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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 leaf 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

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>) (Kato & 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

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	ITS	act	GenBank accession number ²	<i>tef1</i> ; <i>rpb2</i> ; <i>tub2</i>
<i>Pseudocercospora eumusae</i>	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; –		

Table 1. (Continued).

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

Table 1. (Continued).

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

Species **Collection number(s)¹** **Substrate including host, origin and collection year** **GenBank accession number²**

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

Table 1. (Continued).

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

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

Table 1. (Continued).

Species	Collection number(s) ¹	Substrate including host, origin and collection year	GenBank accession number ²		
			ITS	act	tefi; rpb2; tub2
<i>Scolecobasidium bacilliforme</i>	CBS 100442	Biofilm on stainless steel in drinking water; Germany; –	NR_155566.1	KT272051.1	KT272070.1; –; KT272059.1
<i>Scolecobasidium constrictum</i>	CBS 106.65	Soil under <i>Brassica napus</i> ; Germany; –	HQ667518.1	HQ916960.1	JF440551.1; –; –
<i>Scolecobasidium cordanae</i>	CBS 412.51 = MUCL 9472 = QM 373b	–; USA; –	HQ667540.1	KF155907.1	KF155980.1; –; KF156200.1
<i>Scolecobasidium cordanae</i>	CBS 475.80, ex-type	<i>Mauritia minor</i> ; Colombia; 1979	NR_132051.1	HQ916976.1	KF155981.1; –; KF156197.1
<i>Scolecobasidium humicola</i>	CBS 116655 = IMI 110131 = UAMH 10241, ex-type	Peat soil; Canada; –	NR_111437.1	HQ916963.1	JF440553.1; –; HQ877631.1
<i>Scolecobasidium icarus</i>	CBS 116645	Sandy soil; Canada; –	HQ667525.1	LM644599.1	–; –; LM644604.1
	CBS 423.64 = MUCL 10160	Rhizosphere of <i>Solanum tuberosum</i> , 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
<i>Scolecobasidium longiphorum</i>	CBS 435.76 = UAMH 3972	Soil under asphalt paving of car park; Canada; –	KF156038.1	KF155908.1	KF155978.1; –; KF156182.1
<i>Scolecobasidium minimum</i>	CBS 510.71 = ATCC 22631 = IMI 082933, ex-type	Rhizosphere of <i>Gossypium arboreum</i> ; Nigeria; –	NR_145366.1	KF155945.1	KF156007.1; –; KF156172.1
<i>Scolecobasidium musae</i>	CBS 119790 = IMI 138059	Soil; Egypt; –	KT272077.1	KT272053.1	KT272072.1; –; KT272061.1
<i>Scolecobasidium musae</i>	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	<i>Persea americana</i> ; 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 <i>Ochroconis mirabilis</i>	Regulator of diver; –; –	KF156029.1	KF155948.1	KF155999.1; –; KF156171.1
<i>Scolecobasidium musicola</i>	CBS 144441 = CPC 32927, ex-type	<i>Musa</i> ; Malaysia; 2010	NR_160360.1	–	MH327887.1; MH327876.1; MH327898.1
	CPC 37218 = CIRAD-CMR 2064	<i>Musa</i> ; Cameroon; 1999	MW063427.1	MW070776.1	MW071095.1; MW070921.1; MW071115.1
	CPC 37308 = CIRAD-MTQ 0605	<i>Musa</i> ; France; Martinique; 1992	MW063428.1	MW070777.1	MW071096.1; MW070922.1; MW071116.1
	CPC 37309 = CIRAD-MTQ 0606	<i>Musa</i> ; France; Martinique; 1992	MW063429.1	MW070778.1	MW071097.1; MW070923.1; MW071117.1
	CPC 37348 = CIRAD-IND 008	<i>Musa</i> ; India; –	MW063430.1	MW070779.1	MW071098.1; –; –

Species	Collection number(s) ¹	Substrate including host, origin and collection year	GenBank accession number ²		
			ITS	act	tef1; rpb2; tub2
<i>Scolecobasidium ramosum</i>	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
<i>Trochophora simplex</i> (Outgroup)	CBS 124744 = KACC 42362	<i>Daphniophyllum macropodium</i> ; Korea; -	GU269872.1	GU320568.1	GU384580.1; KX462666.1; -
Strains identified based on sequence similarity					
<i>Mycosphaerella musae</i>	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; -
<i>Pantospora guazumae</i>	CPC 37195 = CIRAD-AUS 130	Musa; Australia: Queensland; 1993	MW063438.1	MW070787.1	MW071106.1; MW070930.1; -
<i>Parapallidocercospora thailandica</i>	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; -
<i>Zosmidium musae</i>	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, Bakenham 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 translation elongation factor 1-alpha gene; rpb2: partial DNA-directed RNA polymerase II second largest subunit; tub2: partial beta-tubulin gene.

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).

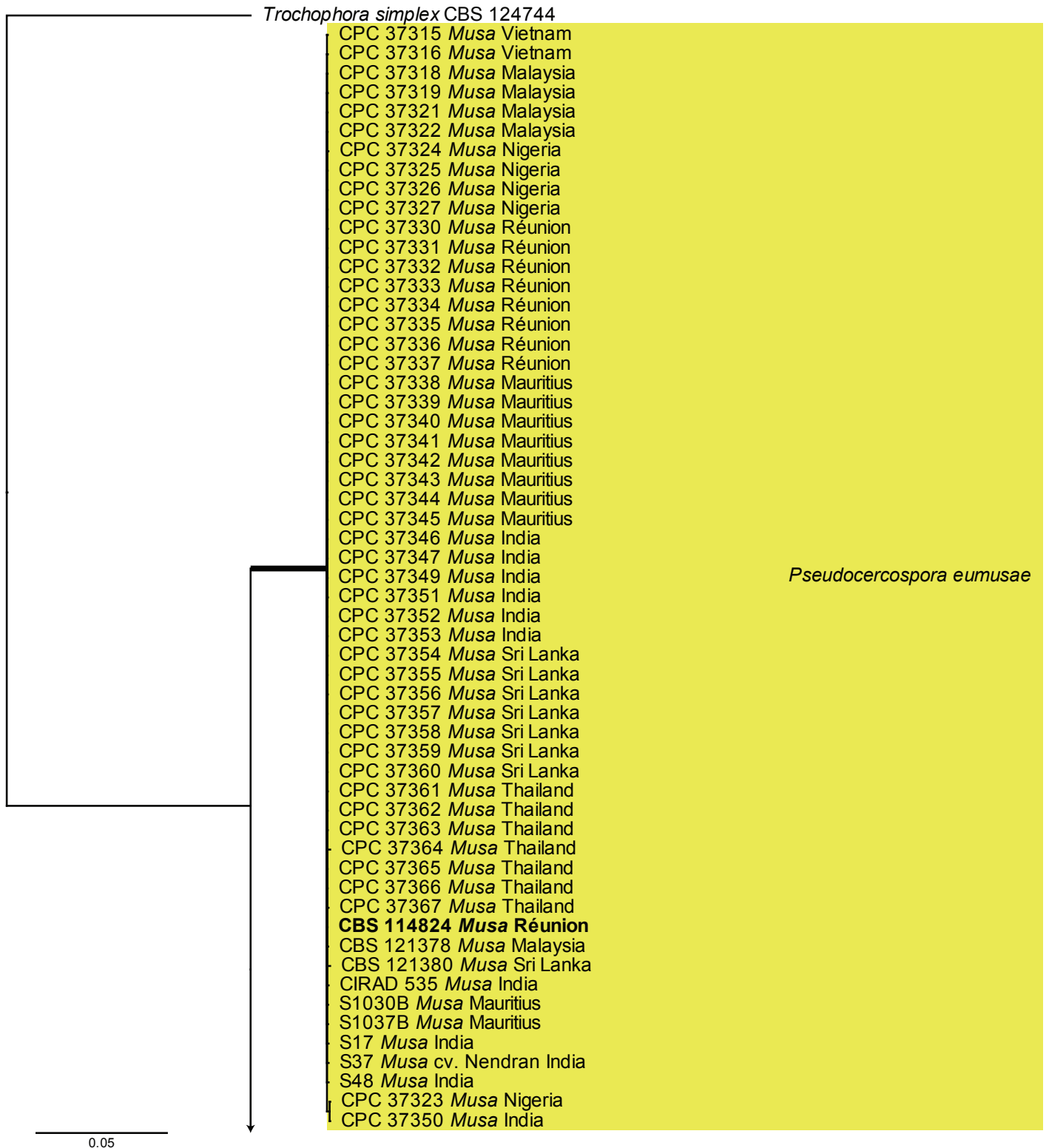


Fig. 1. Consensus phylogram (50 % majority rule) resulting from a Bayesian analysis of the multigene *Pseudocercospora* sequence alignment. Bayesian posterior probabilities (PP) > 0.84 are shown at the nodes and thickened lines represent nodes with PP = 1.00. The scale bar represents the expected changes 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.

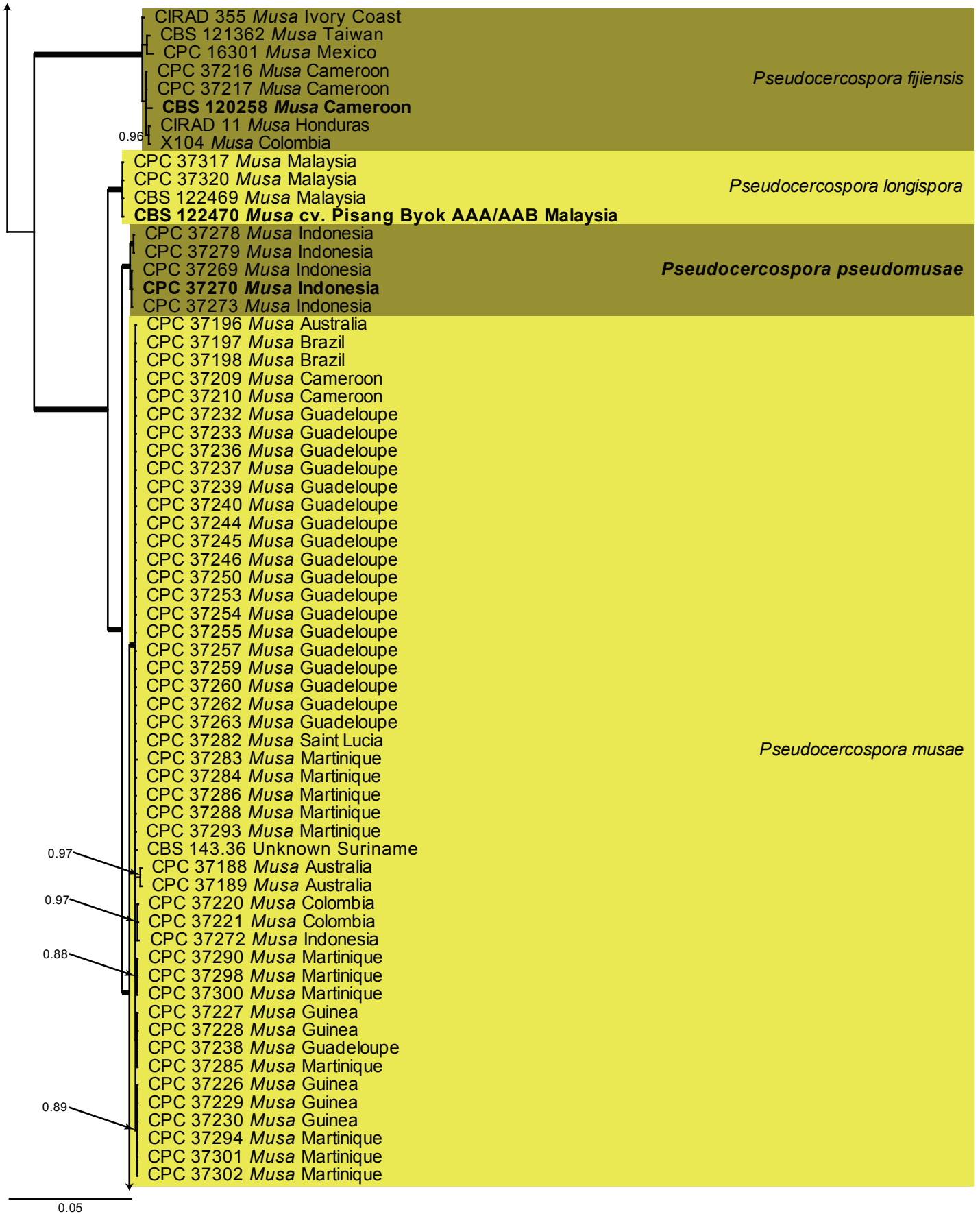


Fig. 1. (Continued).

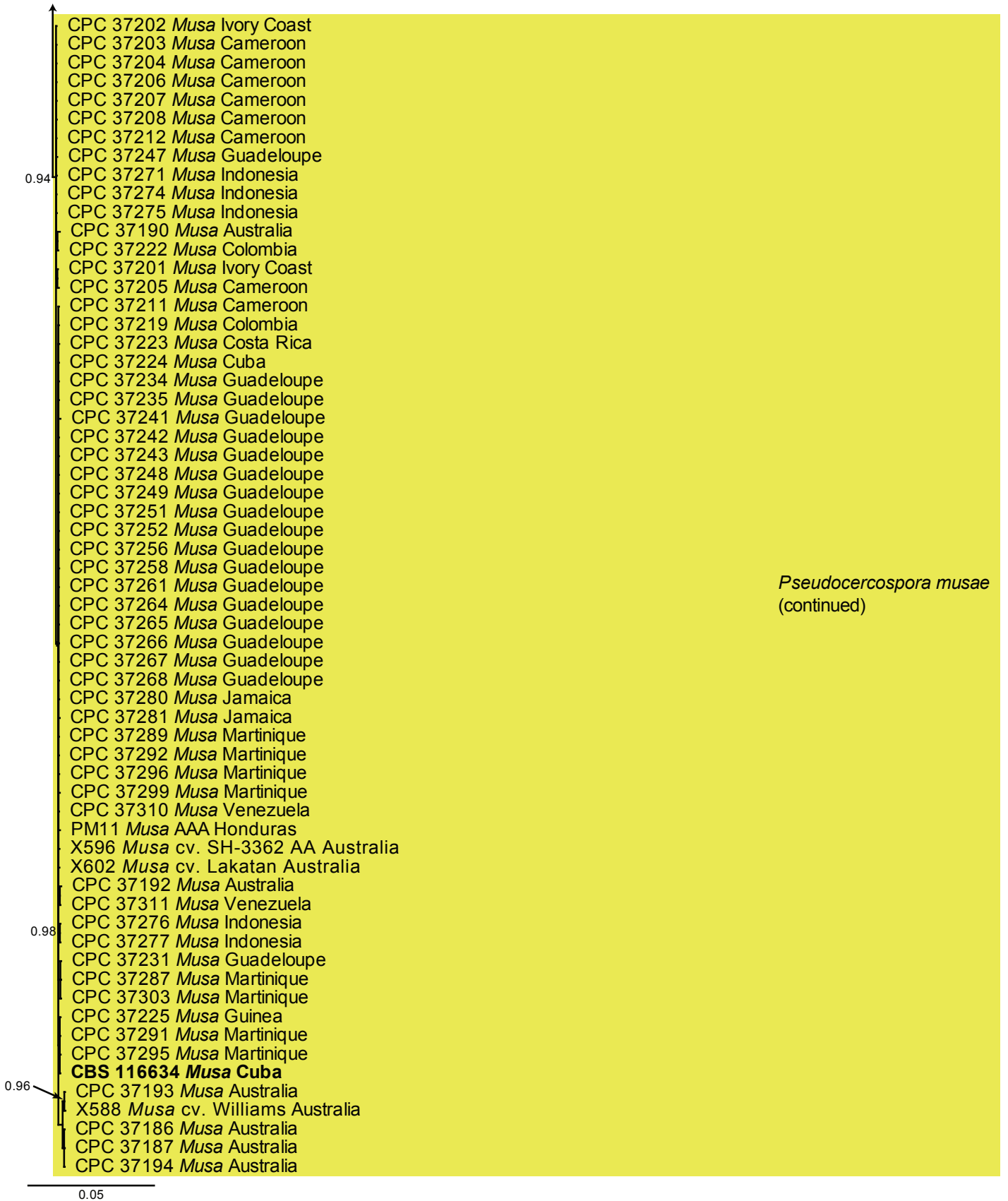


Fig. 1. (Continued).

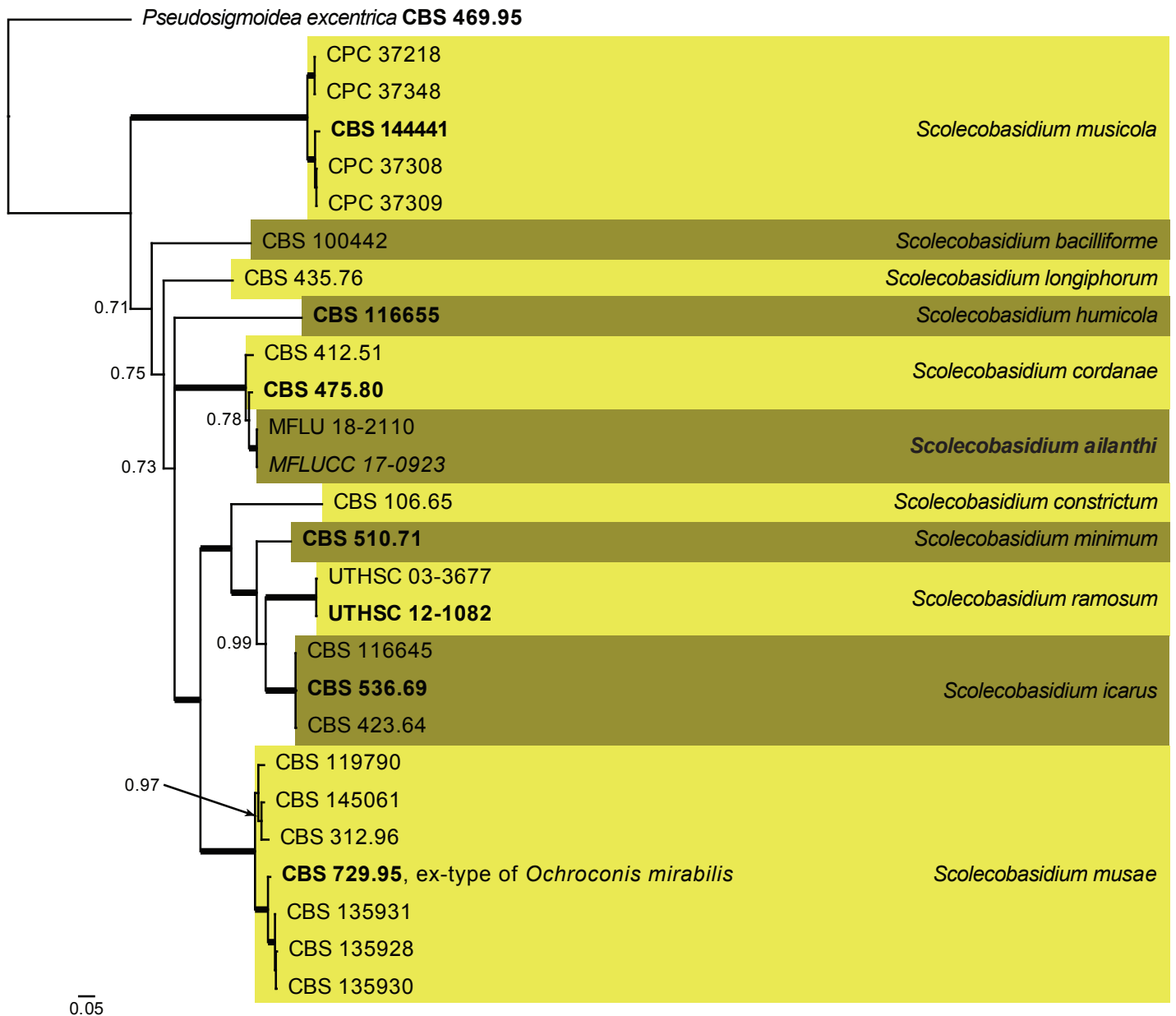


Fig. 2. Consensus phylogram (50 % majority rule) resulting from a Bayesian analysis of the multigene *Scolecobasidium* sequence alignment. Bayesian posterior probabilities (PP) > 0.70 are shown at the nodes and thickened lines represent nodes with PP = 1.00. The scale bar represents the expected changes per site. Species are indicated with coloured blocks to the right of the tree. The tree was rooted to *Pseudosigmaidea 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	<i>act</i>	<i>rpb2</i>	<i>tef1</i>	<i>tub2</i>
<i>Ochroconis</i>	26	100 000	15 002	GTR+I+G; 462	HKY+G; 186	–	HKY+I+G; 332	GTR+I+G; 262
<i>Pseudocercospora</i>	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.

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.]

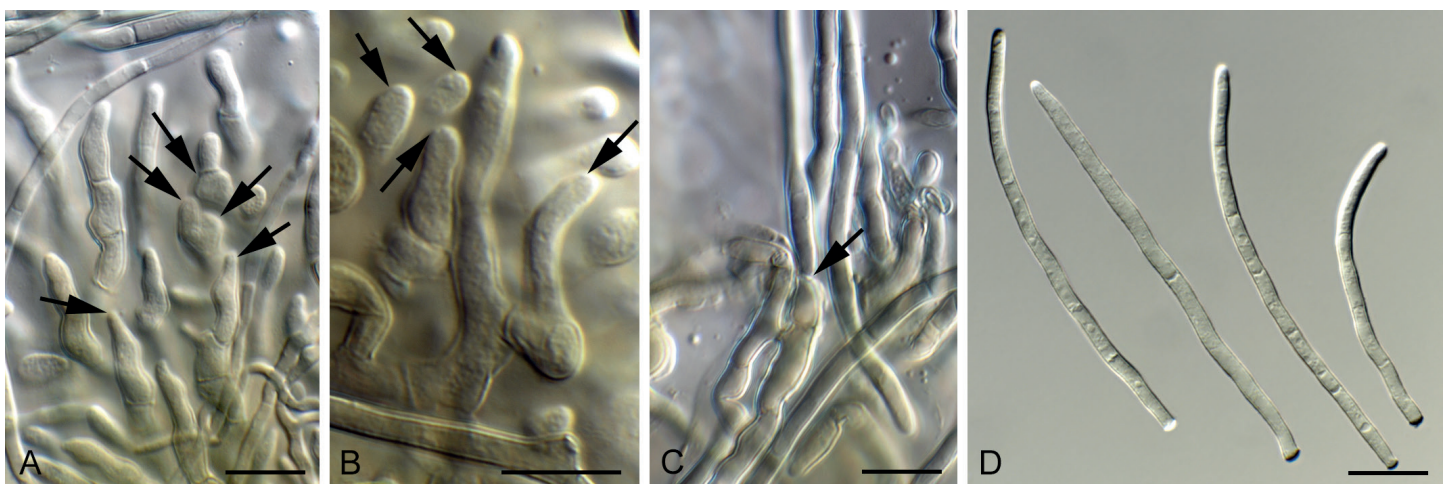


Fig. 3. *Pseudocercospora pseudomusae* (CPC 37270). **A–C.** Conidiogenous cells giving rise to conidia (arrows indicate loci). **D.** Conidia. Scale bars = 10 µm.

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 liukiensis 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)

Pseudocercospora musae-sapientii (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), Marín-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.

Reference: 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

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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