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FULL PAPER

Epitypification of *Colletotrichum musae*, the causative agent of banana anthracnose

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Abstract *Colletotrichum musae* is an important pathogen causing banana anthracnose. The type material (K) had no conidia or sclerotia, and DNA could not be extracted from a darkened area of the herbarium sample. This sample thus provides few characters to delimit this species from other closely related taxa in the "gloeosporioides" species complex. An epitype is therefore designated for *C. musae* to stabilize the application of the species name. A detailed morphological description is provided from the epitype. Multilocus phylogenetic analysis indicates that *C. musae* clusters in a distinct lineage in the "gloeosporioides" species complex and is most closely related to *Colletotrichum fructicola.*

Keywords Disease · Morphology · Phylogeny · Plant pathogen · Taxonomy

Introduction

Anthracnose of banana, caused by *Colletotrichum musae* (Berk. & M.A. Curtis) Arx, is one of the most important and widely distributed diseases of ripe banana fruit (Meredith 1960a; Stover and Simmonds 1987). *Colletotrichum musae* may form lesions on fruits without skin bruising but produces larger lesions when fruits are damaged (Meredith 1960a). This species is also an important pathogen on wounded green banana fruits (Meredith 1960b; Stover and Simmonds 1987), infecting banana fruits at any time during the growing season in the field (Simmonds and Mitchell 1940). *Colletotrichum musae* is also responsible for crown rot, blossom end rot, and tip rot of banana (Nazriya et al. 2007). This taxon has been found on fruits, leaves, and roots of *Musa* spp. (Meredith 1960a; Simmonds 1965; Israeli and Temkin-Gorodeiski 1977; Pereira et al. 1999; Photita et al. 2001; Anthony et al. 2004; Chillet et al. 2006; Nazriya et al. 2007; Nuangmek et al. 2008).

Colletotrichum musae appears to be host specific to *Musa* species; on the other hand, Mahadtanapuk et al. (2007) reported this taxon as an anthracnose pathogen on flowers of *Curcuma alismatifolia* Gagnep. in Thailand. Identification of this fungus on *C. alismatifolia* was based on morphology and should be confirmed by molecular analysis.

Colletotrichum musae was described by Berkeley (1874) as *Myxosporium musae* Berk. & M.A. Curtis with a brief protologue and transferred to *Colletotrichum* by von Arx (1957). Sutton (1980, 1992) accepted it as a distinct species and provided a brief morphological description. Later, Hyde et al. (2009) pointed out that epitypification is needed to clarify its relationships with other closely related taxa.

Traditionally, identification of *C. musae* was based on morphological characters, e.g., the abundant sporulation, straight and cylindrical conidia, and irregularly shaped appressoria (Sutton 1980). These morphological characters, however, are often overlapping and ambiguous among the "gloeosporioides" species complex. Thus, molecular

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analyses are needed for a precise diagnosis. Although molecular data can provide useful information for species delimitation, studies are generally flawed by the fact the type specimens have not been sequenced (Hyde et al. 2009). Then, we examined type material of *C. musae* borrowed from K for morphological characters. Unfortunately, no conidia or sclerotia could be found in this specimen, which consists of a 136-year-old dried banana pericarp. It was also not possible to extract fungal DNA from darkened areas on the banana pericarp of this type material. Therefore, the type of *C. musae* provided few characters to demarcate this species from other closely related taxa in the "gloeosporioides" species complex. An epitype of *C. musae* is therefore designated to stabilize the application of the species name.

The objective of this study was to (1) designate a suitable specimen with living culture as epitype; (2) morphologically characterize the designated epitype; and (3) infer phylogenetic relationships of *C. musae* with closely related taxa.

Materials and methods

Isolation, morphological examination, and reinoculation experiment

A culture of *C. musae* was obtained from CBS (CBS 116870). This culture was isolated from banana fruit in North America, the original geographic locality of this taxon. Three additional strains of *C. musae* were isolated from banana fruits from Bandu, Chiang Rai Province in northern Thailand to provide a comparison with those from North America. Infected fruits were incubated in moist chambers at room temperature to induce sporulation. Strains were isolated by single-spore isolation (Choi et al. 1999). Pure cultures were stored on potato dextrose agar (PDA) slants and deposited in the culture collection of Mae Fah Luang University Culture Collection (MFLUCC), Chiang Rai, Thailand and BIOTEC Culture Collection (BCC), Pathumthani, Thailand.

Mycelial discs (5 mm diameter) were taken from active sporulating areas near the growing edge of 5-day-old cultures, transferred to PDA, and incubated at 25°C, following the methods of Cai et al. (2009). Colony diameter of three replicate cultures growing on PDA was measured daily for 7 days. Growth rate was calculated as the 7-day average of mean daily growth (mm/day). Appressoria were produced using a slide culture technique in which 10 mm^2 squares of PDA were placed in an empty Petri dish. The edge of the agar was inoculated with spores taken from a sporulating culture, and a sterile cover slip was placed over the inoculated agar (Cai et al. 2009). After 3–7 days, the shape and size of the appressoria formed across the underside of cover slips were studied.

To confirm the pathogenicity of the ex-epitype strain, spore suspensions were inoculated back to banana, apple, pear, jujube, and tomato (three replicates). Sterilized distilled water was used as a control. Inoculated fruits were kept in plastic boxes to maintain humidity. Symptoms were examined after 7 days incubation at room temperature. Detailed protocols follow that of Cai et al. (2009).

DNA extraction, polymerase chain reaction, and sequencing

Isolates were grown on PDA and incubated at 27°C for 7 days. Genomic DNA was extracted by using a Biospin Fungus Genomic DNA Extraction Kit (BioFlux) according to the manufacturer's protocol. Quality and quantity of DNA were estimated visually by staining with GelRed on 1% agarose gel electrophoresis.

Partial actin (ACT), calmodulin (CAL), β-tubulin (TUB2), glutamine synthetase (GS), glyceraldehyde-3-phosphate dehydrogenase (GPDH) genes, and the complete rDNA-internal transcribed spacer (ITS) region from the strains were amplified by polymerase chain reaction (PCR). Primer pairs and PCR amplification conditions were followed as previously described (Prihastuti et al. 2009; Crouch et al. 2009a). DNA sequencing was performed at the SinoGenoMax Company, Beijing.

Sequence alignment and phylogenetic analyses

Sequences from forward and backward primers were aligned to obtain a consensus sequence by using BioEdit (Hall 1999). Sequences of the ex-epitype isolate, along with reference sequences obtained from GenBank (Table 1), were aligned by Clustal X (Thompson et al. 1997). Alignments were optimized manually in BioEdit (Hall 1999). To compare *C. musae* with other *Colletotrichum* species, a combined ACT, CAL, GPDH, TUB2, GS, and ITS sequences dataset was used for phylogenetic reconstruction.

Phylogenetic analyses were performed by using PAUP* 4.0b10 (Swofford 2002). Ambiguously aligned regions were excluded from all analyses. Unweighted parsimony (UP) analysis was performed. Trees were inferred using the heuristic search option with TBR branch swapping and 1,000 random sequence additions. Maxtrees were unlimited, branches of zero length were collapsed, and all multiple parsimonious trees were saved. Descriptive tree statistics such as tree length (TL), consistency index (CI), retention index (RI), rescaled consistency index (RC), homoplasy index (HI), and log likelihood [−ln L] (HKY model) were calculated for trees generated under different optimality criteria. Clade stability was assessed in a

Table 1 Sources of isolates and GenBank accession numbers used in this study for genus *Colletotrichum*

Species name	Culture collection no.[a]	GenBank accession number[b]						Reference
		ACT	TUB2	CAL	GS	GPDH	ITS	
C. asianum	MFLUCC 090232	FJ 903188	FJ 907434	FJ 917501	FJ 972586	FJ 972571	FJ 972605	Prihastuti et al. 2009
C. asianum	MFLUCC 090233[b]	FJ 907424	FJ 907439	FJ 917506	FJ 972595	FJ 972576	FJ 972612	Prihastuti et al. 2009
C. asianum	MFLUCC 090234	FJ 907421	FJ 907436	FJ 917503	FJ 972598	FJ 972573	FJ 972615	Prihastuti et al. 2009
C. cordylinicola	BCC 38872[b]	HM470234	HM470249	HM470237	HM470243	HM470240	HM470246	Phoulivong et al. 2010
C. cordylinicola	BCC38864	HM470233	HM470248	HM470236	HM470242	HM470239	HM470245	Phoulivong et al. 2010
C. fructicola	MFLUCC 090227	FJ 907425	FJ 907440	FJ 917507	FJ 972594	FJ 972577	FJ 972611	Prihastuti et al. 2009
C. fructicola	MFLUCC 090228[b]	FJ 907426	FJ 907441	FJ 917508	FJ 972593	FJ 972578	FJ 972603	Prihastuti et al. 2009
C. fructicola	MFLUCC 090226	FJ 907427	FJ 907442	FJ 917509	FJ 972592	FJ 972579	FJ 972602	Prihastuti et al. 2009
C. gloeosporioides	CORCG4	HM034800	HM034810	HM034802	–	HM034806	HM034808	Phoulivong et al. 2010
C. gloeosporioides	CORCG5	HM034801	HM034811	HM034803	–	HM034807	HM034809	Phoulivong et al. 2010
C. gloeosporioides	CBS 953.97[b]	FJ 907430	FJ 907445	FJ 917512	FJ 972589	FJ 972582	FJ 972609	Phoulivong et al. 2010
C. horii	TSG001	GU133374	GU133375	GU133376	GU133377	GQ329682	AY787483	Wikee et al. 2011
C. horii	TSG002	GU133379	GU133380	GU133381	GU133382	GQ329680	AY791890	Wikee et al. 2011
C. jasmini-sambac	MFLUCC10-0277[b]	HM131507	HM153768	HM131492	HM131502	HM131497	HM131511	Wikee et al. 2011
C. jasmini-sambac	HLTX-01	–	HM153769	HM131493	HM131503	HM131498	HM131512	Wikee et al. 2011
C. jasmini-sambac	CLTA-01	HM131510	HM153772	HM131496	HM131506	HM131501	HM131515	Wikee et al. 2011
C. kahawae	IMI 319418[b]	GU133374	GU133375	GU133376	GU133377	GQ329682	AY787483	Prihastuti et al. 2009
C. kahawae	IMI 363578[b]	GU133379	GU133380	GU133381	GU133382	GQ329680	AY791890	Prihastuti et al. 2009
C. musae	**CBS116870[b]**	**HQ596284**	**HQ596280**	**–**	**HQ596288**	**HQ596299**	**HQ596292**	This study
C. musae	**MFLUCC 10-0976**	**HQ596285**	**HQ596281**	**HQ596296**	**HQ596289**	**HQ596300**	**HQ596293**	This study
C. musae	**MFLUCC 10-0977**	**HQ596286**	**HQ596282**	**HQ596297**	**HQ596290**	**HQ596301**	**HQ596294**	This study
C. musae	**MFLUCC 10-0978**	**HQ596287**	**HQ596283**	**HQ596298**	**HQ596291**	**HQ596302**	**HQ596295**	This study
C. siamense	MFLUCC 090231	FJ 907422	FJ 907437	FJ 917504	FJ 972597	FJ 972574	FJ 972614	Prihastuti et al. 2009
C. siamense	MFLUCC 090230[b]	FJ 907423	FJ 907438	FJ 917505	FJ 972596	FJ 972575	FJ 972613	Prihastuti et al. 2009
C. simmondsii	BRIP 28519[b]	FJ 907428	FJ 907443	FJ 917510	FJ 972591	FJ 972580	FJ 972601	Wikee et al. 2011
C. simmondsii	CBS 294.67	FJ 907429	FJ 907444	FJ 917511	FJ 972590	FJ 972581	FJ 972610	Wikee et al. 2011

ACT actin, *TUB-2* β-tubulin (tub2), *CAL* calmoudulin, *GS* glutamine synthetase, *GDPH* glyceraldehyde-3-phosphate dehydrogenase, *ITS* rDNA-internal transcribed spacer (ITS) region

[a] BRIP: Plant Pathology Herbarium, Department of Primary Industries, Queensland, Australia; CBS: Centraalbureau voor Schimmelcultures, Utrecht, The Netherlands; IMI: CABI Europe–UK, Bakeham Lane, Egham, Surrey TW209TY, UK; MFLU: Mae Fah Luang University, Thailand

[b] The ex-type cultures: the newly generated sequences in this study are shown in bold

bootstrap analysis with 1,000 replicates, each with 10 replicates of random stepwise addition of taxa. Kishino–Hasegawa tests (Kishino and Hasegawa 1989) were performed to determine whether trees were significantly different. Trees were figured in Treeview (Page 1996).

Model of evolution (HKY+G) was estimated by using MrModeltest 2.2 (Nylander 2004). Posterior probabilities (PP) (Rannala and Yang 1996; Zhaxybayeva and Gogarten 2002) were determined by Markov Chain Monte Carlo sampling (BMCMC) in MrBayes 3.0b4 (Huelsenbeck and Ronquist 2001), using the estimated model of evolution. Six simultaneous Markov chains were run for 1,000,000 generations, and trees were sampled every 100th generation (resulting in 10,001 total trees). The first 2,001 trees, which represented the burn-in phase of the analyses, were discarded, and the remaining 8,000 trees were used for calculating posterior probabilities (PP) in the majority rule consensus tree.

Results

Sequences of the ex-epitype strain of *C. musae* (CBS 116870) and three strains from Thailand were obtained and deposited in GenBank (see Table 1), except CAL from the ex-epitype strain, which failed in several attempts of amplification. Phylogenetic relationships were inferred using combined ACT, CAL, TUB2, GS, GPDH, and ITS.

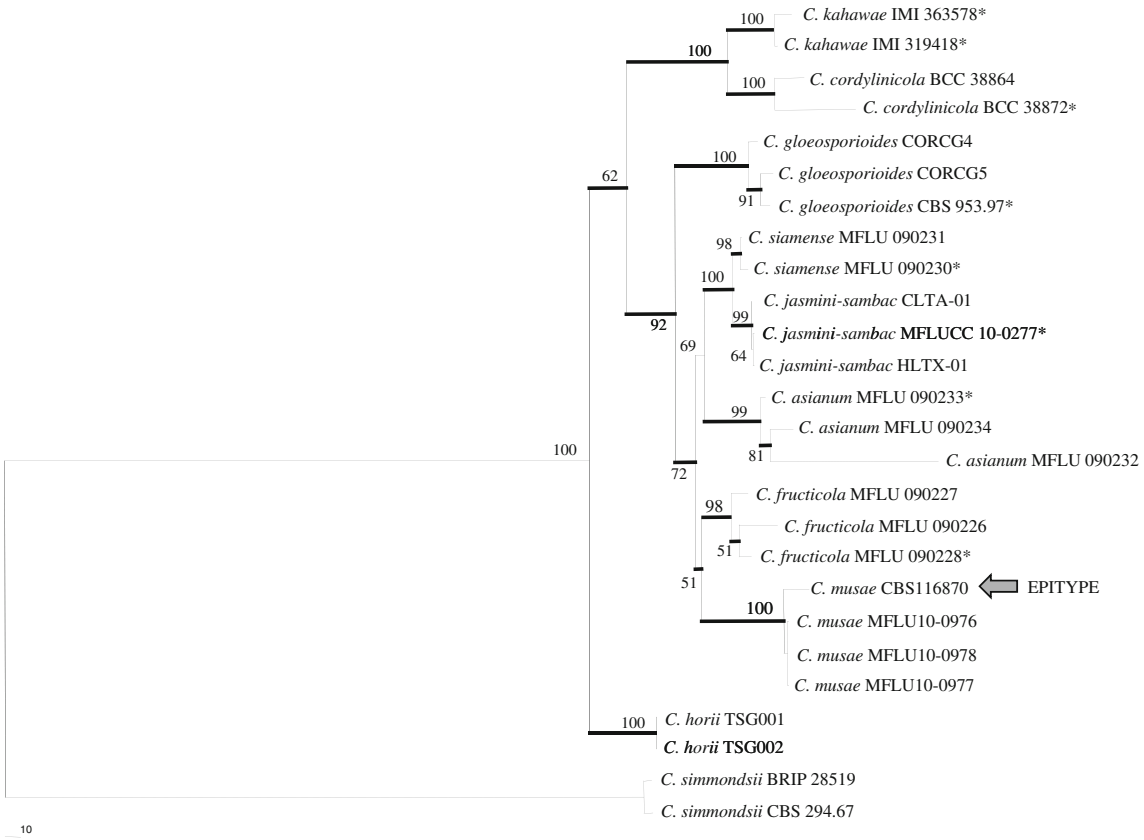

Fig. 1 Phylogram of tree generated from maximum parsimony analysis based on combined actin (ACT), glyceraldehyde-3-phosphate dehydrogenase (GPDH), internal transcribed spacer (ITS), β-tubulin (tub2) (TUB2), glutamine synthetase (GS), and calmoudulin (CAL) sequences, showing the phylogenetic relationships of *Colletotrichum musae*. *Values above the branches* are parsimony bootstrap (>50%); *thickened branches* represent significant Bayesian posterior probability (≥95%). The tree is rooted with *Colletotrichum simmondsii*. *Asterisks* indicate the ex-type strains; *arrow*, epitype

Maximum parsimony analysis generated only one tree (TL = 1,776, CI = 0.882, RI = 0.900, RC = 0.794, HI = 0.118) (Fig. 1). Multilocus sequences analysis shows that *C. musae* appears as a distinct lineage among the "gloeosporioides" species complex of *Colletotrichum*. A close phylogenetic relationship between *C. musae* and *C. fructicola* is supported by this analysis. Cultural characteristics and conidial and appressorial morphology are illustrated in Fig. 2. Three banana fruits inoculated with spore suspensions from the ex-epitype all developed typical anthracnose disease (dark brown necrotic lesions). Apples, pears, jujubes, and tomatoes did not develop symptoms after 7 days of inoculation.

Taxonomy

Colletotrichum musae (Berk. & M.A. Curtis) Arx, Verh. K. Akad. Wet., tweede sect. 51(3): 107 (1957). Fig. 2a–k

MycoBank no.: MB295348.

Colonies on PDA attaining 80 mm diameter in 5 days at 27°C, growth rate 16.9–18.4 mm/day ($\bar{x} = 17.6 \pm 0.6$, $n = 6$); circular, with sparse to abundant, white to grey floccose aerial mycelium, conidial masses well developed, salmon orange; reverse grey-yellowish. Sclerotia absent. Setae absent. Conidiophores cylindrical, tapered toward the apex, hyaline, subhyaline toward the base, up to 31 µm long, 3–5 µm wide. Conidia 11.5–19.5 × 4–5 µm ($\bar{x} = 14.7 \pm 2.13 \times 4.6 \pm 0.41$, $n = 30$), abundant, hyaline, aseptate, guttulate, oval, elliptical or cylindrical, often with a flattened base, apex obtuse. Appressoria in slide cultures 7.5–12.5 × 5–8.75 µm ($\bar{x} = 11.5 \pm 2.5 \times 7.4 \pm 1.5$, $n = 30$), abundant, medium to dark brown, irregular, crenate or lobed.

Epitype designated here: USA, Florida, on *Musa* sp., isolated by M. Arzanlou, dried culture deposited in CBS-H-20515, ex-epitype living culture CBS 116870.

Other materials examined: USA, North Carolina, on *Musa* sp. fruit skin, M.A. Curtis, K(M) 166978 (holotype). Thailand, Chiang Rai, Bandu, on fruit of *Musa* sp., 7 Nov. 2009, MFLU10-0976, living strain isolated by P. Noireung, MFLUCC 10-0115. Thailand, Chiang Rai, Bandu, on fruit of *Musa* sp., 18 July 2009, MFLU10-0977, living strain

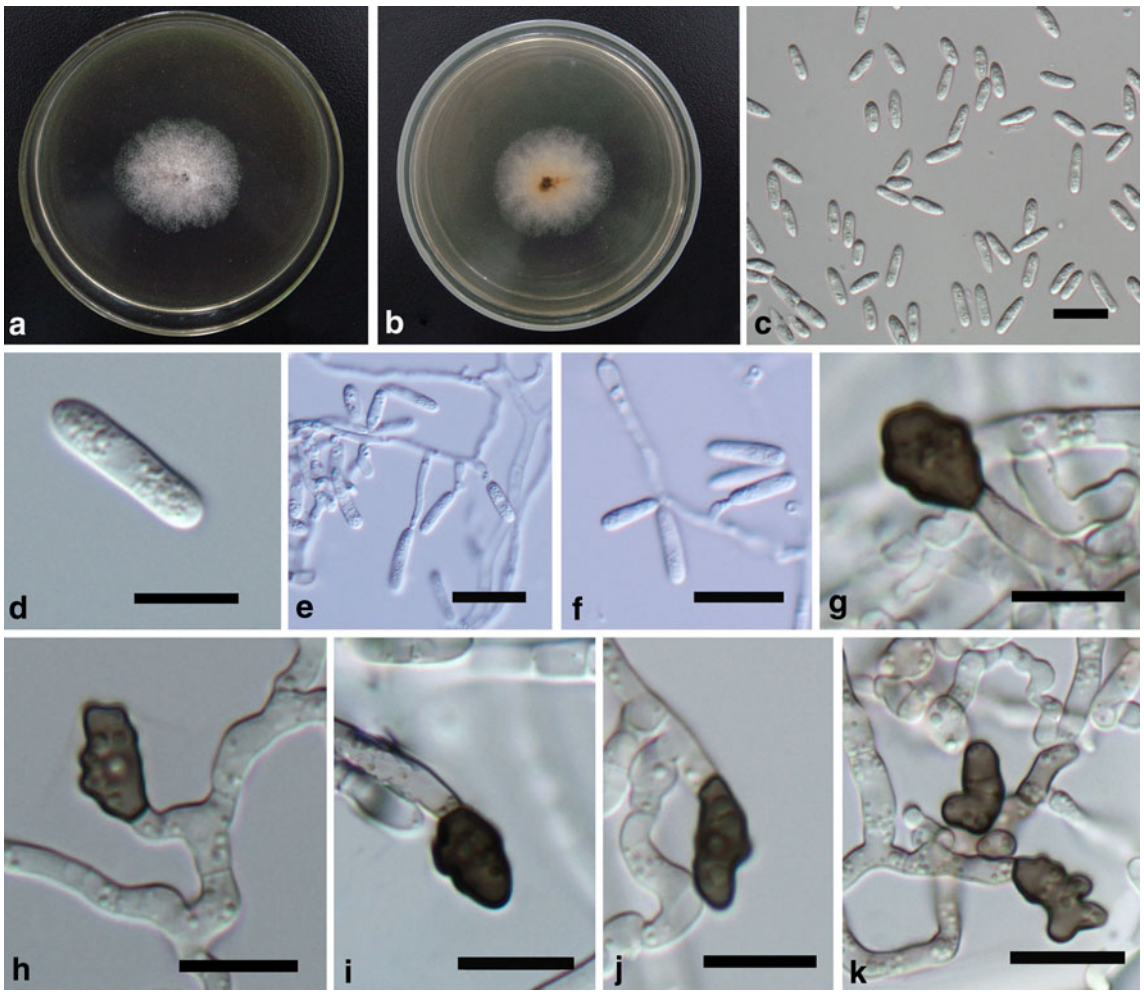

Fig. 2 *Colletotrichum musae* (from CBS 116870). **a**, **b** Upper and reverse view of culture on potato dextrose agar (PDA) 4 days after inoculation. **c**, **d** Conidia. **e**, **f** Conidiophores and conidia. **g–k** Irregularly shaped appressoria. *Bars* **c**, **e**, **f** 20 μm; **d**, **g–k** 10 μm

Fig. 3 *Colletotrichum musae* holotype K(M) 166978

isolated by P. Noireung, MFLUCC 10-0120. Thailand, Chiang Rai, Bandu, on fruit of *Musa* sp., 9 May 2009, MFLU10-0978, living strain isolated by P. Noireung, MFLUCC 10-0121.

Note: The holotype of *Myxosporium musae* K(M) 166978 (Fig. 3) consists of a dried banana pericarp. No conidia or sclerotia could be found on the specimen. Three attempts at DNA extraction from the darkened areas from this specimens were not successful. Berkeley (1874) provided only a brief description of the taxon with very few practical data, and it is impossible to be confident that this specimen is the same as our collections. We have the option of introducing a

new species or using our collection to epitype this old name. The latter option both is sensible and allows us to stabilize the use of the taxon name sensu Sutton (1980, 1992), who treated *C. musae* with conidia with similar characteristics to those of our epitype and thus have been used by most authors since Sutton's publications.

Discussion

Colletotrichum musae has been shown to belong to the "gloeosporioides" species complex, and it is widely recognized as a separate species limited to banana (*Musa* spp.) (Du et al. 2005). Previous phylogenetic analyses of *C. musae* and *Colletotrichum fragariae* A.N. Brooks based on the ITS and the 28S-D2 rDNA gene sequences failed to separate them from *C. gloeosporioides* (Penz.) Penz. & Sacc. (Sreenivasaprasad et al. 1992, 1994; Johnston and Jones 1997). Multilocus phylogeny is now widely applied for the understanding of species relationships in *Colletotrichum* (Damm et al. 2009; Crouch et al. 2009b). For example, Prihastuti et al. (2009) introduced three new species—*Colletotrichum asianum* Prihastuti, L. Cai & K.D. Hyde, *Colletotrichum fructicola* Prihastuti, L. Cai & K.D. Hyde, and *Colletotrichum siamense* Prihastuti, L. Cai & K.D. Hyde—based on multilocus phylogeny and polyphasic phenotypic characters.

In the phylogenetic tree, the epitype and three strains from Asian banana constitute a strongly supported monophyletic clade (see Fig. 1). *Colletotrichum musae* is most closely related to *C. fructicola*, which was originally isolated from coffee berries (Prihastuti et al. 2009) but has since been shown to occur on several other hosts (Yang et al. 2009; Phoulivong et al. 2010). The conidial size of *C. musae* overlaps with that of *C. fructicola*. However, the mean conidial length of *C. musae* is significantly greater (14.7 vs. 11.53 μm), and the shape and size of the appressoria are also different (ovoid and clavate, 7.0 × 4.5 μm, in *C. fructicola* vs. crenate or lobed, 11.5 × 7.4 μm, in *C. musae*).

The *Colletotrichum gloeosporioides* species complex has been shown to contain several genetically and biologically separated species (e.g., *Colletotrichum asianum*, *Colletotrichum fragariae*, *Colletotrichum fructicola*, *Colletotrichum gloeosporioides* sensu stricto, *Colletotrichum horii* B. Weir & P.R. Johnst., *Colletotrichum kahawae* J.M. Waller & Bridge, and *Colletotrichum siamense*). However, these species have few distinguishable morphological characters. Therefore, it is essential to generate sequence data and compare these sequence data to those generated from type specimens. Before this study, there were no sequences generated from the type specimen of *C. musae*, and the current GenBank sequences under the name '*C. musae*' differ one from another (details not shown). Comparison with strains from type specimens is essential for the systematics study and pathogen diagnosis in this group of fungi, and the potential "standard" sample should be based on a properly identified specimen.

The ex-epitype strain infected the banana fruit in a short time and showed typical symptoms. Similar results also occurred in the study of Lim et al. (2002). By formally establishing an ex-epitype culture for *C. musae* that is consistent with the original type with respect to morphology, host and geographic derivation, and generating a multilocus sequence dataset for this strain, we have taken the first and vital step toward informative study of the taxa responsible for this important disease of anthracnose.

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References

Anthony S, Abeywickrama R, Dayananda R, Wilson S, Arambewela L (2004) Fungal pathogens associated with banana fruit in Sri Lanka. Mycopathology 157:91–97

von Arx JA (1957) Die Arten der Gattung *Colletotrichum*. Phytopathology 29:413–468

Berkeley MJ (1874) Notices of North American fungi. Grevillea 3:17

Cai L, Hyde KD, Taylor PWJ, Weir BS, Waller J, Abang MM, Zhang JZ, Yang YL, Phoulivong S, Liu ZY, Prihastuti H, Shivas RG, McKenzie EHC, Johnston PR (2009) A polyphasic approach for studying *Colletotrichum*. Fungal Divers 39:183–204

Chillet M, Hubert O, Rives MJ, de Bellaire L (2006) Effects of the physiological age of bananas on their susceptibility to wound anthracnose due to *Colletotrichum musae*. Plant Dis 90:1181–1185

Choi YW, Hyde KD, Ho WH (1999) Single spore isolation of fungi. Fungal Divers 3:29–38

Crouch JA, Tredway LP, Clarke BB, Hillman BI (2009a) Phylogenetic and population genetic divergence correspond with habitat for the pathogen *Colletotrichum cereale* and allied taxa across diverse grass communities. Mol Ecol 18:123–135

Crouch JA, Clarke BB, White JW, Hillman BI (2009b) Systematic analysis of the falcate-spored graminicolous *Colletotrichum* and a description of six new species of the fungus from warm-season grasses. Mycologia 101:717–732

Damm U, Woudenberg JHC, Cannon PF, Crous PW (2009) *Colletotrichum* species with curved conidia from herbaceous hosts. Fungal Divers 39:45–87

Du M, Schardl CL, Nuckles EM, Vaillancourt LJ (2005) Using mating-type gene sequences for improved phylogenetic resolution of *Colletotrichum* species complexes. Mycologia 97:641–658

Hall TA (1999) BioEdit: a user-friendly biological sequence alignment editor and analysis program for Windows 95/98/NT. Nucleic Acids Symp Ser 41:95–98

Huelsenbeck JP, Ronquist FR (2001) MRBAYES: Bayesian inference of phylogenetic trees. Biometrics 17:754–755

Hyde KD, Cai L, Cannon PF, Crouch JA, Crous PW, Damm U, Goodwin PH, Chen H, Johnston PR, Jones EBG (2009) *Colletotrichum*: names in current use. Fungal Divers 39:147–182

Israeli Y, Temkin-Gorodeiski N (1977) The mode of infection of *Colletotrichum musae* (Cke. and Massee) causing tip rot of banana fruits in the plantation. Phytoparasitica 5:167–172

Johnston PR, Jones D (1997) Relationships among *Colletotrichum* isolates from fruit-rots assessed using rDNA sequences. Mycologia 89:420–430

Kishino H, Hasegawa M (1989) Evaluation of the maximum likelihood estimate of the evolutionary tree topologies from DNA sequence data, and the branching order of Hominoidea. J Mol Evol 29:170–179

Lim J, Lim TH, Cha B (2002) Isolation and identification of *Colletotrichum musae* from imported bananas. Plant Pathol J 18:161–164

Mahadtanapuk S, Sanguansermsri M, Cutler RW, Sardsud V, Anuntalabhochai S (2007) Control of anthracnose caused by *Colletotrichum musae* on *Curcuma alismatifolia* Gagnep. using antagonistic *Bacillus* spp. Am J Agric Biol Sci 2:54–61

Meredith DS (1960a) Studies on *Gloeosporium musarum* Cke. and Massee causing storage rots of Jamaican bananas. I. Anthracnose and its chemical control. Ann Appl Biol 48:279–290

Meredith DS (1960b) Studies on *Gloeosporium musarum* Cke. & Mass. causing storage rots of Jamaican banana. II. Some factors influencing anthracnose development. Ann Appl Biol 48:518–528

Nazriya NF, Costa DMD, Azhaar AS (2007) Genomic variations of *Colletotrichum musae* morphotypes infecting banana varieties of Sri Lanka. Proc Perad Univ Res Ses 12:1–2

Nuangmek W, McKenzie EHC, Lumyong S (2008) Endophytic fungi from wild banana (*Musa acuminata* Colla) works against anthracnose disease caused by *Colletotrichum musae*. Res J Microbiol 3:368–374

Nylander JAA (2004) MrModeltest v2. Program distributed by the author. Evolutionary Biology Centre, Uppsala University, Uppsala

Page RDM (1996) TREEVIEW: an application to display phylogenetic trees on personal computers. Comput Appl Biosci 12:357–358

Pereira JO, Carneiro Vieira ML, Azevedo JL (1999) Endophytic fungi from *Musa acuminata* and their reintroduction into axenic plants. World J Microbiol Biotechnol 15:43–46

Photita W, Lumyong S, Lumyong P, Hyde KD (2001) Endophytic fungi of wild banana (*Musa acuminata*) at Doi Suthep Pui National Park, Thailand. Mycol Res 105:1508–1513

Phoulivong S, Cai L, Chen H, McKenzie EHC, Abd-Elsalam K, Chukeatirote E, Hyde KD (2010) *Colletotrichum gloeosporioides* is not a common pathogen on tropical fruits. Fungal Divers 44:33–43

Prihastuti H, Cai L, Chen H, McKenzie EHC, Hyde KD (2009) Characterization of *Colletotrichum* species associated with coffee berries in northern Thailand. Fungal Divers 39:89–109

Rannala B, Yang Z (1996) Probability distribution of molecular evolutionary trees: a new method of phylogenetic inference. J Mol Evol 43:304–311

Simmonds JH (1965) A study of the species of *Colletotrichum* causing ripe fruit rots in Queensland. Queensl J Agric Anim Sci 22:437–459

Simmonds TH, Mitchell RS (1940) Black end and anthracnose of the banana with special reference to *Gloeosporium musarum* Cke. & Mass. Bull Coun Sci Industr Res Aust 131:6–63

Sreenivasaprasad S, Brown AE, Mills PR (1992) DNA sequence variation and interrelationships among *Colletotrichum* species causing strawberry anthracnose. Physiol Mol Plant Pathol 41:265–281

Sreenivasaprasad S, Mills PR, Brown AE (1994) Nucleotide sequence of the rDNA spacer 1 enables identification of isolates of *Colletotrichum* as *C. acutatum*. Mycol Res 98:186–188

Stover RH, Simmonds NW (1987) Bananas, 3rd edn. Longman, London

Sutton BC (1980) The coelomycetes. Commonwealth Mycological Institute, Kew

Sutton BC (1992) The genus *Glomerella* and its anamorph *Colletotrichum*. In: Bailey JA, Jeger MJ (eds) *Colletotrichum*: biology, pathology and control. CAB International, Wallingford, pp 1–26

Swofford DL (2002) PAUP*. Phylogenetic analysis using parsimony (*and other methods), 4th edn. Sinauer Associates, Sunderland

Thompson JD, Gibson TJ, Plewniak F, Jeanmougin F, Higgins DG (1997) The Clustal X windows interface: flexible strategies for multiple sequence alignment aided by quality analysis tools. Nucleic Acids Res 24:4876–4882

Wikee S, Cai L, Pairin N, McKenzie EHC, Su YY, Chukeatirote E, Thi HN, Bahkali AH, Moslem MA, Abdelsalam K (2011) *Colletotrichum* species from jasmine (*Jasminum sambac*). Fungal Divers 46:171–182

Yang YL, Liu ZY, Cai L, Hyde KD, Yu ZN, McKenzie EHC (2009) *Colletotrichum anthracnose* of Amaryllidaceae. Fungal Divers 39:123–146

Zhaxybayeva O, Gogarten JP (2002) Bootstrap, Bayesian probability and maximum likelihood mapping: exploring new tools for comparative genome analyses. Genomics 3:1–15