063299.1**	**MW070648.1**	**MW070969.1**; **MW070829.1**; –
	CPC 37354 = CIRAD-LKA 001	*Musa*; Sri Lanka; –	**MW063300.1**	**MW070649.1**	**MW070970.1**; **MW070830.1**; –
	CPC 37355 = CIRAD-LKA 002	*Musa*; Sri Lanka; 1999	**MW063301.1**	**MW070650.1**	**MW070971.1**; **MW070831.1**; –
	CPC 37356 = CIRAD-LKA 003	*Musa*; Sri Lanka; 1999	**MW063302.1**	**MW070651.1**	**MW070972.1**; –; –
	CPC 37357 = CIRAD-LKA 006	*Musa*; Sri Lanka; 1995	**MW063303.1**	**MW070652.1**	**MW070973.1**; **MW070832.1**; –
	CPC 37358 = CIRAD-LKA 007	*Musa*; Sri Lanka; 1995	**MW063304.1**	**MW070653.1**	**MW070974.1**; **MW070833.1**; –
	CPC 37359 = CIRAD-LKA 016	*Musa*; Sri Lanka; 1995	**MW063305.1**	**MW070654.1**	**MW070975.1**; **MW070834.1**; –
	CPC 37360 = CIRAD-LKA 017	*Musa*; Sri Lanka; 1995	**MW063306.1**	**MW070655.1**	**MW070976.1**; **MW070835.1**; –
	CPC 37361 = CIRAD-THA 001	*Musa*; Thailand; 1994	**MW063307.1**	**MW070656.1**	**MW070977.1**; –; –
	CPC 37362 = CIRAD-THA 002	*Musa*; Thailand; 1994	**MW063308.1**	**MW070657.1**	**MW070978.1**; **MW070836.1**; –
	CPC 37363 = CIRAD-THA 005	*Musa*; Thailand; 1994	**MW063309.1**	**MW070658.1**	–; **MW070837.1**; –
	CPC 37364 = CIRAD-THA 006	*Musa*; Thailand; 1994	**MW063310.1**	**MW070659.1**	**MW070979.1**; **MW070838.1**; –
	CPC 37365 = CIRAD-THA 007	*Musa*; Thailand; 1994	**MW063311.1**	**MW070660.1**	**MW070980.1**; **MW070839.1**; –
	CPC 37366 = CIRAD-THA 008	*Musa*; Thailand; 1994	**MW063312.1**	**MW070661.1**	**MW070981.1**; **MW070840.1**; –
	CPC 37367 = CIRAD-THA 009	*Musa*; Thailand; 1994	**MW063313.1**	**MW070662.1**	**MW070982.1**; **MW070841.1**; –
	S1030B	*Musa*; Mauritius; –	EU514233.1	EU514300.1	–; –; –
	S1037B	*Musa*; Mauritius; –	EU514234.1	EU514301.1	–; –; –
	S17	*Musa*; India; –	MN860088.1	–	–; –; –
	S37	*Musa* cv. Nendran; India; –	MN901997.1	–	–; –; –
	S48	*Musa*; India; –	MN947254.1	–	–; –; –
Pseudocercospora fijiensis	CBS 120258 = CIRAD 86, ex-epitype	*Musa*; Cameroon; –	EU514248.1	NW_006921533.1	NW_006921532.1; NW_006921535.1; –
	CBS 121362 = CIRAD 364 = X847	*Musa*; Taiwan; –	EU514254.1	EU514316.1	–; –; –
	CIRAD 11 = X843	*Musa*; Honduras; –	EU514253.1	EU514315.1	–; –; –
	CIRAD 355 = X850	*Musa*; Ivory Coast; –	EU514255.1	–	–; –; –
	CPC 16301	*Musa*; Mexico; –	KX462581.1	KX462548.1	KX462667.1; KX462613.1; –
	CPC 37216 = CMR 1853	*Musa*; Cameroon; 2007	**MW063314.1**	**MW070663.1**	**MW070983.1**; **MW070842.1**; –
	CPC 37217 = CIRAD-CMR 1861	*Musa*; Cameroon; 1996	**MW063315.1**	**MW070664.1**	**MW070984.1**; **MW070843.1**; –

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Table 1. (Continued).

Species	Collection number(s)[1]	Substrate including host, origin and collection year	GenBank accession number[2]		
			ITS	*act*	*tef1*; *rpb2*; *tub2*
	X104	*Musa*; Colombia; –	EU514251.1	–	–; –; –
Pseudocercospora longispora	CBS 122469 = X474	*Musa*; Malaysia; 1988	EU514284.1	EU514341.1	–; –; –
	CBS 122470 = X475, ex-type	*Musa* cv. Pisang Byok AAA/AAB; Malaysia; 1988	NR_156515.1	EU514342.1	GU384447.1; –; –
	CPC 37317 = CIRAD-MYS 001	*Musa*; Malaysia; 1988	**MW063316.1**	**MW070665.1**	**MW070985.1**; –; –
	CPC 37320 = CIRAD-MYS 017	*Musa*; Malaysia; 1988	**MW063317.1**	**MW070666.1**	–; –; –
Pseudocercospora musae	CBS 116634 = IMI 123823 = X42, ex-epitype	*Musa*; Cuba; –	EU514265.1	LFZO01000469.1	LFZO01000001.1; LFZO01000453.1; –
	CBS 143.36 = ATCC 10688	–; Suriname; –	MH855742.1	–	–; –; –
	CPC 37186 = CIRAD-AUS 001	*Musa*; Australia: New South Wales; 1999	**MW063318.1**	**MW070667.1**	**MW070986.1**; **MW070844.1**; –
	CPC 37187 = CIRAD-AUS 002	*Musa*; Australia: New South Wales; 1999	**MW063319.1**	**MW070668.1**	**MW070987.1**; **MW070845.1**; –
	CPC 37188 = CIRAD-AUS 007	*Musa*; Australia: Queensland; 1999	**MW063320.1**	**MW070669.1**	**MW070988.1**; **MW070846.1**; –
	CPC 37189 = CIRAD-AUS 008	*Musa*; Australia: Queensland; 1999	**MW063321.1**	**MW070670.1**	**MW070989.1**; **MW070847.1**; –
	CPC 37190 = CIRAD-AUS 012	*Musa*; Australia; 1999	**MW063322.1**	**MW070671.1**	**MW070990.1**; **MW070848.1**; –
	CPC 37192 = CIRAD-AUS 127	*Musa*; Australia: Queensland; 1994	**MW063323.1**	**MW070672.1**	**MW070991.1**; **MW070849.1**; –
	CPC 37193 = CIRAD-AUS 128	*Musa*; Australia; 1992	**MW063324.1**	**MW070673.1**	**MW070992.1**; **MW070850.1**; –
	CPC 37194 = CIRAD-AUS 129	*Musa*; Australia: Queensland; 1992	**MW063325.1**	**MW070674.1**	**MW070993.1**; **MW070851.1**; –
	CPC 37196 = CIRAD-AUS 131	*Musa*; Australia: Queensland; 1993	**MW063326.1**	**MW070675.1**	**MW070994.1**; **MW070852.1**; –
	CPC 37197 = CIRAD-BRA 003	*Musa*; Brazil; 1983	**MW063327.1**	**MW070676.1**	**MW070995.1**; **MW070853.1**; –
	CPC 37198 = CIRAD-BRA 004	*Musa*; Brazil; 1983	**MW063328.1**	**MW070677.1**	**MW070996.1**; –; –
	CPC 37201 = CIRAD-CIV 091	*Musa*; Cote d'ivoire (Ivory Coast); 1985	**MW063329.1**	**MW070678.1**	**MW070997.1**; **MW070854.1**; –
	CPC 37202 = CIRAD-CIV 092	*Musa*; Cote d'ivoire (Ivory Coast); 1986	**MW063330.1**	**MW070679.1**	**MW070998.1**; **MW070855.1**; –
	CPC 37203 = CIRAD-CMR 1175	*Musa*; Cameroon; 1999	**MW063331.1**	**MW070680.1**	**MW070999.1**; **MW070856.1**; –
	CPC 37204 = CIRAD-CMR 1176	*Musa*; Cameroon; 1999	**MW063332.1**	**MW070681.1**	**MW071000.1**; **MW070857.1**; –
	CPC 37205 = CIRAD-CMR 1292	*Musa*; Cameroon; 1999	**MW063333.1**	**MW070682.1**	**MW071001.1**; **MW070858.1**; –
	CPC 37206 = CIRAD-CMR 1293	*Musa*; Cameroon; 1999	**MW063334.1**	**MW070683.1**	**MW071002.1**; **MW070859.1**; –
	CPC 37207 = CIRAD-CMR 1328	*Musa*; Cameroon; 1999	**MW063335.1**	**MW070684.1**	**MW071003.1**; –; –
	CPC 37208 = CIRAD-CMR 1329	*Musa*; Cameroon; 1999	**MW063336.1**	**MW070685.1**	**MW071004.1**; –; –
	CPC 37209 = CIRAD-CMR 2857	*Musa*; Cameroon; 1988	**MW063337.1**	**MW070686.1**	**MW071005.1**; **MW070860.1**; –
	CPC 37210 = CIRAD-CMR 2856	*Musa*; Cameroon; 1988	**MW063338.1**	**MW070687.1**	**MW071006.1**; **MW070861.1**; –

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Table 1. (Continued).

Species	Collection number(s)[1]	Substrate including host, origin and collection year	GenBank accession number[2]		
			ITS	*act*	*tef1*; *rpb2*; *tub2*
	CPC 37211 = CIRAD-CMR 2859	*Musa*; Cameroon; 1987	**MW063339.1**	**MW070688.1**	**MW071007.1**; **MW070862.1**; –
	CPC 37212 = CIRAD-CMR 2861	*Musa*; Cameroon; 1987	**MW063340.1**	**MW070689.1**	**MW071008.1**; **MW070863.1**; –
	CPC 37219 = CIRAD-COL 056	*Musa*; Colombia; 1987	**MW063341.1**	**MW070690.1**	**MW071009.1**; **MW070864.1**; –
	CPC 37220 = CIRAD-COL 057	*Musa*; Colombia; 1988	**MW063342.1**	**MW070691.1**	**MW071010.1**; –; –
	CPC 37221 = CIRAD-COL 059	*Musa*; Colombia; 1989	**MW063343.1**	**MW070692.1**	**MW071011.1**; –; –
	CPC 37222 = CIRAD-COL 067	*Musa*; Colombia; 1990	**MW063344.1**	**MW070693.1**	**MW071012.1**; –; –
	CPC 37223 = CIRAD-CRI 001	*Musa*; Costa Rica; 1991	**MW063345.1**	**MW070694.1**	**MW071013.1**; –; –
	CPC 37224 = CIRAD-CUB 0459	*Musa*; Cuba; 1986	**MW063346.1**	**MW070695.1**	**MW071014.1**; **MW070865.1**; –
	CPC 37225 = CIRAD-GIN 002	*Musa*; Guinea; 1994	**MW063347.1**	**MW070696.1**	**MW071015.1**; –; –
	CPC 37226 = CIRAD-GIN 003	*Musa*; Guinea; 1994	**MW063348.1**	**MW070697.1**	**MW071016.1**; –; –
	CPC 37227 = CIRAD-GIN 004	*Musa*; Guinea; 1994	**MW063349.1**	**MW070698.1**	**MW071017.1**; –; –
	CPC 37228 = CIRAD-GIN 005	*Musa*; Guinea; 1994	**MW063350.1**	**MW070699.1**	**MW071018.1**; –; –
	CPC 37229 = CIRAD-GIN 007	*Musa*; Guinea; 1994	**MW063351.1**	**MW070700.1**	**MW071019.1**; –; –
	CPC 37230 = CIRAD-GIN 008	*Musa*; Guinea; 1994	**MW063352.1**	**MW070701.1**	**MW071020.1**; –; –
	CPC 37231 = CIRAD-GLP 0101	*Musa*; Guadeloupe; 2003	**MW063353.1**	**MW070702.1**	**MW071021.1**; –; –
	CPC 37232 = CIRAD-GLP 0102	*Musa*; Guadeloupe; 2003	**MW063354.1**	**MW070703.1**	**MW071022.1**; –; –
	CPC 37233 = CIRAD-GLP 0130	*Musa*; Guadeloupe; 2003	**MW063355.1**	**MW070704.1**	**MW071023.1**; **MW070866.1**; –
	CPC 37234 = CIRAD-GLP 0131	*Musa*; Guadeloupe; 2003	**MW063356.1**	**MW070705.1**	**MW071024.1**; **MW070867.1**; –
	CPC 37235 = CIRAD-GLP 0160	*Musa*; Guadeloupe; 2003	**MW063357.1**	**MW070706.1**	**MW071025.1**; **MW070868.1**; –
	CPC 37236 = CIRAD-GLP 0775	*Musa*; Guadeloupe; 2003	**MW063358.1**	**MW070707.1**	**MW071026.1**; **MW070869.1**; –
	CPC 37237 = CIRAD-GLP 0162	*Musa*; Guadeloupe; 2003	**MW063359.1**	**MW070708.1**	**MW071027.1**; **MW070870.1**; –
	CPC 37238 = CIRAD-GLP 0163	*Musa*; Guadeloupe; 2003	**MW063360.1**	**MW070709.1**	**MW071028.1**; **MW070871.1**; –
	CPC 37239 = CIRAD-GLP 0192	*Musa*; Guadeloupe; 2003	**MW063361.1**	**MW070710.1**	**MW071029.1**; **MW070872.1**; –
	CPC 37240 = CIRAD-GLP 0193	*Musa*; Guadeloupe; 2003	**MW063362.1**	**MW070711.1**	**MW071030.1**; –; –
	CPC 37241 = CIRAD-GLP 0222	*Musa*; Guadeloupe; 2003	**MW063363.1**	**MW070712.1**	**MW071031.1**; –; –
	CPC 37242 = CIRAD-GLP 0223	*Musa*; Guadeloupe; 2003	**MW063364.1**	**MW070713.1**	**MW071032.1**; **MW070873.1**; –
	CPC 37243 = CIRAD-GLP 0254	*Musa*; Guadeloupe; 1992	**MW063365.1**	**MW070714.1**	**MW071033.1**; **MW070874.1**; –
	CPC 37244 = CIRAD-GLP 0255	*Musa*; Guadeloupe; 1992	**MW063366.1**	**MW070715.1**	**MW071034.1**; **MW070875.1**; –
	CPC 37245 = CIRAD-GLP 0261	*Musa*; Guadeloupe; 1992	**MW063367.1**	**MW070716.1**	**MW071035.1**; **MW070876.1**; –
	CPC 37246 = CIRAD-GLP 0256	*Musa*; Guadeloupe; 1992	**MW063368.1**	**MW070717.1**	**MW071036.1**; **MW070877.1**; –
	CPC 37247 = CIRAD-GLP 0257	*Musa*; Guadeloupe; 1992	**MW063369.1**	**MW070718.1**	**MW071037.1**; **MW070878.1**; –
	CPC 37248 = CIRAD-GLP 0258	*Musa*; Guadeloupe; 1992	**MW063370.1**	**MW070719.1**	**MW071038.1**; **MW070879.1**; –
	CPC 37249 = CIRAD-GLP 0262	*Musa*; Guadeloupe; 1992	**MW063371.1**	**MW070720.1**	**MW071039.1**; **MW070880.1**; –

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Table 1. (Continued).

Species	Collection number(s)[1]	Substrate including host, origin and collection year	GenBank accession number[2]		
			ITS	*act*	*tef1*; *rpb2*; *tub2*
	CPC 37250 = CIRAD-GLP 0263	*Musa*; Guadeloupe; 1992	**MW063372.1**	**MW070721.1**	**MW071040.1**; **MW070881.1**; –
	CPC 37251 = CIRAD-GLP 0265	*Musa*; Guadeloupe; 1992	**MW063373.1**	**MW070722.1**	**MW071041.1**; **MW070882.1**; –
	CPC 37252 = CIRAD-GLP 0266	*Musa*; Guadeloupe; 1992	**MW063374.1**	**MW070723.1**	**MW071042.1**; **MW070883.1**; –
	CPC 37253 = CIRAD-GLP 0267	*Musa*; Guadeloupe; 1992	**MW063375.1**	**MW070724.1**	**MW071043.1**; **MW070884.1**; –
	CPC 37254 = CIRAD-GLP 0268	*Musa*; Guadeloupe; 1992	**MW063376.1**	**MW070725.1**	**MW071044.1**; **MW070885.1**; –
	CPC 37255 = CIRAD-GLP 0269	*Musa*; Guadeloupe; 1992	**MW063377.1**	**MW070726.1**	**MW071045.1**; **MW070886.1**; –
	CPC 37256 = CIRAD-GLP 0270	*Musa*; Guadeloupe; 1992	**MW063378.1**	**MW070727.1**	**MW071046.1**; **MW070887.1**; –
	CPC 37257 = CIRAD-GLP 0271	*Musa*; Guadeloupe; 1992	**MW063379.1**	**MW070728.1**	**MW071047.1**; **MW070888.1**; –
	CPC 37258 = CIRAD-GLP 0273	*Musa*; Guadeloupe; 1992	**MW063380.1**	**MW070729.1**	**MW071048.1**; –; –
	CPC 37259 = CIRAD-GLP 0274	*Musa*; Guadeloupe; 1992	**MW063381.1**	**MW070730.1**	**MW071049.1**; **MW070889.1**; –
	CPC 37260 = CIRAD-GLP 0275	*Musa*; Guadeloupe; 1992	**MW063382.1**	**MW070731.1**	**MW071050.1**; **MW070890.1**; –
	CPC 37261 = CIRAD-GLP 0276	*Musa*; Guadeloupe; 1992	**MW063383.1**	**MW070732.1**	**MW071051.1**; **MW070891.1**; –
	CPC 37262 = CIRAD-GLP 0277	*Musa*; Guadeloupe; 1992	**MW063384.1**	**MW070733.1**	**MW071052.1**; –; –
	CPC 37263 = CIRAD-GLP 0278	*Musa*; Guadeloupe; 1992	**MW063385.1**	**MW070734.1**	**MW071053.1**; **MW070892.1**; –
	CPC 37264 = CIRAD-GLP 0279	*Musa*; Guadeloupe; 1992	**MW063386.1**	**MW070735.1**	**MW071054.1**; **MW070893.1**; –
	CPC 37265 = CIRAD-GLP 0281	*Musa*; Guadeloupe; 1992	**MW063387.1**	**MW070736.1**	**MW071055.1**; **MW070894.1**; –
	CPC 37266 = CIRAD-GLP 0282	*Musa*; Guadeloupe; 1992	**MW063388.1**	**MW070737.1**	**MW071056.1**; **MW070895.1**; –
	CPC 37267 = CIRAD-GLP 0773	*Musa*; Guadeloupe; 1998	**MW063389.1**	**MW070738.1**	**MW071057.1**; **MW070896.1**; –
	CPC 37268 = CIRAD-GLP 0774	*Musa*; Guadeloupe; 1998	**MW063390.1**	**MW070739.1**	**MW071058.1**; **MW070897.1**; –
	CPC 37271 = CIRAD-IDN 06	*Musa*; Indonesia; 1988	**MW063391.1**	**MW070740.1**	**MW071059.1**; –; –
	CPC 37272 = CIRAD-IDN 07	*Musa*; Indonesia; 1988	**MW063392.1**	**MW070741.1**	**MW071060.1**; –; –
	CPC 37274 = CIRAD-IDN 30	*Musa*; Indonesia; 2010	**MW063393.1**	**MW070742.1**	**MW071061.1**; **MW070898.1**; –
	CPC 37275 = CIRAD-IDN 31	*Musa*; Indonesia; 2010	**MW063394.1**	**MW070743.1**	**MW071062.1**; –; –
	CPC 37276 = CIRAD-IDN 52	*Musa*; Indonesia; 2010	**MW063395.1**	**MW070744.1**	**MW071063.1**; **MW070899.1**; –
	CPC 37277 = CIRAD-IDN 53	*Musa*; Indonesia; 2010	**MW063396.1**	**MW070745.1**	**MW071064.1**; **MW070900.1**; –
	CPC 37280 = CIRAD-JAM 002	*Musa*; Jamaica; 1995	**MW063397.1**	**MW070746.1**	**MW071065.1**; –; –
	CPC 37281 = CIRAD-JAM 003	*Musa*; Jamaica; 1995	**MW063398.1**	**MW070747.1**	**MW071066.1**; **MW070901.1**; –
	CPC 37282 = CIRAD-LCA 001	*Musa*; Saint Lucia; 1986	**MW063399.1**	**MW070748.1**	**MW071067.1**; **MW070902.1**; –
	CPC 37283 = CIRAD-MTQ 1033	*Musa*; France: Martinique; 2003	**MW063400.1**	**MW070749.1**	**MW071068.1**; **MW070903.1**; –
	CPC 37284 = CIRAD-MTQ 1034	*Musa*; France: Martinique; 2003	**MW063401.1**	**MW070750.1**	**MW071069.1**; –; –
	CPC 37285 = CIRAD-MTQ 1063	*Musa*; France: Martinique; 2003	**MW063402.1**	**MW070751.1**	**MW071070.1**; –; –
	CPC 37286 = CIRAD-MTQ 1064	*Musa*; France: Martinique; 2003	**MW063403.1**	**MW070752.1**	**MW071071.1**; **MW070904.1**; –
	CPC 37287 = CIRAD-MTQ 1093	*Musa*; France: Martinique; 2003	**MW063404.1**	**MW070753.1**	**MW071072.1**; –; –

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Table 1. (Continued).

Species	Collection number(s)[1]	Substrate including host, origin and collection year	GenBank accession number[2]		
			ITS	*act*	*tef1*; *rpb2*; *tub2*
	CPC 37288 = CIRAD-MTQ 1094	*Musa*; France: Martinique; 2003	**MW063405.1**	**MW070754.1**	**MW071073.1**; **MW070905.1**; –
	CPC 37289 = CIRAD-MTQ 1123	*Musa*; France: Martinique; 2003	**MW063406.1**	**MW070755.1**	**MW071074.1**; **MW070906.1**; –
	CPC 37290 = CIRAD-MTQ 1124	*Musa*; France: Martinique; 2003	**MW063407.1**	**MW070756.1**	**MW071075.1**; –; –
	CPC 37291 = CIRAD-MTQ 1153	*Musa*; France: Martinique; 2003	**MW063408.1**	**MW070757.1**	**MW071076.1**; **MW070907.1**; –
	CPC 37292 = CIRAD-MTQ 1154	*Musa*; France: Martinique; 2003	**MW063409.1**	**MW070758.1**	**MW071077.1**; **MW070908.1**; –
	CPC 37293 = CIRAD-MTQ 1183	*Musa*; France: Martinique; 2003	**MW063410.1**	**MW070759.1**	**MW071078.1**; **MW070909.1**; –
	CPC 37294 = CIRAD-MTQ 1184	*Musa*; France: Martinique; 2003	**MW063411.1**	**MW070760.1**	**MW071079.1**; **MW070910.1**; –
	CPC 37295 = CIRAD-MTQ 1213	*Musa*; France: Martinique; 1988	**MW063412.1**	**MW070761.1**	**MW071080.1**; –; –
	CPC 37296 = CIRAD-MTQ 1214	*Musa*; France: Martinique; 1988	**MW063413.1**	**MW070762.1**	**MW071081.1**; –; –
	CPC 37298 = CIRAD-MTQ 1221	*Musa*; France: Martinique; 1988	**MW063414.1**	**MW070763.1**	**MW071082.1**; **MW070911.1**; –
	CPC 37299 = CIRAD-MTQ 1222	*Musa*; France: Martinique; 1988	**MW063415.1**	**MW070764.1**	**MW071083.1**; **MW070912.1**; –
	CPC 37300 = CIRAD-MTQ 1223	*Musa*; France: Martinique; 1988	**MW063416.1**	**MW070765.1**	**MW071084.1**; **MW070913.1**; –
	CPC 37301 = CIRAD-MTQ 1225	*Musa*; France: Martinique; 1988	**MW063417.1**	**MW070766.1**	**MW071085.1**; **MW070914.1**; –
	CPC 37302 = CIRAD-MTQ 1226	*Musa*; France: Martinique; 1988	**MW063418.1**	**MW070767.1**	**MW071086.1**; **MW070915.1**; –
	CPC 37303 = CIRAD-MTQ 1227	*Musa*; France: Martinique; 1988	**MW063419.1**	**MW070768.1**	**MW071087.1**; –; –
	CPC 37310 = CIRAD-VEN 001	*Musa*; Venezuela; 1986	**MW063420.1**	**MW070769.1**	**MW071088.1**; **MW070916.1**; –
	CPC 37311 = CIRAD-VEN 002	*Musa*; Venezuela; 1989	**MW063421.1**	**MW070770.1**	**MW071089.1**; **MW070917.1**; –
	PM11 = ATCC 36143	*Musa* AAA; Honduras; –	AY266148.1	–	–; –; –
	X588	*Musa* cv. Williams; Australia; –	EU514268.1	EU514326.1	–; –; –
	X596	*Musa* cv. SH-3362 AA; Australia; –	EU514270.1	EU514328.1	–; –; –
	X602	*Musa* cv. Lakatan; Australia; –	EU514271.1	EU514329.1	–; –; –
Pseudocercospora pseudomusae	CBS 147147 = CPC 37270 = CIRAD-IDN 02, ex-type	*Musa*; Indonesia; 1988	**MW063423.1**	**MW070772.1**	**MW071091.1**; **MW070919.1**; –
	CBS 147148 = CPC 37269 = CIRAD-IDN 01	*Musa*; Indonesia; 1988	**MW063422.1**	**MW070771.1**	**MW071090.1**; **MW070918.1**; –
	CBS 147149 = CPC 37273 = CIRAD-IDN 29	*Musa*; Indonesia; 1988	**MW063424.1**	**MW070773.1**	**MW071092.1**; –; –
	CBS 147150 = CPC 37278 = CIRAD-IDN 57	*Musa*; Indonesia; 1989	**MW063425.1**	**MW070774.1**	**MW071093.1**; –; –
	CBS 147151 = CPC 37279 = CIRAD-IDN 58	*Musa*; Indonesia; 1989	**MW063426.1**	**MW070775.1**	**MW071094.1**; **MW070920.1**; –
Pseudosigmoidea excentrica (Outgroup)	CBS 469.95 = INIFAT C94/202 = MUCL 39227, ex-type	*Lauraceae* leaf litter; Cuba; 1994	NR_156545.1	KF155934.1	KF155975.1; –; KF156196.1
Scolecobasidium ailanthi	MFLU 18-2110	*Ailanthus* sp.; Thailand; 2017	MK347731.1	MK412892.1	–; –; MK412881.1
	MFLUCC 17-0923, ex-type	*Ailanthus* sp.; Thailand; 2017	NR_163326.1	MK412893.1	–; –; MK412883.1

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Species	Collection number(s)[1]	Substrate including host, origin and collection year	GenBank accession number[2]		
			ITS	*act*	*tef1*; *rpb2*; *tub2*
Scolecobasidium bacilliforme	CBS 100442	Biofilm on stainless steel in drinking water; Germany; –	NR_155566.1	KT272051.1	KT272070.1; –; KT272059.1
Scolecobasidium constrictum	CBS 106.65	Soil under *Brassica napus*; Germany; –	HQ667518.1	HQ916960.1	JF440551.1; –; –
Scolecobasidium cordanae	CBS 412.51 = MUCL 9472 = QM 373b	–; USA; –	HQ667540.1	KF155907.1	KF155980.1; –; KF156200.1
Scolecobasidium cordanae	CBS 475.80, ex-type	*Mauritia minor*; Colombia; 1979	NR_132051.1	HQ916976.1	KF155981.1; –; KF156197.1
Scolecobasidium humicola	CBS 116655 = IMI 110131 = UAMH 10241, ex-type	Peat soil; Canada; –	NR_111437.1	HQ916963.1	JF440553.1; –; HQ877631.1
Scolecobasidium icarus	CBS 116645	Sandy soil; Canada; –	HQ667525.1	LM644599.1	–; –; LM644604.1
	CBS 423.64 = MUCL 10160	Rhizosphere of *Solanum tuberosum*, in sandy soil; Netherlands; –	HQ667523.1	HQ916965.1	KF156008.1; –; –
	CBS 536.69 = MUCL 15054 = OAC 10212, ex-type	Forest soil; Canada; –	NR_145367.1	KF155944.1	–; –; KF156174.1
Scolecobasidium longiphorum	CBS 435.76 = UAMH 3972	Soil under asphalt paving of car park; Canada; –	KF156038.1	KF155908.1	KF155978.1; –; KF156182.1
Scolecobasidium minimum	CBS 510.71 = ATCC 22631 = IMI 082933, ex-type	Rhizosphere of *Gossypium arboreum*; Nigeria; –	NR_145366.1	KF155945.1	KF156007.1; –; KF156172.1
Scolecobasidium musae	CBS 119790 = IMI 138059	Soil; Egypt; –	KT272077.1	KT272053.1	KT272072.1; –; KT272061.1
Scolecobasidium musae	CBS 135928	Black biofilm, washing machine, detergent drawer, private residence; Germany; –	KT272080.1	KT272056.1	KT272074.1; –; KT272064.1
	CBS 135930	Black biofilm, sink drain, private residence; Germany; –	KT272082.1	KT272058.1	KT272076.1; –; KT272066.1
	CBS 135931	Black biofilm, bathtub, water tap; Germany; –	KT272081.1	KT272057.1	KT272075.1; –; KT272065.1
	CBS 145061 = CPC 33947	*Persea americana*; Thailand; 2008	MK442605.1	MK442639.1	MK442698.1; –; –
	CBS 312.96	Desert soil; Israel; 1996	KT272078.1	KT272055.1	KF156002.1; –; KT272063.1
	CBS 729.95, ex-type of *Ochroconis mirabilis*	Regulator of diver; –; –	KF156029.1	KF155948.1	KF155999.1; –; KF156171.1
Scolecobasidium musicola	CBS 144441 = CPC 32927, ex-type	*Musa*; Malaysia; 2010	NR_160360.1	–	MH327887.1; MH327876.1; MH327898.1
	CPC 37218 = CIRAD-CMR 2064	*Musa*; Cameroon; 1999	**MW063427.1**	**MW070776.1**	**MW071095.1**; **MW070921.1**; **MW071115.1**
	CPC 37308 = CIRAD-MTQ 0605	*Musa*; France: Martinique; 1992	**MW063428.1**	**MW070777.1**	**MW071096.1**; **MW070922.1**; **MW071116.1**
	CPC 37309 = CIRAD-MTQ 0606	*Musa*; France: Martinique; 1992	**MW063429.1**	**MW070778.1**	**MW071097.1**; **MW070923.1**; **MW071117.1**
	CPC 37348 = CIRAD-IND 008	*Musa*; India; –	**MW063430.1**	**MW070779.1**	**MW071098.1**; –; –

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Table 1. (Continued).

Species	Collection number(s)[1]	Substrate including host, origin and collection year	GenBank accession number[2]		
			ITS	*act*	*tef1*; *rpb2*; *tub2*
Scolecobasidium ramosum	CBS 137171 = FMR 12512 = UTHSC 03-3677	Human skin; USA: Pennsylvania; 2003	LM644522.1	LM644601.1	–; –; LM644606.1
	CBS 137173 = FMR 12514 = UTHSC 12-1082, ex-type	Human nail; USA: California; 2012	NR_155606.1	LM644603.1	–; –; LM644608.1
Trochophora simplex (Outgroup)	CBS 124744 = KACC 42362	*Daphiniphyllum macropodum*; Korea; –	GU269872.1	GU320568.1	GU384580.1; KX462666.1; –
Strains identified based on sequence similarity					
Mycosphaerella musae	CPC 37191 = CIRAD-AUS 126	*Musa*; Australia: New South Wales; 1993	**MW063431.1**	**MW070780.1**	**MW071099.1**; –; –
	CPC 37199 = CIRAD-BRA 001	*Musa*; Brazil; 1989	**MW063432.1**	**MW070781.1**	**MW071100.1**; **MW070924.1**; –
	CPC 37213 = CIRAD-CMR 2862	*Musa*; Cameroon; 1987	**MW063433.1**	**MW070782.1**	**MW071101.1**; **MW070925.1**; –
	CPC 37215 = CIRAD-CMR 2863	*Musa*; Cameroon; 1987	**MW063434.1**	**MW070783.1**	**MW071102.1**; **MW070926.1**; –
	CPC 37307 = CIRAD-MTQ 1241	*Musa*; France: Martinique; 1986	**MW063435.1**	**MW070784.1**	**MW071103.1**; **MW070927.1**; –
	CPC 37312 = CIRAD-COK 002	*Musa*; Cook Islands; 1989	**MW063436.1**	**MW070785.1**	**MW071104.1**; **MW070928.1**; –
	CPC 37313 = CIRAD-COK 003	*Musa*; Cook Islands; 1989	**MW063437.1**	**MW070786.1**	**MW071105.1**; **MW070929.1**; –
Pantospora guazumae	CPC 37195 = CIRAD-AUS 130	*Musa*; Australia: Queensland; 1993	**MW063438.1**	**MW070787.1**	**MW071106.1**; **MW070930.1**; –
Parapallidocercospora thailandica	CPC 37200 = CIRAD-BRA 002	*Musa*; Brazil; 1988	**MW063439.1**	**MW070788.1**	**MW071107.1**; **MW070931.1**; –
	CPC 37214 = CIRAD-CMR 0043	*Musa*; Cameroon; –	**MW063440.1**	**MW070789.1**	**MW071108.1**; **MW070932.1**; –
	CPC 37305 = CIRAD-MTQ 1235	*Musa*; France: Martinique; 1988	**MW063441.1**	**MW070790.1**	**MW071109.1**; **MW070933.1**; –
Zasmidium musae	CPC 37304 = CIRAD-MTQ 1228	*Musa*; France: Martinique; 1987	**MW063442.1**	**MW070791.1**	**MW071110.1**; –; –
	CPC 37306 = CIRAD-MTQ 1240	*Musa*; France: Martinique; 1986	**MW063443.1**	**MW070792.1**	**MW071111.1**; –; –
	CPC 37314 = CIRAD-TON 007	*Musa*; Tonga; 1990	**MW063444.1**	**MW070793.1**	**MW071112.1**; **MW070934.1**; –
	CPC 37328 = CIRAD-GAB 030	*Musa*; Gabon; 1998	**MW063445.1**	**MW070794.1**	**MW071113.1**; **MW070935.1**; –
	CPC 37329 = CIRAD-GAB 031	*Musa*; Gabon; 1998	**MW063446.1**	**MW070795.1**	**MW071114.1**; **MW070936.1**; –

[1] ATCC: American Type Culture Collection, Virginia, USA; CBS: Westerdijk Fungal Biodiversity Institute, Utrecht, The Netherlands; CIRAD: Centre de coopération internationale en recherche agronomique pour le développement, Montpellier, France; CPC: Culture collection of Pedro Crous, housed at CBS; IMI: International Mycological Institute, CABI-Bioscience, Egham, Bakeham Lane, UK; INIFAT: Alexander Humboldt Institute for Basic Research in Tropical Agriculture, Ciudad de La Habana, Cuba; KACC: Korean Agricultural Culture Collection, National Institute of Agricultural Biotechnology, Rural Development Administration, Suwon, Republic of Korea; MFLUCC: Mae Fah Luang University Culture Collection, Chiang Rai, Thailand; MUCL: Université Catholique de Louvain, Louvain-la-Neuve, Belgium; OAC: Department of Botany and Genetics, University of Guelph, Ont., Canada; STE-U: Department of Plant Pathology, University of Stellenbosch, South Africa; UAMH: University of Alberta Microfungus Collection and Herbarium, Edmonton, Alberta, Canada; UTHSC: Fungus Testing Laboratory at the University of Texas Health Science Center, San Antonio, TX, USA.

[2] ITS: internal transcribed spacer regions and intervening 5.8S nrRNA gene; *act*: partial actin gene; *tef1*: partial translation elongation factor 1-alpha gene; *rpb2*: partial DNA-directed RNA polymerase II second largest subunit; *tub2*: partial beta-tubulin gene.

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lineage sister to *Pseudocercospora musae* and representing a novel species which is described below. All five species clades were fully supported in the Bayesian analyses (posterior probability value of 1.0). Based on the *Scolecobasidium* phylogeny (Fig. 2), two strains are very closely related to the ex-type strain of *Scolecobasidium musicola* while two other strains form a closely related sister lineage. The two lineages have the following numbers of fixed nucleotide differences: ITS (19 substitutions and one indel), *act* (13 substitutions; no sequence available for the ex-type), *tef1* (23 substitutions) and *tub2* (8 substitutions and one indel; no sequence available for CPC 37348).

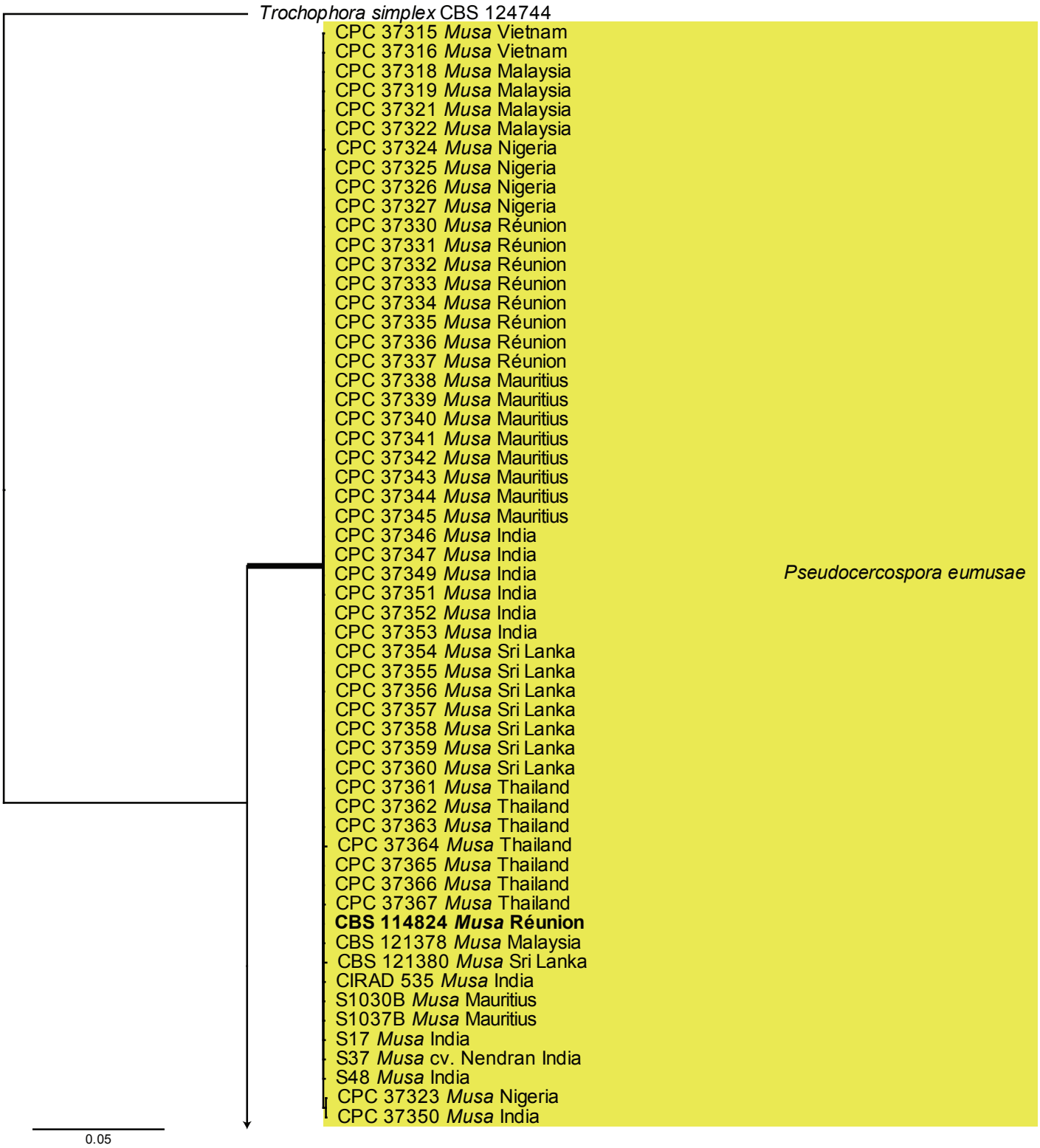

Fig. 1. Consensus phylogram (50 % majority rule) resulting from a Bayesian analysis of the multigene *Pseudocercospora* sequence alignment. Bayesian posterior probabilities (PP) > 0.84 are shown at the nodes and thickened lines represent nodes with PP = 1.00. The scale bar represents the expected changes per site. Species are indicated with coloured blocks to the right of the tree. Culture collection numbers are followed by the host and origin, where known. The tree was rooted to *Trochophora simplex* (culture CBS 124744). The taxonomic novelty described in this study and cultures with type status are indicated in bold face.

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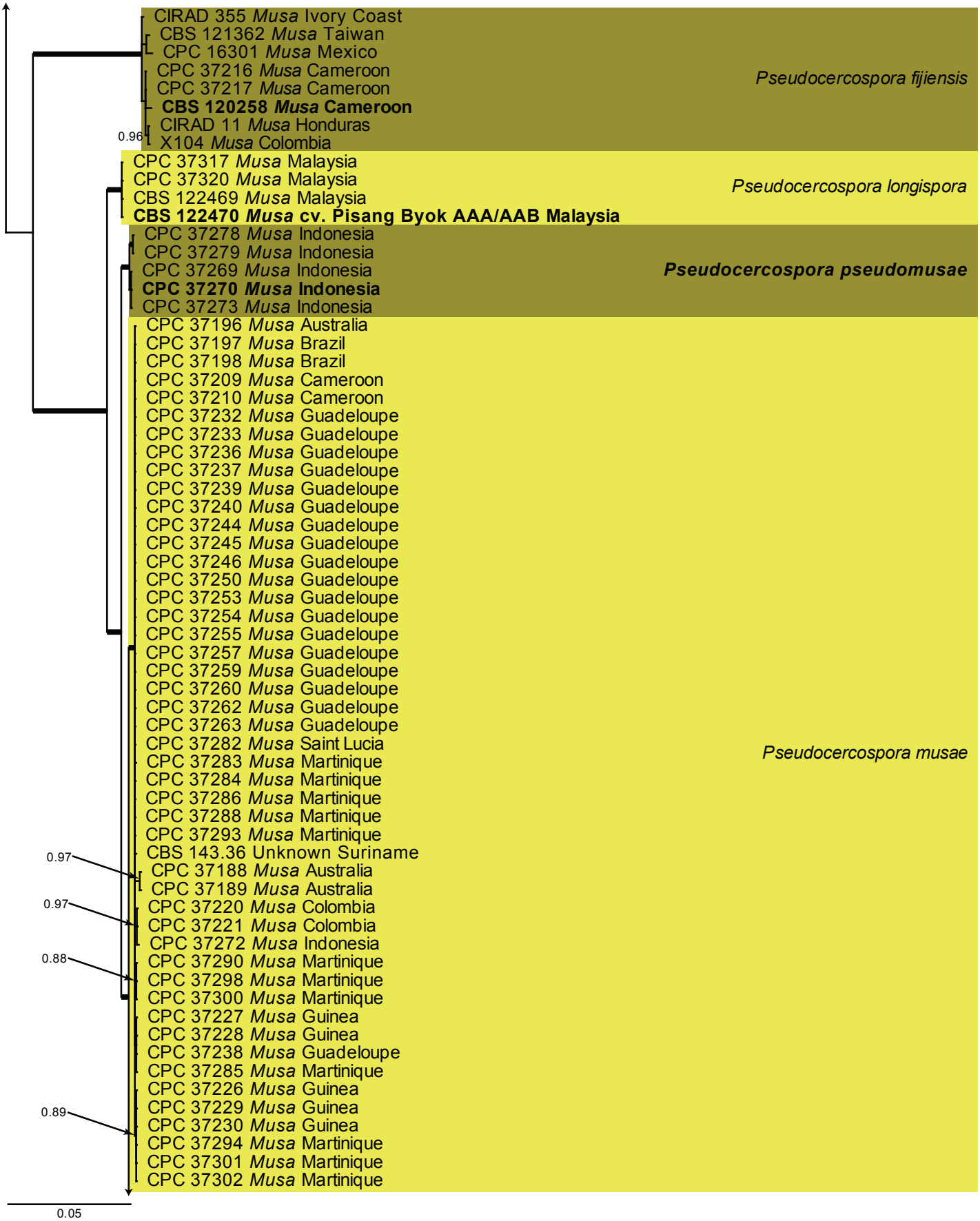

Fig. 1. (Continued).

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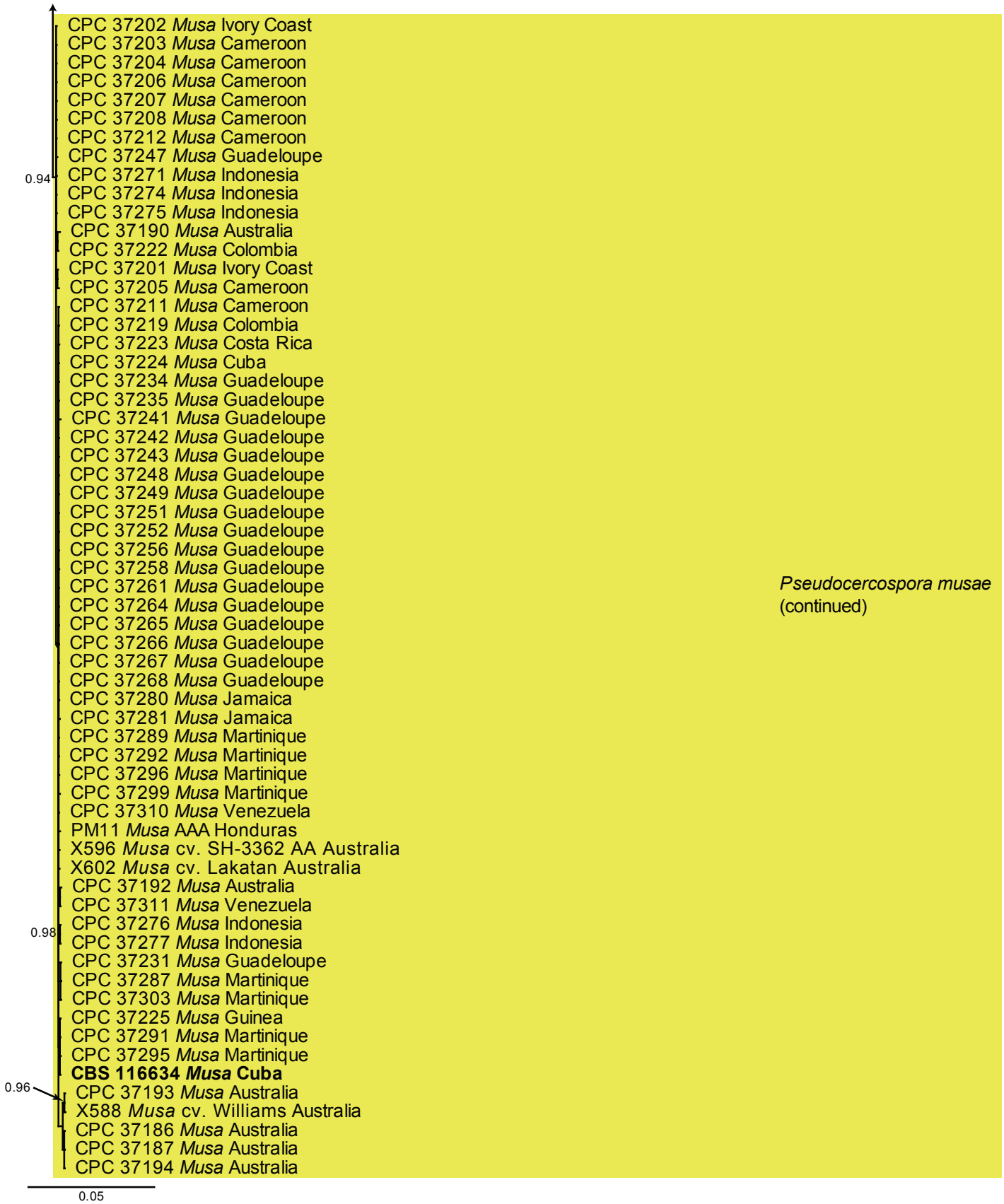

Fig. 1. (Continued).

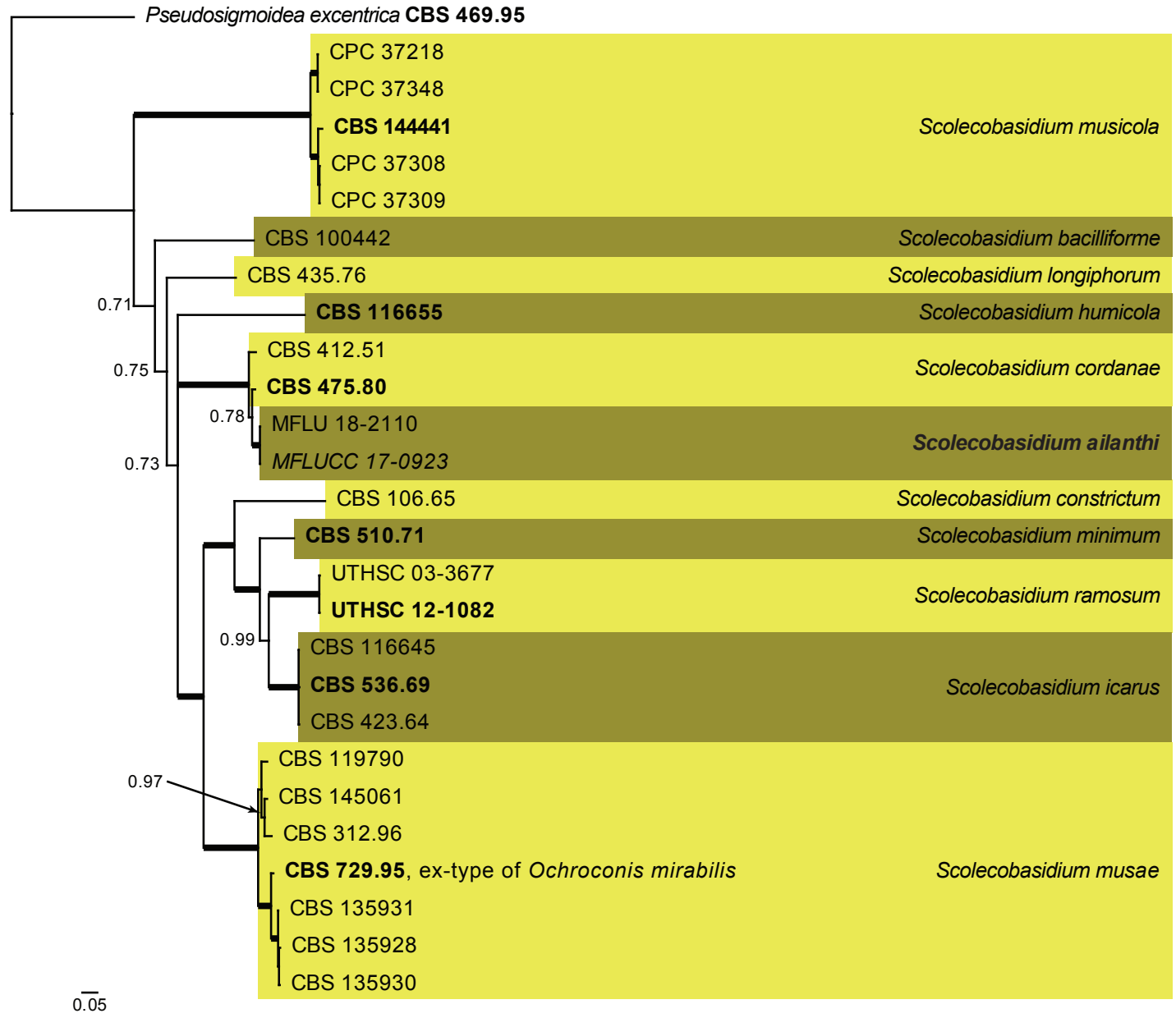

Fig. 2. Consensus phylogram (50 % majority rule) resulting from a Bayesian analysis of the multigene *Scolecobasidium* sequence alignment. Bayesian posterior probabilities (PP) > 0.70 are shown at the nodes and thickened lines represent nodes with PP = 1.00. The scale bar represents the expected changes per site. Species are indicated with coloured blocks to the right of the tree. The tree was rooted to *Pseudosigmoidea excentrica* (= *Scolecobasidium excentricum*; culture CBS 469.95). The taxonomic novelty described in this study and the cultures with a type status are indicated in bold face.

Table 2. Substitution models and other statistical measures used for Bayesian analyses in this study.

Analysis	Number of ingroup sequences	Number of generations	Number of trees used	[1]Substitution models used for Bayesian analyses; Number of unique site patterns				
				ITS	*act*	*rpb2*	*tef1*	*tub2*
Ochroconis	26	100 000	15 002	GTR+I+G; 462	HKY+G; 186	–	HKY+I+G; 332	GTR+I+G; 262
Pseudocercospora	184	6 680 000	100 202	HKY+I; 75	HKY+G; 69	GTR+I; 178	HKY+G; 183	–

[1] ITS: internal transcribed spacer regions and intervening 5.8S nrRNA gene; *act*: partial actin gene; *tef1*: partial translation elongation factor 1-alpha gene; *rpb2*: partial DNA-directed RNA polymerase II second largest subunit; *tub2*: partial beta-tubulin gene.

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Taxonomy

Pseudocercospora pseudomusae Crous & Carlier, ***sp. nov.*** MycoBank MB837605. Fig. 3.

Etymology: Name reflects the genetic similarity to *Pseudocercospora musae*.

Colonies sporulating on PDA. *Conidiophores* aggregated in dense fascicles forming sporodochia on agar surface; consisting of septate, medium brown, thin-walled, smooth, subcylindrical conidiophores frequently branched below, 20–60 × 3–5 µm. *Conidiogenous cells* integrated, terminal and intercalary, proliferating sympodially, subcylindrical, smooth, olivaceous, 13–20 × 3–4 µm. *Conidia* solitary, olivaceous, thin-walled, smooth, subcylindrical, straight to curved, apex obtuse, base truncate, (60–)70–80(–100) × (2.5–)3 µm, (2–)4–5(–6)-septate.

Culture characteristics: Colonies erumpent, spreading, surface folded, with sparse to moderate aerial mycelium and even, lobate margins, reaching 8 mm after 2 wk at 25 °C in the dark. On MEA and PDA surface olivaceous grey, reverse iron-grey. On OA surface olivaceous grey with diffuse yellow pigment in agar (more prominent in isolates CPC 37273, 37378 and 37279).

Typus: **Indonesia**, on leaves of *Musa* sp., 1988, *J. Carlier* (**holotype** CBS H-24557, culture ex-type CPC 37270 = IDN 02 = CBS 147147).

Additional materials examined: **Indonesia**, on leaves of *Musa* sp., 1988, *J. Carlier* CPC 37269 = IDN 01 = CBS 147148; on leaves of *Musa* sp., 1988, *J. Carlier*, 37273 = IDN 29 = CBS 147149; on leaves of *Musa* sp., 1989, *J. Carlier*, CPC 37278 = IDN 57 = CBS 147150, CPC 37279 = IDN 58 = CBS 147151.

Notes: *Pseudocercospora pseudomusae* is closely related to *P. musae*, which has more obclavate-cylindrical conidia, that are (10–)20–80(–110) × (2–)2.5–5(–6) µm, (0–)2–7(–9)-septate (Braun *et al.* 2014). Conidia of *P. pseudomusae* differ in being more subcylindrical (not obclavate), and on average being longer than those of *P. pseudomusae.*

The five isolates of *P. pseudomusae* clustered together with full support in the multi-gene phylogeny (Fig. 1). In the individual gene phylogenies based on distance and parsimony analyses (data not shown), the species can be distinguished from *P. musae* based on ITS and *rpb2* while the distinction is less well-defined for *tef1* and the strains are intermingled on *act*. The ITS sequence of CPC 37270 is 455/468 (97 %, including one indel) to 460/468 (98 %, no indels) similar to the included *P. musae* ITS sequences. The *act* sequence of CPC 37270 is 545/550 (99 %, no indels) to 498/501 (99 %, no indels) similar to the included *P. musae act* sequences. The *rpb2* sequence of CPC 37270 is 588/592 (99 %, no indels) to 647/650 (99 %, no indels) similar to the included *P. musae rpb2* sequences. The *tef1* sequence of CPC 37270 is 448/453 (99 %, no indels) to 449/453 (99 %, no indels) similar to the included *P. musae tef1* sequences.

Several of the isolates associated leaf speckle turned out to be representative of the genus *Scolecobasidium*, which together with its generic synonym, *Ochroconis*, were recently treated by Shen *et al.* (2020). All species of *Ochroconis* for which DNA data are available have since been transferred to *Scolecobasidium*, except *O. ailanthi*, which is thus treated below.

Scolecobasidium ailanthi (Jayasiri *et al.*) Crous, ***comb. nov.*** MB837607.
Basionym: *Ochroconis ailanthi* Jayasiri *et al.*, *Mycosphere* **10**: 171. 2019.

Description and illustration: Jayasiri *et al.* (2019).

List of Cercosporoid taxa associated with leaf spots of *Musa*

Cercospora apii Fresen. (= *Cercospora hayi* Calp.)
Type: *Musa paradisiaca* var. *sapientum*, Cuba (ex-type culture of *C. hayi*, ATCC 12234); *Musa* cv. Cavendish, India (CBS H-20035, culture CBS 119395).
Disease: Leaf spots.
Reference: Groenewald *et al*. (2013).

Cercospora musae var. ***paradisiaca*** Bat. & R. Garnier
Type: *Musa paradisiaca*, Brazil.
Disease: Leaf spots.
Reference: Braun *et al.* (2014).
[Not known from culture.]

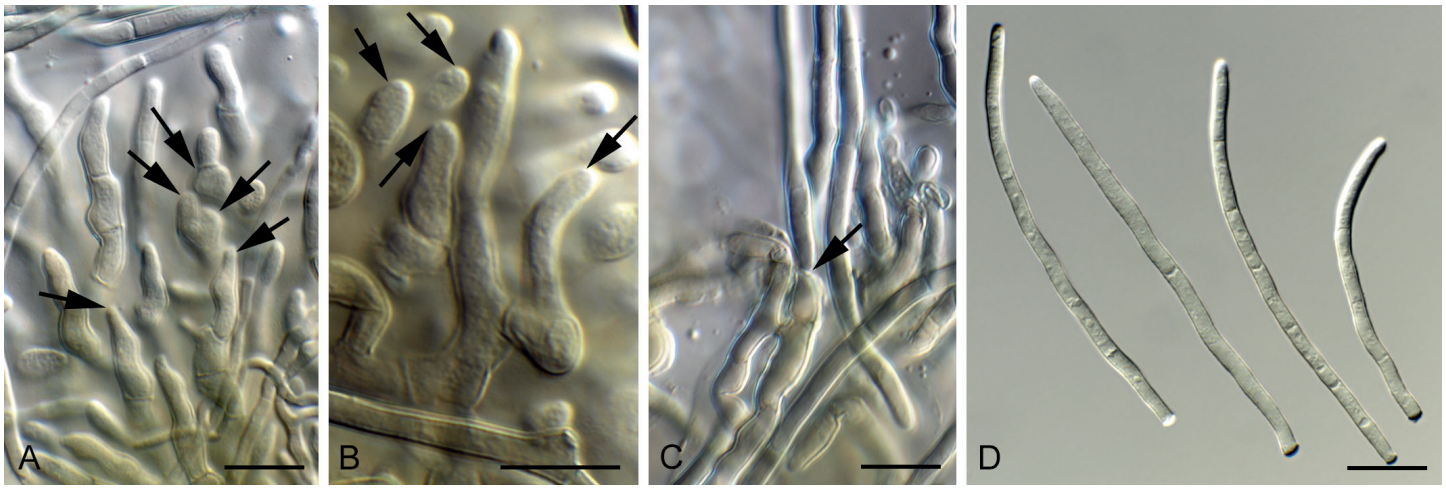

Fig. 3. *Pseudocercospora pseudomusae* (CPC 37270). **A–C.** Conidiogenous cells giving rise to conidia (arrows indicate loci). **D.** Conidia. Scale bars = 10 µm.

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Cercospora pingtungensis T.Y. Lin & J.M. Yen
Type: *Musa acuminata, M. cavendishii*, China, Taiwan.
Disease: Leaf spots.
Reference: Braun *et al.* (2014), tentatively reduced to synonymy with *Pseudocercospora fijiensis*.
[Not known from culture.]

Cladocillium musae Chun-Hao Chen & R. Kirschner
Type: *Musa itinerans,* Taiwan (TNM, culture BCRC FU30634).
Disease: Not associated with distinct leaf spots; secondary coloniser.
Reference: Chen *et al*. (2020).

Metulocladosporiella chiangmaiensis Y. Marín, Cheew. & Crous
Type: Thailand, *Musa* sp. (holotype CBS H-23393, culture ex-type CBS 143918 = CPC 18646).
Disease: Metulocladosporiella leaf speckle.
Reference: Marin-Felix *et al.* (2019).

Metulocladosporiella malaysiana Y. Marín & Crous
Type: Malaysia, *Musa* sp. (holotype CBS H-23394, culture ex-type CBS 143919 = CPC 18131).
Disease: Metulocladosporiella leaf speckle.
Reference: Marin-Felix *et al.* (2019).

Metulocladosporiella musae (E.W. Mason) Crous *et al*. (= *Cladosporium musae* E.W. Mason)
Type: Honduras, *Musa* sp. (epitype CBS H-14788, CBS 161.74 = ATCC 36973).
Disease: Metulocladosporiella leaf speckle.
Reference: Marin-Felix *et al.* (2019).

Metulocladosporiella musicola Crous, Schroers & J.Z. Groenew.
Type: Africa, *Musa acuminata* subgr. Cavendish 'Grand Nain' (holotype CBS H-14787, culture ex-type CBS 110960 = CPC 4629).
Disease: Metulocladosporiella leaf speckle.
Reference: Crous *et al*. (2006).

Metulocladosporiella musigena Y. Marín, Cheew. & Crous
Type: Thailand, *Musa* sp. (holotype CBS H-23395, culture ex-type CBS 143920 = CPC 31490).
Disease: Metulocladosporiella leaf speckle.
Reference: Marin-Felix *et al.* (2019).

Metulocladosporiella samutensis Y. Marín, Luangsa-ard & Crous
Type: Thailand, *Musa* sp. (holotype CBS H-23396, culture ex-type CBS 143921 = CPC 33939).
Disease: Metulocladosporiella leaf speckle.
Reference: Marin-Felix *et al.* (2019).

Mycosphaerella formosana T.Y. Lin & J.M. Yen
Type: Taiwan, *Musa* sp.
Disease: Leaf spots.
Reference: Aptroot (2006).
[Not known from culture.]

Mycosphaerella henriquesiana G. Winter
Type: Africa, *Musa* sp.
Disease: Leaf spots.
Reference: Aptroot (2006).
[Not known from culture.]

Mycosphaerella liukiuensis Sawada
Type: Taiwan, *Musa formosana*.
Disease: Leaf spots.
Reference: Aptroot (2006).
[Not known from culture.]

Mycosphaerella musae (Speg.) Syd. & P. Syd.
Type: Argentina, *Musa sapientum* (holotype LPS, slide ex-type IMI 91165).
Disease: Leaf speckle.
Reference: Aptroot (2006), Arzanlou *et al.* (2008).
[Not known from culture.]

Pseudocercospora assamensis Arzanlou & Crous
Type: India, *Musa* cv. Nanderan (Plantain) (holotype CBS H-20044, culture ex-type X988 = CBS 122467).
Disease: Leaf spots.
Reference: Arzanlou *et al*. (2008).

Pseudocercospora eumusae Crous & Mour. (= *Mycosphaerella eumusae* Crous & Mour.)
Type: Réunion (France), *Musa* sp. (holotype PREM 57315, cultures ex-type (CIRAD 1156, 1157 = CPC 4579, 4580 = CBS 114824, CBS 114825).
Disease: Eumusae leaf spot.
Reference: Crous & Mourichon (2002).

Pseudocercospora fengshanensis (T.Y. Lin & J.M. Yen) J.M. Yen & S.K. Sun
Type: China, Taiwan, *Musa acuminata*.
Disease: Leaf spots.
Reference: Braun *et al.* (2014).
[Not known from culture.]

Pseudocercospora fijiensis (M. Morelet) Deighton (= *Mycosphaerella fijiensis* M. Morelet)
Type: Cameroon, *Musa* sp. (epitype CBS H-20037, culture ex-epitype CIRAD 86 = CBS 120258).
Disease: Black Sigatoka or black leaf streak disease.
Reference: Arzanlou *et al*. (2008).

Pseudocercospora indonesiana Arzanlou & Crous
Type: Indonesia, *Musa* cv. Buai (holotype CBS H-20045, culture ex-type X992 = CBS 122473).
Disease: Leaf spots.
Reference: Arzanlou *et al*. (2008).

Pseudocercospora longispora Arzanlou & Crous
Type: Malaysia, *Musa* cv. Pisang Byok AAA/AAB (holotype CBS H-20043, culture ex-type X475 = CBS 122470).
Disease: Leaf spots.
Reference: Arzanlou *et al*. (2008).

Pseudocercospora musae (Zimm.) Deighton (= *Mycosphaerella musicola* R. Leach ex J.L. Mulder)
Type: Cuba, *Musa* sp. (epitype CBS H-20038, culture ex-epitype IMI 123823 = CBS 116634).
Disease: Yellow Sigatoka disease.
Reference: Arzanlou *et al*. (2008)

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Pseudocercospora musae-sapienti (A.K. Kar & M. Mandal) U. Braun & Mouch.
Type: India, Wallis, *Musa paradisiaca*.
Disease: Leaf spots.
Reference: Braun *et al.* (2014).
[Not known from culture.]

Pseudocercospora musicola U. Braun
Type: Taiwan, *Musa acuminata*.
Disease: Leaf spots.
Reference: Braun *et al.* (2014).
[Not known from culture.]

Pseudocercospora pseudomusae Crous & Carlier
Type: Indonesia, *Musa* sp. (holotype CBS H-24557, culture ex-type CPC 37270 = IDN 02 = CBS 147147).
Disease: Leaf spots.
Reference: Present study.

Rhachisphaerella mozambica (Arzanlou & Crous) Videira & Crous (= *Mycosphaerella mozambica* Arzanlou & Crous)
Type: Mozambique, *Musa* sp. (holotype CBS H-20039, culture ex-type X34 = CBS 122464).
Disease: Leaf spots.
Reference: Arzanlou *et al*. (2008), Videira *et al.* (2017).

Scolecobasidium musae G.Y. Sun & Lu Hao [= *Ochroconis musae* (G.Y. Sun & Lu Hao) Samerp. & de Hoog]
Type: China, *Musa basjoo* (holotype HMAS 243664, culture ex-type CGMCC 3.14990 = 0HLHKBJ-22).
Disease: Leaf speckle.
Reference: Samerpitak *et al.* (2015).

Scolecobasidium musicola (Crous) Crous, M. Shen & Y. Zhang ter (= *Ochroconis musicola* Crous)
Type: Malaysia, *Musa* sp. (holotype CBS H-23562, culture ex-type CBS 144441).
Disease: Leaf speckle.
Reference: Shen *et al.* (2020).

Uwebraunia musae (Arzanlou & Crous) Crous (= *Dissoconium musae* Arzanlou & Crous)
Type: India, *Musa* cv. Nendran (Plantain) AAB (holotype CBS H-20036, culture ex-type X1021 = CBS 122453).
Disease: Leaf spots.
Reference: Arzanlou *et al.* (2008).

Zasmidium biverticillatum (Arzanlou & Crous) Videira & Crous (= *Ramichloridium biverticillatum* Arzanlou & Crous)
Type: Surinam, *Musa sapientum* (reference strain CBS 335.36).
Disease: Zasmidium leaf speckle.
References: Arzanlou *et al.* (2007), Videira *et al.* (2017).

Zasmidium ducassei (R.G. Shivas *et al.*) Y. Marín & Crous (= *Ramichloridium ducassei* R.G. Shivas *et al.*)
Type: Australia, *Musa acuminata* × *balbisiana* (holotype and ex-type culture BRIP 53367).
Disease: Zasmidium leaf speckle.
References: Shivas *et al*. (2011), Marin-Felix *et al*. (2019).

Zasmidium musae (Arzanlou & Crous) Crous & U. Braun (= *Stenella musae* Arzanlou & Crous)
Type: Tonga, Wind Ward Isles, *Musa* cv. TU8 AAAA, *Musa* cv. (holotype CBS H-20047, culture ex-type X745 = CBS 122477).
Disease: Zasmidium leaf speckle.
Reference: Arzanlou *et al.* (2008).

Zasmidium musae-banksii Videira & Crous (= *Ramichloridium australiense* Arzanlou & Crous)
Type: Australia, *Musa banksii* (holotype CBS H-19928, culture ex-type CBS 121710).
Disease: Zasmidium leaf speckle.
Referencse: Arzanlou *et al.* (2007), Videira *et al.* (2017).

Zasmidium musicola (Arzanlou & Crous) Crous & U. Braun (= *Stenella musicola* Arzanlou & Crous)
Type: India, *Musa* cv. Grand Nain AAA (holotype CBS H-20046, culture ex-type X1019 = CBS 122479).
Disease: Zasmidium leaf speckle.
Reference: Arzanlou *et al.* (2008).

Zasmidium musigenum Videira & Crous [= *Ramichloridium musae* (M.B. Ellis) de Hoog]
Type: Surinam, *Musa sapientum* (ex-type culture CBS 365.36 = JCM 6973 = MUCL 9556).
Disease: Zasmidium leaf speckle.
References: Arzanlou *et al.* (2007), Videira *et al.* (2017).

Zasmidium queenslandicum (Arzanlou & Crous) Crous & U. Braun (= *Stenella queenslandica* Arzanlou & Crous)
Type: Australia, *Musa banksii* (holotype CBS H-20050, culture ex-type CBS 122475).
Disease: Zasmidium leaf speckle.
Reference: Arzanlou *et al.* (2008)

DISCUSSION

The Sigatoka leaf spot complex is the most important complex of leaf diseases of banana (Mourichon & Fullerton 1990, Jones 2019). A revision of the taxonomy of this complex by Arzanlou *et al.* (2008) saw the introduction of eight new species, although their importance as foliar pathogens remains largely unknown. Many isolates that were in the past identified as *P. musae* based on general symptomatology, are now ascribed to one of these new taxa. The aim of the present study, therefore, was to revisit a global set of 228 isolates identified as *P. musae, P. eumusae* or other close relatives based on preliminary morphological analysis and ITS sequencing, and resolve their identity by employing multigene DNA sequence analysis and deep morphological observations. Based on these results (Fig. 1), 48 isolates were confirmed as *P. eumusae*, from India, Malaysia, Mauritius, Nigeria, Réunion (France), Sri Lanka, Thailand and Vietnam, while 104 isolates originally identified as *P. musae* were confirmed as this taxon from Australia, Brazil, Cameroon, Colombia, Costa Rica, Cuba, Guadeloupe, Guinea, Indonesia, Ivory Coast, Jamaica, Martinique (France), Saint Lucia and Venezuela, and two isolates as *P. fijiensis* (Cameroon), two isolates as *P. longispora* (Malaysia) and five isolates as a new species, *P. pseudomusae*, which is thus far only known from Indonesia. The remainder of the strains studied belonged to

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Zasmidium musae (five strains), *Scolecobasidium musicola* (four strains, Fig. 2), *Parapallidocercospora thailandica* (three strains), while one strain was identical to *Pantospora guazumae* and the last strain represented a *Penicillium* infection and was discarded from further analyses (Table 1). Seven strains were tentatively identified as *Mycosphaerella musae* (Australia, Brazil, Cameroon, Martinique and the Cook Islands) (Table 1). Although leaf speckle of *Musa* spp. has traditionally been ascribed to *M. musae*, this species was originally described from a sexual morph collected on *Musa sapientum* in Argentina, and its exact identity remains to be determined (Arzanlou *et al.* 2008).

Other than the Sigatoka disease complex, several other disease complexes have also recently been revised. "Cladosporium leaf speckle" was shown to be caused by several species of *Metulocladosporiella* (Marin-Felix et al. 2019) and should better be renamed as "Metulocladosporiella leaf speckle", and "Taiwan leaf speckle" ascribed to a complex of various *Zasmidium* spp. (Videira *et al.* 2017), which would in future be better referred to as "Zasmidium leaf speckle", as these taxa have a wider distribution than Taiwan only. Several other species also causing leaf speckle symptoms have been assigned to *Scolecobasidium* (Shen *et al.* 2020), but the majority of foliar pathogens on banana have to date simply been recorded as causing "leaf spots". A complicating factor is that many of the taxa listed here have not been recorded since they were initially described, and more needs to be done to resolve their phylogeny and ecology.

Conflict of interest: The authors declare that there is no conflict of interest.

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