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The *Colletotrichum gloeosporioides* species complex

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Abstract: The limit of the *Colletotrichum gloeosporioides* species complex is defined genetically, based on a strongly supported clade within the *Colletotrichum* ITS gene tree. All taxa accepted within this clade are morphologically more or less typical of the broadly defined *C. gloeosporioides*, as it has been applied in the literature for the past 50 years. We accept 22 species plus one subspecies within the *C. gloeosporioides* complex. These include *C. asianum*, *C. cordylinicola*, *C. fructicola*, *C. gloeosporioides*, *C. horii*, *C. kahawae* subsp. *kahawae*, *C. musae*, *C. nupharicola*, *C. psidii*, *C. siamense*, *C. theobromicola*, *C. tropicale*, and *C. xanthorrhoeae*, along with the taxa described here as new, *C. aenigma*, *C. aeschynomenes*, *C. alatae*, *C. alienum*, *C. aotearoa*, *C. clidemiae*, *C. kahawae* subsp. *ciggaro*, *C. salsolae*, and *C. ti*, plus the nom. nov. *C. queenslandicum* (for *C. gloeosporioides* var. *minus*). All of the taxa are defined genetically on the basis of multi-gene phylogenies. Brief morphological descriptions are provided for species where no modern description is available. Many of the species are unable to be reliably distinguished using ITS, the official barcoding gene for fungi. Particularly problematic are a set of species genetically close to *C. musae* and another set of species genetically close to *C. kahawae*, referred to here as the Musae clade and the Kahawae clade, respectively. Each clade contains several species that are phylogenetically well supported in multi-gene analyses, but within the clades branch lengths are short because of the small number of phylogenetically informative characters, and in a few cases individual gene trees are incongruent. Some single genes or combinations of genes, such as glyceraldehyde-3-phosphate dehydrogenase and glutamine synthetase, can be used to reliably distinguish most taxa and will need to be developed as secondary barcodes for species level identification, which is important because many of these fungi are of biosecurity significance. In addition to the accepted species, notes are provided for names where a possible close relationship with *C. gloeosporioides sensu lato* has been suggested in the recent literature, along with all subspecific taxa and *formae speciales* within *C. gloeosporioides* and its putative teleomorph *Glomerella cingulata*.

Key words: anthracnose, *Ascomycota,* barcoding, *Colletotrichum gloeosporioides*, *Glomerella cingulata*, phylogeny, systematics.
Taxonomic novelties: Name replacement - *C. queenslandicum* B. Weir & P.R. Johnst. **New species -** *C. aenigma* B. Weir & P.R. Johnst., *C. aeschynomenes* B. Weir & P.R. Johnst., *C. alatae* B. Weir & P.R. Johnst., C. *alienum* B. Weir & P.R. Johnst, *C. aotearoa* B. Weir & P.R. Johnst., *C. clidemiae* B. Weir & P.R. Johnst., *C. salsolae* B. Weir & P.R. Johnst., *C. ti* B. Weir & P.R. Johnst. **New subspecies -** *C. kahawae* subsp. *ciggaro* B. Weir & P.R. Johnst. **Typification: Epitypification -** *C. queenslandicum* B. Weir & P.R. Johnst.

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INTRODUCTION

The name *Colletotrichum gloeosporioides* was first proposed in Penzig (1882), based on *Vermicularia gloeosporioides*, the type specimen of which was collected from *Citrus* in Italy. Much of the early literature used this name to refer to fungi associated with various diseases of *Citrus*, with other species established for morphologically similar fungi from other hosts. However, several early papers discussed the morphological similarity between many of the *Colletotrichum* spp. that had been described on the basis of host preference, and used inoculation tests to question whether or not the species were distinct. Some of these papers investigated in culture the link between the various *Colletotrichum* species and their sexual *Glomerella* state (*e.g.* Shear & Wood 1907, Ocfemia & Agati 1925). Authors such as Shear & Wood (1907, 1913) and Small (1926) concluded that many of the species described on the basis of host preference were in fact the same, rejecting apparent differences in host preference as a basis for taxonomic segregation. Small (1926) concluded that the names *Glomerella cingulata* and *Colletotrichum gloeosporioides* should be used for the sexual and asexual morphs, respectively, of the many *Colletotrichum* spp. they regarded as conspecific. *Colletotrichum gloeosporioides* was stated to be the earliest name with a proven link to what they regarded as a biologically diverse *G. cingulata*. The studies of von Arx & Müller (1954) and von Arx (1957, 1970) taxonomically formalised this concept.

The "von Arxian" taxonomic concept for *Colletotrichum* saw large numbers of species synonymised with the names *C. graminicola* (for grass-inhabiting species) and *C. gloeosporioides* (for non-grass inhabiting species with straight conidia). The genetic and biological diversity encompassed by these names was so broad that they became of little practical use to plant pathologists, conveying no information about pathogenicity, host range, or other attributes. The von Arx & Müller (1954) and von Arx (1957) studies were not based on direct examination of type material of all species and some of the synonymy proposed in these papers has subsequently been found to be incorrect. Examples include the segregation of *C. acutatum* (Simmonds 1965) and *C. boninense* (Moriwaki *et al.* 2003) from *C. gloeosporioides sensu* von Arx (1957). Other studies published elsewhere in this volume (Damm *et al.* 2012a, b) show that several species regarded as synonyms of *C. gloeosporioides* by von Arx (1957) are members of the *C. acutatum* complex (*e.g. C. godetiae*, *Gloeosporium limetticola*, *G. lycopersici*, and *G. phormii*) or the *C. boninense* complex (*e.g. C. dracaenae*). Recent molecular studies have resulted in a much better understanding of phylogenetic relationships amongst the

grass-inhabiting species of the *C. graminicola* group and the development of a more useful taxonomy for this group of fungi (*e.g.* Hsiang & Goodwin 2001, Du *et al.* 2005, and Crouch *et al.* 2006). This group is now recognised as comprising several host-specialised, genetically well characterised species, but a modern taxonomy for *C. gloeosporioides* has yet to be resolved.

Von Arx (1970) and Sutton (1980) distinguished the *C. gloeosporioides* group using conidial shape and size. A few apparently host-specialised, *C. gloeosporioides*-like taxa were retained by these authors, but the basis of their identification was often difficult to understand. Prior to the availability of DNA sequence data, taxonomic concepts within *Colletotrichum* were based on features such as host species, substrate, conidial size and shape, shape of appressoria, growth rate in culture, colour of cultures, presence or absence of setae, whether or not the teleomorph develops, etc. Some studies have found characters such as these useful for distinguishing groups within *C. gloeosporioides* (*e.g.* Higgins 1926, Gorter 1956, Hindorf 1973, and Johnston & Jones 1997). However, problems arise because many of these morphological features change under different conditions of growth (dependent upon growth media, temperature, light regime, etc.), or can be lost or change with repeated subculturing. Host preference is poorly controlled — even good, well-defined pathogens causing a specific disease can be isolated by chance from other substrates (*e.g.* Johnston 2000). *Colletotrichum* conidia will germinate on most surfaces, form an appressorium, remain attached to that surface as a viable propagule or perhaps as a minor, endophytic or latent infection, and grow out from there into senescing plant tissue or onto agar plates if given the opportunity. In addition, the same disease can be caused by genetically distinct sets of isolates, the shared pathogenicity presumably independently evolved, *e.g.* the bitter rot disease of apple is caused by members of both the *C. acutatum* and *C. gloeosporioides* species complexes (Johnston *et al.* 2005).

Sutton (1992) commented on *C. gloeosporioides* that "No progress in the systematics and identification of isolates belonging to this complex is likely to be made based on morphology alone". A start was made towards a modern understanding of this name with the designation of an epitype specimen with a culture derived from it to stabilise the application of the name (Cannon *et al.* 2008). Based on ITS sequences, the ex-epitype isolate belongs in a strongly supported clade, distinct from other taxa that have been confused with *C. gloeosporioides* in the past, such as *C. acutatum* and *C. boninense* (*e.g.* Abang *et al.* 2002, Martinez-Culebras *et al.* 2003, Johnston *et al*. 2005, Chung *et al.* 2006, Farr *et al.* 2006, Than *et al.* 2008). However, biological and genetic relationships within the broad *C. gloeosporioides* clade remain confused and ITS sequences alone are insufficient to resolve them.

In this study we define the limits of the *C. gloeosporioides* species complex on the basis of ITS sequences, the species we accept within the complex forming a strongly supported clade in the ITS gene tree (fig. 1 in Cannon *et al.* 2012, this issue). In all cases the taxa we include in the *C. gloeosporioides* complex would fit within the traditional morphological concept of the *C. gloeosporioides* group (*e.g.* von Arx 1970, Mordue 1971, and Sutton 1980). Commonly used species names within the *C. gloeosporioides* complex include *C. fragariae*, *C. musae*, and *C. kahawae*. Since the epitype paper (Cannon *et al.* 2008), several new *C. gloeosporioides*-like species have been described in regional studies, where multi-gene analyses have shown the new species to be phylogenetically distinct from the ex-epitype strain of *C. gloeosporioides* (*e.g.* Rojas *et al.* 2010, Phoulivong *et al.* 2011, and Wikee *et al.* 2011).

The regional nature of most of these studies, the often restricted genetic sampling across the diversity of *C. gloeosporioides* globally, and the minimal overlap between isolates treated and gene regions targeted in the various studies, means that the relationship between the newly described species is often poorly understood.

While some authors have embraced a genetically highly restricted concept for *C. gloeosporioides*, many applied researchers continue to use the name in a broad, group-species concept (*e.g.* Bogo *et al.* 2012, Deng *et al.* 2012, Kenny *et al.* 2012, Parvin *et al.* 2012, and Zhang *et al.* 2012). In this paper we accept both concepts as useful and valid. When used in a broad sense, we refer to the taxon as the *C. gloeosporioides* species complex or *C. gloeosporioides s. lat*.

This paper aims to clarify the genetic and taxonomic relationships within the *C. gloeosporioides* species complex using a set of isolates that widely samples its genetic, biological and geographic diversity. Type specimens, or cultures derived from type specimens, have been examined wherever possible. Although we do not treat all of the names placed in synonymy with *C. gloeosporioides* or *Glomerella cingulata* by von Arx & Müller (1954) and von Arx (1957, 1970), we treat all names for which a possible close relationship with *C. gloeosporioides* has been suggested in the recent literature, along with all subspecific taxa and *formae speciales* within *C. gloeosporioides* and *G. cingulata*.

ITS sequences, the official barcoding gene for fungi (Seifert 2009, Schoch *et al.* 2012), do not reliably resolve relationships within the *C. gloeosporioides* complex. We define species in the complex genetically rather than morphologically, on the basis of phylogenetic analyses of up to eight genes. Following Cannon *et al.* (2012, this issue) the generic name *Colletotrichum* is used as the preferred generic name for all species wherever possible throughout this paper, whether or not a *Glomerella* state has been observed for that fungus, and whether or not the *Glomerella* state has a formal name.

MATERIALS AND METHODS

Specimen isolation and selection

An attempt was made to sample the genetic diversity across *C. gloeosporioides* as widely as possible, with isolates from diverse hosts from around the world selected for more intensive study. A BLAST search of GenBank using the ITS sequence of the epitype culture of *C. gloeosporioides* (Cannon *et al*. 2008) provided a coarse estimate for the genetic limit of the *C. gloeosporioides* complex and ITS diversity across the complex was used to select a genetically diverse set of isolates. Voucher cultures were obtained from the research groups who deposited the GenBank records. To these were added isolates representing the known genetic and morphological diversity of *C. gloeosporioides* from New Zealand, isolated from rots of native and introduced fruits, from diseased exotic weeds, and as endophytes from leaves of native podocarps. Additional isolates representing ex-type and authentic cultures of as many named taxa and *formae speciales* within the *C. gloeosporioides* complex as possible were obtained from international culture collections. Approximately 400 isolates belonging to the *C. gloeosporioides* complex were obtained. GAPDH gene sequences were generated for all isolates as an initial measure of genetic diversity. A subset of 156 isolates, selected to represent the range of genetic, geographic, and host plant diversity,

was used in this research (Table 1).

Most of the New Zealand isolates had been stored as conidial suspensions made from single conidium or ascospore cultures and then stored at -80 °C in a 5 % glycerol/water suspension. Additional isolates from New Zealand were obtained from the ICMP culture collection, where isolates are stored as lyophilised (freeze-dried) ampoules or in a metabolically inactive state in liquid nitrogen at -196 °C. The storage history of most of the isolates received from other research groups is not known. Table 1 lists the isolates studied. All those supplying cultures are acknowledged at the end of this manuscript, and additional details on each culture are available on the ICMP website (http://www.landcareresearch.co.nz/resources/collections/icmp).

Culture collection and fungal herbarium (fungarium) abbreviations used herein are: CBS = Centraalbureau voor Schimmelcultures (Netherlands), ICMP = International Collection of Microorganisms from Plants, MFLU = Mae Fah Luang University Herbarium (Thailand) MFLUCC = Mae Fah Luang University Culture Collection (Thailand), GCREC = University of Florida, Gulf Coast Research and Education Centre (USA), HKUCC = The University of Hong Kong Culture Collection (China), IMI = CABI Genetic Resource Collection (UK), MAFF = Ministry of Agriculture, Forestry and Fisheries (Japan), DAR = Plant Pathology Herbarium (Australia), NBRC = Biological Resource Center, National Institute of Technology and Evaluation (Japan), BCC = BIOTEC Culture Collection (Thailand), GZAAS = Guizhou Academy of Agricultural Sciences herbarium (China), MUCL = Belgian Co-ordinated Collections of Micro-organisms, (agro)industrial fungi & yeasts (Belgium), BRIP = Queensland Plant Pathology Herbarium (Australia), PDD = New Zealand Fungal and Plant Disease Collection (New Zealand), BPI = U.S. National Fungus Collections (USA), STE-U = Culture collection of the Department of Plant Pathology, University of Stellenbosch (South Africa), and MCA = M. Catherine Aime's collection series, Louisiana State University (USA).

DNA extraction, amplification, and sequencing

Mycelium was collected from isolates grown on PDA agar, and manually comminuted with a micropestle in 420 µL of Quiagen DXT tissue digest buffer; 4.2 µL of proteinase K was added and incubated at 55 °C for 1 h. After a brief centrifugation 220 µL of the supernatant was placed in a Corbett X-tractorGene automated nucleic acid extraction robot. The resulting 100 µL of pure DNA in TE buffer was stored at -30 °C in 1.5 mL tubes until use.

Gene sequences were obtained from eight nuclear gene regions, actin (ACT) [316 bp], calmodulin (CAL) [756 bp], chitin synthase (CHS-1) [229 bp], glyceraldehyde-3-phosphate dehydrogenase (GAPDH) [308 bp], the ribosomal internal transcribed spacer (ITS) [615 bp], glutamine synthetase (GS) [907 bp], manganese-superoxide dismutase (SOD2) [376 bp], and β-tubulin 2 (TUB2) [716 bp].

PCR Primers used during this study are shown in Table 2. The standard CAL primers (O'Donnell *et al*. 2000) gave poor or non-specific amplification for most isolates, thus new primers (CL1C, CL2C) were designed for *Colletotrichum* based on the *C. graminicola* M1.001 genome sequence. The standard GS primers (Stephenson *et al*. 1997) sequenced poorly for some isolates due to an approx. 9 bp homopolymer T run 71 bp in from the end of the GSF1 primer binding site. A new primer, GSF3, was designed 41 bp downstream of this region to eliminate the homopolymer slippage error from sequencing. The reverse primer GSR2 was designed in the same location as GSR1 with one nucleotide change. Both new GS primers were based on similarity with a *C. theobromicola* UQ62 sequence (GenBank L78067, as *C. gloeosporioides*).

The PCRs were performed in an Applied Biosystems Veriti Thermal Cycler in a total volume of 25 µL. The PCR mixtures contained 15.8 µL of UV-sterilised ultra-filtered water, 2.5 µL of 10× PCR buffer (with 20 mM $MgCl_2$), 2.5 µL of dNTPs (each 20 µM), 1 µL of each primer (10 µM), 1 µL of BSA, 1 µL of genomic DNA, and 0.2 µL (1 U) of Roche FastStart Taq DNA Polymerase.

The PCR conditions for ITS were 4 min at 95 °C, then 35 cycles of 95 °C for 30 s, 52 °C for 30 s, 72 °C for 45 s, and then 7 min at 72 °C. The annealing temperatures differed for the other genes, with the optimum for each; ACT: 58 °C, CAL: 59 °C, CHS-1: 58 °C, GAPDH: 60 °C, GS: 54 °C, SOD2: 54 °C, TUB2: 55 °C. Some isolates required altered temperatures and occasionally gave multiple bands, which were excised separately from an electrophoresis gel and purified. PCR Products were purified on a Qiagen MinElute 96 UF PCR Purification Plate.

DNA sequences were obtained in both directions on an Applied Biosystems 3130*xl* Avant Genetic analyzer using BigDye v. 3.1 chemistry, electropherograms were analysed and assembled in Sequencher v. 4.10.1 (Gene Codes Corp.).

Phylogenetic analyses

Multiple sequence alignments of each gene were made with ClustalX v. 2.1 (Larkin *et al*. 2007), and manually adjusted where necessary with Geneious Pro v. 5.5.6 (Drummond *et al*. 2011).

Bayesian inference (BI) was used to reconstruct most of the phylogenies using MrBayes v. 3.2.1 (Ronquist *et al*. 2012). Bayesian inference has significant advantages over other methods of analysis such as maximum likelihood and maximum parsimony (Archibald *et al*. 2003) and provides measures of clade support as posterior probabilities rather than random resampling bootstraps. jModelTest v. 0.1.1 (Posada 2008) was used to carry out statistical selection of best-fit models of nucleotide substitution using the corrected Akaike information criteria (AICc) (Table 3). Initial analyses showed that individual genes were broadly congruent, thus nucleotide alignments of all genes were concatenated using Geneious, and separate partitions created for each gene with their own model of nucleotide substitution. Analyses on the full data set were run twice for 5 x 10^7 generations, and twice for 2 x 10^7 generations for the clade trees. Samples were taken from the posterior every 1000 generations. Convergence of all parameters was checked using the internal diagnostics of the standard deviation of split frequencies and performance scale reduction factors (PSRF), and then externally with Tracer v. 1.5 (Rambaut & Drummond 2007). On this basis the first 25 % of generations were discarded as burn-in.

An initial BI analysis treated all 158 isolates using a concatenated alignment for five of the genes, ACT, CAL, CHS-1, GAPDH, and ITS. *Colletotrichum boninense* and *C. hippeastri* were used as outgroups. A second BI analysis, restricted to ex-type or authentic isolates of each of the accepted species, was based on a concatenated alignment of all eight genes. A third set of BI analyses treated focussed on taxa within the Musae clade and the Kahawae clade. For each clade, the ex-type or authentic isolates, together with 2–3 additional selected isolates of each accepted taxon where available, were analysed using a concatenated alignment of all eight genes, with *C. gloeosporioides* used as the outgroup for both analyses.

Table 1. A list of strains used in this study.

Species	Culture*	Host	Country	GenBank accession number							
				ITS	GAPDH	CAL	ACT	CHS-1	GS	SOD2	TUB2
C. aenigma	ICMP 18608*	*Persea americana*	Israel	JX010244	JX010044	JX009683	JX009443	JX009774	JX010078	JX010311	JX010389
	ICMP 18686	*Pyrus pyrifolia*	Japan	JX010243	JX009913	JX009684	JX009519	JX009789	JX010079	JX010312	JX010390
C. aeschynomenes	ICMP 17673*, ATCC 201874	*Aeschynomene virginica*	USA	JX010176	JX009930	JX009721	JX009483	JX009799	JX010081	JX010314	JX010392
C. alatae	CBS 304.67*, ICMP 17919	*Dioscorea alata*	India	JX010190	JX009990	JX009738	JX009471	JX009837	JX010065	JX010305	JX010383
	ICMP 18122	*Dioscorea alata*	Nigeria	JX010191	JX010011	JX009739	JX009470	JX009846	JX010136	JX010371	JX010449
C. alienum	IMI 313842, ICMP 18691	*Persea americana*	Australia	JX010217	JX010018	JX009664	JX009580	JX009754	JX010074	JX010307	JX010385
	ICMP 18703	*Persea americana*	New Zealand	JX010252	JX010030	JX009656	JX009528	JX009885			
	ICMP 12071*	*Malus domestica*	New Zealand	JX010251	JX010028	JX009654	JX009572	JX009882	JX010101	JX010333	JX010411
	ICMP 17972	*Diospyros kaki*	New Zealand	JX010247	JX009944	JX009655	JX009497	JX009750			
	ICMP 18704	*Persea americana*	New Zealand	JX010253	JX010045	JX009658	JX009456	JX009886			
	ICMP 18621	*Persea americana*	New Zealand	JX010246	JX009959	JX009657	JX009552	JX009755	JX010075	JX010308	JX010386
	ICMP 12068	*Malus domestica*	New Zealand	JX010255	JX009925	JX009660	JX009492	JX009889			
	ICMP 18725	*Malus domestica*	New Zealand	JX010254	JX009943	JX009659	JX009530	JX009887			
C. aotearoa	ICMP 18532	*Vitex lucens*	New Zealand	JX010220	JX009906	JX009614	JX009544	JX009764	JX010108	JX010338	JX010421
	ICMP 18734	*Agathis australis*	New Zealand	JX010211	JX010004	JX009627	JX009569	JX009878			
	ICMP 18528	*Berberis glaucocarpa*	New Zealand	JX010199	JX009977	JX009615	JX009527	JX009879			
	ICMP 17324	*Kunzea ericoides*	New Zealand	JX010198	JX009991	JX009619	JX009538	JX009770	JX010109	JX010344	JX010418
	ICMP 18533	*Prumnopitys ferruginea*	New Zealand	JX010197	JX010026	JX009624	JX009522	JX009769	JX010110	JX010340	JX010416
	ICMP 18535	*Dacrycarpus dacrydioides*	New Zealand	JX010201	JX009968	JX009617	JX009545	JX009766	JX010107	JX010364	JX010423
	ICMP 18577	*Coprosma* sp.	New Zealand	JX010203	JX009978	JX009612	JX009567	JX009851	JX010111	JX010360	JX010417
	ICMP 18529	*Acmena smithii*	New Zealand	JX010222	JX009956	JX009618	JX009539	JX009883			
	ICMP 18537*	*Coprosma* sp.	New Zealand	JX010205	JX010005	JX009611	JX009564	JX009853	JX010113	JX010345	JX010420
	ICMP 18536	*Coprosma* sp.	New Zealand	JX010204	JX009907	JX009610	JX009577	JX009852			
	ICMP 18748	*Ligustrum lucidum*	New Zealand	JX010209	JX009918	JX009613	JX009453	JX009858			
	ICMP 17326	*Podocarpus totara*	New Zealand	JX010202	JX010049	JX009616	JX009578	JX009768	JX010106	JX010341	JX010422
	ICMP 18540	*Geniostoma ligustrifolium*	New Zealand	JX010207	JX010043	JX009622	JX009514	JX009855			
	ICMP 18541	*Coprosma* sp.	New Zealand	JX010208	JX009960	JX009607	JX009513	JX009856			
	ICMP 18742	*Meryta sinclairii*	New Zealand	JX010210	JX010025	JX009626	JX009477	JX009862			
	ICMP 18740	*Dysoxylum spectabile*	New Zealand	JX010218	JX009988	JX009625	JX009517	JX009763	JX010135	JX010368	JX010446
	ICMP 18530	*Vitex lucens*	New Zealand	JX010268	JX009911	JX009623	JX009521	JX009884	JX010112	JX010339	JX010419
	ICMP 18735	*Hedychium gardnerianum*	New Zealand	JX010221	JX010023	JX009620	JX009500	JX009880	JX010115	JX010343	JX010424

Table 1. (Continued).

Species	Culture*	Host	Country	GenBank accession number							
				ITS	GAPDH	CAL	ACT	CHS-1	GS	SOD2	TUB2
	ICMP 18736	*Lonicera japonica*	New Zealand	JX010200	JX009912	JX009608	JX009454	JX009894			
	ICMP 18548	*Coprosma* sp.	New Zealand	JX010206	JX009961	JX009609	JX009854	JX009445	JX010114	JX010342	JX010425
	ICMP 18543	*Melicytus ramiflorus*	New Zealand	JX010156	JX009983	JX009621	JX009524	JX009859			
C. asianum	IMI 313839, ICMP 18696	*Mangifera indica*	Australia	JX010192	JX009915	JX009723	JX009576	JX009753	JX010073	JX010306	JX010384
	MAFF 306627, ICMP 18603	*Mangifera indica*	Philippines	JX010195	JX009938	JX009725	JX009579	JX009825			
	HKUCC 10862, ICMP 18605	*Mangifera indica*	Thailand	JX010194	JX010021	JX009726	JX009465	JX009787			
	ICMP 18580*, CBS 130418	*Coffea arabica*	Thailand	**FJ972612**	JX010053	**FJ917506**	JX009584	JX009867	JX010096	JX010328	JX010406
	CBS 124960, ICMP 18648	*Mangifera indica*	Panama	JX010193	JX010017	JX009724	JX009546	JX009871			
C. boninense	MAFF 305972*, ICMP 17904, CBS 123755	*Crinum asiaticum* var. *sinicum*	Japan	JX010292	JX009905		JX009583	JX009827			
C. clidemiae	ICMP 18706	*Vitis* sp.	USA	JX010274	JX009909	JX009639	JX009476	JX009777	JX010128	JX010353	JX010439
	ICMP 18658*	*Clidemia hirta*	USA, Hawaii	JX010265	JX009989	JX009645	JX009537	JX009877	JX010129	JX010356	JX010438
C. cordylinicola	MFLUCC 090551*, ICMP 18579	*Cordyline fruticosa*	Thailand	JX010226	JX009975	**HM470238**	**HM470235**	JX009864	JX010122	JX010361	JX010440
C. fructicola	ICMP 12568	*Persea americana*	Australia	JX010166	JX009946	JX009680	JX009529	JX009762			
	ICMP 17787	*Malus domestica*	Brazil	JX010164	JX009958	JX009667	JX009439	JX009807			
	ICMP 17788	*Malus domestica*	Brazil	JX010177	JX009949	JX009672	JX009458	JX009808			
	IMI 345051, ICMP 17819	*Fragaria* × *ananassa*	Canada	JX010180	JX009997	JX009668	JX009469	JX009820			
	ICMP 18613	*Limonium sinuatum*	Israel	JX010167	JX009998	JX009675	JX009491	JX009772	JX010077	JX010310	JX010388
	ICMP 18698	*Limonium* sp.	Israel	JX010168	JX010052	JX009677	JX009585	JX009773			
	ICMP 18667	*Limonium* sp.	Israel	JX010169	JX009951	JX009679	JX009464	JX009775			
	ICMP 18615	*Limonium* sp.	Israel	JX010170	JX010016	JX009678	JX009511	JX009776			
	ICMP 18610	*Pyrus pyrifolia*	Japan	JX010174	JX010034	JX009681	JX009526	JX009788			
	ICMP 18120	*Dioscorea alata*	Nigeria	JX010182	JX010041	JX009670	JX009436	JX009844	JX010091	JX010323	JX010401
	CBS 125395, ICMP 18645	*Theobroma cacao*	Panama	JX010172	JX009992	JX009666	JX009543	JX009873	JX010098	JX010330	JX010408
	ICMP 18581*, CBS 130416	*Coffea arabica*	Thailand	JX010165	JX010033	**FJ917508**	**FJ907426**	JX009866	JX010095	JX010327	JX010405
	ICMP 18727	*Fragaria* × *ananassa*	USA	JX010179	JX010035	JX009682	JX009565	JX009812	JX010083	JX010316	JX010394
	CBS 120005, ICMP 18609	*Fragaria* × *ananassa*	USA	JX010175	JX009926	JX009673	JX009534	JX009792			
	ICMP 17789	*Malus domestica*	USA	JX010178	JX009914	JX009665	JX009451	JX009809			
	ICMP 18125	*Dioscorea alata*	Nigeria	JX010183	JX010009	JX009669	JX009468	JX009847			
C. fructicola (syn. *C. ignotum*)	CBS 125397(*), ICMP 18646	*Tetragastris panamensis*	Panama	JX010173	JX010032	JX009674	JX009581	JX009874	JX010099	JX010331	JX010409
C. fructicola (syn. *Glomerella cingulata* var. *minor*)	CBS 238.49(*), ICMP 17921	*Ficus edulis*	Germany	JX010181	JX009923	JX009671	JX009495	JX009839	JX010090	JX010322	JX010400

Table 1. (Continued).

Species	Culture*	Host	Country	GenBank accession number							
				ITS	GAPDH	CAL	ACT	CHS-1	GS	SOD2	TUB2
C. gloeosporioides	DAR 76936, ICMP 18738	*Carya illinoinensis*	Australia	JX010151	JX009976	JX009730	JX009542	JX009797			
	IMI 356878*, ICMP 17821, CBS 112999	*Citrus sinensis*	Italy	JX010152	JX010056	JX009731	JX009531	JX009818	JX010085	JX010365	JX010445
	ICMP 12939	*Citrus* sp.	New Zealand	JX010149	JX009931	JX009728	JX009462	JX009747			
	ICMP 12066	*Ficus* sp.	New Zealand	JX010158	JX009955	JX009734	JX009550	JX009888			
	ICMP 18730	*Citrus* sp.	New Zealand	JX010157	JX009981	JX009737	JX009548	JX009861			
	ICMP 12938	*Citrus sinensis*	New Zealand	JX010147	JX009935	JX009732	JX009560	JX009746			
	ICMP 18694	*Mangifera indica*	South Africa	JX010155	JX009980	JX009729	JX009481	JX009796			
	CBS 119204, ICMP 18678	*Pueraria lobata*	USA	JX010150	JX010013	JX009733	JX009502	JX009790			
	ICMP 18695	*Citrus* sp.	USA	JX010153	JX009979	JX009735	JX009494	JX009779			
	ICMP 18697	*Vitis vinifera*	USA	JX010154	JX009987	JX009736	JX009557	JX009780			
C. gloeosporioides (syn. *Gloeosporium pedemontanum*)	CBS 273.51(*), ICMP 19121	*Citrus limon*	Italy	JX010148	JX010054	JX009745	JX009558	JX009903			
C. hippeastri	CBS 241.78, ICMP 17920	*Hippeastrum* sp.	Netherlands	JX010293	JX009932	JX009740	JX009485	JX009838			
C. horii	ICMP 12942	*Diospyros kaki*	New Zealand	**GQ329687**	**GQ329685**	JX009603	JX009533	JX009748	JX010072	JX010296	JX010375
	ICMP 12951	*Diospyros kaki*	New Zealand	**GQ329689**	**GQ329683**	JX009602	JX009466	JX009751			
	NBRC 7478*, ICMP 10492	*Diospyros kaki*	Japan	**GQ329690**	**GQ329681**	JX009604	JX009438	JX009752	JX010137	JX010370	JX010450
	ICMP 17968	*Diospyros kaki*	China	JX010212	**GQ329682**	JX009605	JX009547	JX009811	JX010068	JX010300	JX010378
	MAFF 306429, ICMP 17970	*Diospyros kaki*	Japan	JX010213	**GQ329686**	JX009606	JX009467	JX009824			
C. kahawae subsp. *ciggaro*	ICMP 18539*	*Olea europaea*	Australia	JX010230	JX009966	JX009635	JX009523	JX009800	JX010132	JX010346	JX010434
	ICMP 18728	*Miconia* sp.	Brazil	JX010239	JX010048	JX009643	JX009525	JX009850			
	ICMP 18741	*Kunzea ericoides*	New Zealand	JX010229	JX010039	JX009631	JX009472	JX009767			
	ICMP 18534	*Kunzea ericoides*	New Zealand	JX010227	JX009904	JX009634	JX009473	JX009765	JX010116	JX010351	JX010427
	ICMP 18544	*Toronia toru*	New Zealand	JX010240	JX009920	JX009632	JX009430	JX009860			
	ICMP 18531	*Persea americana*	New Zealand	JX009463	JX009999	JX009647	JX009463	JX009749			
	ICMP 12952	*Persea americana*	New Zealand	JX010214	JX009971	JX009648	JX009431	JX009757	JX010126	JX010348	JX010426
	ICMP 12953	*Persea americana*	New Zealand	JX010215	JX009928	JX009646	JX009499	JX009758			
	CBS 112984, ICMP 17932	*Dryandra* sp.	South Africa	JX010237	JX009973	JX009633	JX009434	JX009833			
	IMI 359911, ICMP 17931, CBS 12988	*Dryas octopetala*	Switzerland	JX010236	JX009965	JX009637	JX009475	JX009832	JX010121	JX010354	JX010428
C. kahawae subsp. *ciggaro* (syn. *Glomerella cingulata* var. *migrans*)	CBS 237.49(*), ICMP 17922	*Hypericum perforatum*	Germany	JX010238	JX010042	JX009636	JX009450	JX009840	JX010120	JX010355	JX010432

Table 1. (Continued).

Species	Culture*	Host	Country	GenBank accession number							
				ITS	GAPDH	CAL	ACT	CHS-1	GS	SOD2	TUB2
C. kahawae subsp. *ciggaro* (syn. *Glomerella rufomaculans* var. *vaccinii*)	CBS 124.22(*), ICMP 19122	*Vaccinium* sp.	USA	JX010228	JX009950	JX009744	JX009536	JX009902	JX010134	JX010367	JX010433
C. kahawae subsp. *kahawae*	CBS 982.69, ICMP 17915	*Coffea arabica*	Angola	JX010234	JX010040	JX009638	JX009474	JX009829	JX010125	JX010352	JX010435
	IMI 361501, ICMP 17905	*Coffea arabica*	Cameroon	JX010232	JX010046	JX009644	JX009561	JX009816	JX010127	JX010349	JX010431
	IMI 319418*, ICMP 17816	*Coffea arabica*	Kenya	JX010231	JX010012	JX009642	JX009452	JX009813	JX010130	JX010350	JX010444
	CBS 135.30, ICMP 17928	*Coffea* sp.	Kenya	JX010235	JX010037	JX009640	JX009554	JX009831			
	IMI 301220, ICMP 17811	*Coffea arabica*	Malawi	JX010233	JX009970	JX009641	JX009555	JX009817	JX010131	JX010347	JX010430
C. musae	CBS 192.31, ICMP 17923	*Musa* sp.	Indonesia	JX010143	JX009929	JX009690	JX009587	JX009841			
	IMI 52264, ICMP 17817	*Musa sapientum*	Kenya	JX010142	JX010015	JX009689	JX009432	JX009815	JX010084	JX010317	JX010395
	ICMP 12931	*Musa* sp.	New Zealand (imported)	JX010140	JX009995	JX009688	JX009442	JX009756			
	ICMP 18600	*Musa* sp.	Philippines	JX010144	JX010038	JX009686	JX009556	JX009848			
	ICMP 12930	*Musa* sp.	New Zealand	JX010141	JX009986	JX009685	JX009566	JX009881			
	ICMP 18701	*Musa* sp.	Philippines	JX010145	JX010047	JX009687	JX009551	JX009849			
	CBS 116870*, ICMP 19119	*Musa* sp.	USA	JX010146	JX010050	JX009742	JX009433	JX009896	JX010103	JX010335	**HQ596280**
C. nupharicola	CBS 469.96, ICMP 17938	*Nuphar lutea* subsp. *polysepala*	USA	JX010189	JX009936	JX009661	JX009486	JX009834	JX010087	JX010319	JX010397
	CBS 470.96*, ICMP 18187	*Nuphar lutea* subsp. *polysepala*	USA	JX010187	JX009972	JX009663	JX009437	JX009835	JX010088	JX010320	JX010398
	CBS 472.96, ICMP 17940	*Nymphaea ordorata*	USA	JX010188	JX010031	JX009662	JX009582	JX009836	JX010089	JX010321	JX010399
C. psidii	CBS 145.29*, ICMP 19120	*Psidium* sp.	Italy	JX010219	JX009967	JX009743	JX009515	JX009901	JX010133	JX010366	JX010443
C. queenslandicum	ICMP 1778*	*Carica papaya*	Australia	JX010276	JX009934	JX009691	JX009447	JX009899	JX010104	JX010336	JX010414
	ICMP 1780	*Carica* sp.	Australia	JX010186	JX010010	JX009693	JX009504	JX009900			
	ICMP 12564	*Persea americana*	Australia	JX010184	JX009919	JX009692	JX009573	JX009759			
	ICMP 18705	*Coffea* sp.	Fiji	JX010185	JX010036	JX009694	JX009490	JX009890	JX010102	JX010334	JX010412
C. salsolae	ICMP 19051*	*Salsola tragus*	Hungary	JX010242	JX009916	JX009696	JX009562	JX009863	JX010093	JX010325	JX010403
	CBS 119296, ICMP 18693	*Glycine max* (inoculated)	Hungary	JX010241	JX009917	JX009695	JX009559	JX009791			
C. siamense	ICMP 12567	*Persea americana*	Australia	JX010250	JX009940	JX009697	JX009541	JX009761	JX010076	JX010309	JX010387
	DAR 76934, ICMP 18574	*Pistacia vera*	Australia	JX010270	JX010002	JX009707	JX009535	JX009798	JX010080	JX010313	JX010391
	ICMP 12565	*Persea americana*	Australia	JX010249	JX009937	JX009698	JX009571	JX009760			
	CBS 125379, ICMP 18643	*Hymenocallis americana*	China	JX010258	JX010060	**GQ849451**	**GQ856776**	**GQ856729**			
	ICMP 18121	*Dioscorea rotundata*	Nigeria	JX010245	JX009942	JX009715	JX009460	JX009845	JX010092	JX010324	JX010402
	ICMP 18118	*Commelina* sp.	Nigeria	JX010163	JX009941	JX009701	JX009505	JX009843			

Table 1. (Continued).

Species	Culture*	Host	Country	GenBank accession number							
				ITS	GAPDH	CAL	ACT	CHS-1	GS	SOD2	TUB2
	ICMP 18117	*Dioscorea rotundata*	Nigeria	JX010266	JX009954	JX009700	JX009574	JX009842			
	ICMP 18739	*Carica papaya*	South Africa	JX010161	JX009921	JX009716	JX009484	JX009794			
	ICMP 18570	*Persea americana*	South Africa	JX010248	JX009969	JX009699	JX009510	JX009793			
	ICMP 18569	*Persea americana*	South Africa	JX010262	JX009963	JX009711	JX009459	JX009795			
	ICMP 18578*, CBS 130417	*Coffea arabica*	Thailand	JX010171	JX009924	**FJ917505**	**FJ907423**	JX009865	JX010094	JX010326	JX010404
	HKUCC 10884, ICMP 18575	*Capsicum annuum*	Thailand	JX010256	JX010059	JX009717	JX009455	JX009785			
	HKUCC 10881, ICMP 18618	*Capsicum annuum*	Thailand	JX010257	JX009945	JX009718	JX009512	JX009786			
	ICMP 18572	*Vitis vinifera*	USA	JX010160	JX010061	JX009705	JX009487	JX009783			
	ICMP 18571	*Fragaria* × *ananassa*	USA	JX010159	JX009922	JX009710	JX009482	JX009782			
	ICMP 18573	*Vitis vinifera*	USA	JX010271	JX009996	JX009712	JX009435	JX009784			
	ICMP 17795	*Malus domestica*	USA	JX010162	JX010051	JX009703	JX009506	JX009805	JX010082	JX010315	JX010393
	ICMP 17791	*Malus domestica*	USA	JX010273	JX009933	JX009708	JX009508	JX009810			
	ICMP 17797	*Malus domestica*	USA	JX010263	JX009984	JX009704	JX009461	JX009806			
	ICMP 17785	*Malus domestica*	USA	JX010272	JX010051	JX009706	JX009446	JX009804			
C. siamense (syn. *C. hymenocallidis*)	CBS 125378(*), ICMP 18642	*Hymenocallis americana*	China	JX010278	JX010019	JX009709	**GQ856775**	**GQ856730**	JX010100	JX010332	JX010410
C. siamense (syn. *C. jasmini-sambac*)	CBS 130420(*), ICMP 19118	*Jasminum sambac*	Vietnam	**HM131511**	**HM131497**	JX009713	**HM131507**	JX009895	JX010105	JX010337	JX010415
C. theobromicola	MUCL 42295, ICMP 17958, CBS 124250	*Stylosanthes guianensis*	Australia	JX010291	JX009948	JX009598	JX009498	JX009822	JX010067	JX010303	JX010381
	ICMP 18566	*Olea europaea*	Australia	JX010282	JX009953	JX009593	JX009496	JX009801	JX010071	JX010297	JX010376
	ICMP 18565	*Olea europaea*	Australia	JX010283	JX010029	JX009594	JX009449	JX009802	JX010070	JX010298	JX010374
	ICMP 18567	*Olea europaea*	Australia	JX010287	JX009985	JX009599	JX009457	JX009803	JX010069	JX010299	JX010377
	ICMP 18576	*Limonium* sp.	Israel	JX010279	JX010022	JX009595	JX009532	JX009771			
	ICMP 17895	*Annona diversifolia*	Mexico	JX010284	JX010057	JX009600	JX009568	JX009828	JX010066	JX010304	JX010382
	ICMP 15445	*Acca sellowiana*	New Zealand	JX010290	JX010027	JX009601	JX009509	JX009893			
	CBS 125393, ICMP 18650	*Theobroma cacao*	Panama	JX010280	JX009982	JX009590	JX009503	JX009872			
	CBS 124945*, ICMP 18649	*Theobroma cacao*	Panama	JX010294	JX010006	JX009591	JX009444	JX009869	JX010139	JX010372	JX010447
	ICMP 17099	*Fragaria* × *ananassa*	USA	JX010285	JX009957	JX009588	JX009493	JX009778			
	ICMP 17100	*Quercus* sp.	USA	JX010281	JX009947	JX009596	JX009507	JX009781			
	IMI 348152, ICMP 17814	*Fragaria vesca*	USA	JX010288	JX010003	JX009589	JX009448	JX009819	JX010062	JX010301	JX010379
C. theobromicola (syn. *C. fragariae*)	CBS 142.31(*), ICMP 17927	*Fragaria* × *ananassa*	USA	JX010286	JX010024	JX009592	JX009516	JX009830	JX010064	JX010295	JX010373
C. theobromicola (syn. *C. gloeosporioides* f. *stylosanthis*)	MUCL 42294(*), ICMP 17957, CBS 124251	*Stylosanthes viscosa*	Australia	JX010289	JX009962	JX009597	JX009575	JX009821	JX010063	JX010302	JX010380

Table 1. (Continued).

Species	Culture*	Host	Country	GenBank accession number						
				ITS	GAPDH	CAL	ACT	CHS-1	GS	SOD2	TUB2
C. ti	ICMP 5285	*Cordyline australis*	New Zealand	JX010267	JX009910	JX009650	JX009553	JX009897	JX010124	JX010363	JX010441
	ICMP 4832*	*Cordyline* sp.	New Zealand	JX010269	JX009952	JX009649	JX009520	JX009898	JX010123	JX010362	JX010442
C. tropicale	MAFF 239933, ICMP 18672	*Litchi chinensis*	Japan	JX010275	JX010020	JX009722	JX009480	JX009826	JX010086	JX010318	JX010396
	CBS 124949*, ICMP 18653	*Theobroma cacao*	Panama	JX010264	JX010007	JX009719	JX009489	JX009870	JX010097	JX010329	JX010407
	CBS 124943, ICMP 18651	*Annona muricata*	Panama	JX010277	JX010014	JX009720	JX009570	JX009868			
C. xanthorrhoeae	BRIP 45094*, ICMP 17903, CBS 127831	*Xanthorrhoea preissii*	Australia	JX010261	JX009927	JX009653	JX009478	JX009823	JX010138	JX010369	JX010448
	IMI 350817a, ICMP 17820	*Xanthorrhoea* sp.	Australia	JX010260	JX010008	JX009652	JX009479	JX009814			
Glomerella cingulata "f.sp. *camelliae*"	ICMP 10643	*Camellia* × *williamsii*	UK	JX010224	JX009908	JX009630	JX009540	JX009891	JX010119	JX010358	JX010436
	ICMP 18542	*Camellia sasanqua*	USA	JX010223	JX009994	JX009628	JX009488	JX009857	JX010118	JX010357	JX010429
	ICMP 10646	*Camellia sasanqua*	USA	JX010225	JX009993	JX009629	JX009563	JX009892	JX010117	JX010359	JX010437

* = ex-type or authentic culture, (*) = ex-type or authentic culture of synonymised taxon. Sequences downloaded from GenBank, not generated as part of this project are in bold font. Collection abbreviations are listed in the methods.

Several species-trees analyses were conducted using BEAST v. 1.7.1 (Drummond *et al*. 2012). Species-trees combine multi-gene and multiple isolate data to reconstruct the evolutionary history of hypothesised species, rather than individual isolates. BEAST does not use concatenation, but rather co-estimates the individual gene trees embedded inside the summary species tree. It also estimates the time since each species shared a common ancestor (divergence times). For these analyses the species tree ancestral reconstruction option was selected (Heled & Drummond 2010), the gene data partitioned as for BI and the substitution model for each gene was selected based on the models selected using jModelTest. The individual isolates were grouped into sets of species by setting species names as trait values. A strict clock was used for the GAPDH gene (as an all intronic sequence it was assumed to be accumulating mutations at a steady rate) and the other gene clock rates were estimated relative to GAPDH, using an uncorrelated lognormal relaxed clock. The species tree prior used for all genes was the Yule process, with the ploidy type set to nuclear autosomal. Uninformative priors were used for all parameters, and were allowed to auto optimise.

The first species-tree analysis was conducted using the 158 isolate, five gene dataset, with *C. boninense* and *C. hippeastri* as the outgroups. The MCMC chain was set to 1×10^8 generations for the species complex tree and samples were taken from the posterior every 1000 generations. The analysis was run twice independently. The effective sample size (ESS) and traces of all parameters and convergence of the two runs was checked with Tracer and a summary maximum clade credibility species tree was built with TreeAnnotator v. 1.7.1 (Drummond *et al*. 2012) using a 10 % burn-in and a posterior probability limit of 0.5, setting the heights of each node in the tree to the mean height across the entire sample of trees for that clade. Separate analyses were conducted using all eight genes and the same restricted set of isolates chosen to represent taxa within the Musae clade and the Kahawae clade as were used for the BI analyses of the eight gene concatenated analyses outlined above. For each of the Musae and Kahawae clade analyses, the MCMC chain was set to 5×10^7 generations, but otherwise run as for the five gene dataset.

To illustrate the potential limitations of ITS to discriminate species within the *C. gloeosporioides* complex, an UPGMA tree was built of all 158 ITS sequences, using the Geneious tree builder tool. A UPGMA tree visually approximates a BLAST search, which is based on distances (and sequence length) rather than corrected nucleotide substitutions of more sophisticated, model-based analyses.

Sequences derived in this study were lodged in GenBank (Table 1), the concatenated alignment and trees in TreeBASE (www.treebase.org) study number S12535, and taxonomic novelties in MycoBank (Crous *et al.* 2004).

Morphology

Detailed morphological descriptions are provided only for those species with no recently published description. Few specimens were examined from infected host material; the descriptions provided are mostly from agar cultures. Cultures were grown on Difco PDA from single conidia, or from single hyphal tips for the few specimens where no conidia were formed, with culture diameter measured and appearance described after 10 d growth at 18–20 °C under mixed white and UV fluorescent tubes, 12 h light/12 h dark. Colour codes follow Kornerup & Wanscher (1963).

Table 2. Primers used in this study, with sequences and sources.

Gene	Product name	Primer	Direction	Sequence (5'–3')	Reference
ACT	Actin	ACT-512F	Foward	ATG TGC AAG GCC GGT TTC GC	Carbone & Kohn 1999
		ACT-783R	Reverse	TAC GAG TCC TTC TGG CCC AT	Carbone & Kohn 1999
CAL	Calmodulin	CL1	Foward	GAR TWC AAG GAG GCC TTC TC	O'Donnell *et al.* 2000
		CL2A	Reverse	TTT TTG CAT CAT GAG TTG GAC	O'Donnell *et al.* 2000
		CL1C	Foward	GAA TTC AAG GAG GCC TTC TC	This study
		CL2C	Reverse	CTT CTG CAT CAT GAG CTG GAC	This study
CHS-1	Chitin synthase	CHS-79F	Foward	TGG GGC AAG GAT GCT TGG AAG AAG	Carbone & Kohn 1999
		CHS-345R	Reverse	TGG AAG AAC CAT CTG TGA GAG TTG	Carbone & Kohn 1999
GAPDH	Glyceraldehyde-3-phosphate dehydrogenase	GDF	Foward	GCC GTC AAC GAC CCC TTC ATT GA	Templeton *et al.* 1992
		GDR	Reverse	GGG TGG AGT CGT ACT TGA GCA TGT	Templeton *et al.* 1992
GS	Glutamine synthetase	GSF1	Foward	ATG GCC GAG TAC ATC TGG	Stephenson *et al.* 1997
		GSF3	Foward	GCC GGT GGA GGA ACC GTC G	This study
		GSR1	Reverse	GAA CCG TCG AAG TTC CAG	Stephenson *et al.* 1997
		GSR2	Reverse	GAA CCG TCG AAG TTC CAC	This study
ITS	Internal transcribed spacer	ITS-1F	Foward	CTT GGT CAT TTA GAG GAA GTA A	Gardes & Bruns 1993
		ITS-4	Reverse	TCC TCC GCT TAT TGA TAT GC	White *et al.* 1990
SOD2	Manganese-superoxide dismutase	SODglo2-F	Foward	CAG ATC ATG GAG CTG CAC CA	Moriwaki & Tsukiboshi 2009
		SODglo2-R	Reverse	TAG TAC GCG TGC TCG GAC AT	Moriwaki & Tsukiboshi 2009
TUB2	β-Tubulin 2	T1	Foward	AAC ATG CGT GAG ATT GTA AGT	O'Donnell & Cigelnik 1997
		T2	Reverse	TAG TGA CCC TTG GCC CAGT TG	O'Donnell & Cigelnik 1997
		Bt2b	Reverse	ACC CTC AGT GTA GTG ACC CTT GGC	Glass & Donaldson 1995

Table 3. Nucleotide substitution models used in phylogenetic analyses.

Gene	All taxa	Musae clade	Kahawae clade
ITS	TrNef+G	TrNef+G	TrNef
GAPDH	HKY+G	TPM1uf+G	TrN
CAL	TIM1+G	TIM1+G	TrN+G
ACT	HKY+G	TrN	JC
CHS-1	TrNef+G	TrNef+G	K80
GS		TIM2+G	TIM3+G
SOD2		HKY+G	GTR+I+G
TUB2		TrN+G	HKY+G

Conidia were measured and described using conidia taken from the conidial ooze on acervuli and mounted in lactic acid, at least 24 conidia were measured for each isolate, range measurements are provided in the form (lower extreme–) 25 % quartile – 75 % quartile (–upper extreme), all ranges were rounded to the nearest 0.5 µm. Cultures were examined periodically for the development of perithecia. Ascospores were measured and described from perithecia crushed in lactic acid.

Appressoria were producing using a slide culture technique. A small square of agar was inoculated on one side with conidia and immediately covered with a sterile cover slip. After 14 d the cover slip was removed and placed in a drop of lactic acid on a glass slide.

All morphological character measurements were analysed with the statistical programme "R" v. 2.14.0 (R Development Core Team 2011). The R package ggplot2 (Wickham 2009) was used for graphical plots. The box plots show the median, upper and lower quartiles, and the 'whisker' extends to the outlying data, or to a maximum of 1.5× the interquartile range, individual outliers outside this range are shown as dots.

Taxa treated in the taxonomic section

Species, subspecific taxa, and *formae speciales* within the *C. gloeosporioides* species complex are treated alphabetically by epithet. The names of *formae speciales* are not governed by the International Code of Botanical Nomenclature (ICBN) (McNeill *et al.* 2006, Art. 4, Note 4), and are hence enclosed in quotation marks to indicate their invalid status. Other invalid names that are governed by the ICBN are also enclosed in quotation marks. Accepted names are marked with an asterisk (*). The breadth of the taxonomic names treated includes:

all taxonomic names with DNA sequence data in GenBank that place them in the *C. gloeosporioides* complex as it has been defined here on the basis of the ITS gene tree. The sense that the names were used in GenBank may have been misapplied;

names that have been used in the literature in recent years for which a possible relationship to *C. gloeosporioides* has been suggested;

all subspecific taxa and *formae speciales* within *C. gloeosporioides* and *Glomerella cingulata*.

We have not considered the full set of species in *Colletotrichum*, *Gloeosporium* and *Glomerella* that were placed in synonymy with *C. gloeosporioides* or *Glomerella cingulata* by von Arx & Müller (1954) or von Arx (1957, 1970).

For each accepted species, comments are provided regarding the limitations of ITS, the official barcoding gene for fungi, to distinguish that species from others within the *C. gloeosporioides* complex.

RESULTS

Phylogenetics

DNA sequences of five genes were obtained from all 158 isolates included in the study and concatenated to form a supermatrix of 2294 bp. The gene boundaries in the alignment were: ACT: 1–316, CAL: 317–1072, CHS-1: 1073–1371, GAPDH: 1372–1679, ITS: 1680–2294. A BI analysis of the concatenated dataset is presented in Fig.1. This tree is annotated with the species boundaries of the taxa that we accept in the *C. gloeosporioides* complex, and the clades representing these taxa formed the basis for investigating the morphological and biological diversity of our species. Ex-type and authentic isolates are highlighted in bold and labelled with the names under which they were originally described. The posterior probability (PP) support for the grouping of most species ranges from 1 to 0.96, however support for deeper nodes is often lower, *e.g.* 0.53 for the root of *C. ti* and *C. aotearoa,* indicating that the branching may be uncertain for the root of these species. Branch lengths and node PP are typically lower within a species than between species.

The large number of taxa in Fig. 1 makes it difficult to visualise the interspecific genetic distance between the recognised species. The unrooted tree in Fig. 2 represents the results of a BI analysis based on a concatenation of all eight genes, but restricted to the ex-type or authentic cultures from each of the accepted taxa. The analysis was done without out-group taxa and clearly shows two clusters of closely related species that we informally label the Musae clade, and the Kahawae clade.

To better resolve relationships within the Musae and Kahawae clades a further set of BI analyses included eight genes and, wherever possible, several representative isolates of each of the accepted species. All eight gene sequences were concatenated to form a supermatrix for each clade. For the Musae clade of 32 isolates the alignment was 4199 bp and the gene boundaries were: ACT: 1–292, TUB2: 293–1008, CAL: 1009–1746, CHS-1: 1747–2045, GAPDH: 2046–2331, GS: 2332–3238, ITS: 3239–3823, SOD2: 3824–4199. For the Kahawae clade of 30 isolates the alignment was 4107 bp and the gene boundaries were: ACT: 1–281, TUB2: 282–988, CAL: 989–1728, CHS-1: 1729–2027, GAPDH: 2028–2311, GS: 2312–3179, ITS: 3198–3733, SOD2: 3734–4107. The additional genes sequenced provided additional support for our initial species delimitations with better resolution for some closely related species. For example, the highly pathogenic coffee berry isolates (referred to here as *C. kahawae* subsp. *kahawae*) were distinguished from other *C. kahawae* isolates.

Analyses based on concatenated data sets can mask incongruence between individual gene trees. The low levels of support within some parts of the species-tree analysis (Fig. 3), in part reflects incongruence between gene trees. The levels of support for the Kahawae clade and for the Musae clade are strong (PP=1) but the species that we accept within these clades have lower levels of support than is shown between the other species outside of the clades. The scale bar in Fig. 3 represents a time scale, calibrated at zero for the present day, and at 1 for the last common ancestor (LCA) of the *C. gloeosporioides* and *C. boninense* species complexes. The separate species-tree analyses for the Musae and Kahawae clades provide a finer resolution of evolutionary history within each clade, the time scale based on the same calibration as Fig. 3.

The UPGMA-based ITS gene tree (Fig 6). shows that *C. theobromicola*, *C. horii*, *C. gloeosporioides, G. cingulata* "f. sp. *camelliae*"*, C. asianum, C. musae, C. alatae, C. xanthorrhoeae* all form monophyletic clades and may be distinguished with ITS, but many species are unable to be discriminated using this gene alone. Note that *C. cordylinicola* and *C. psidii* are represented by a single isolate, meaning that variation within ITS sequences across these species has not been tested.

Morphology and biology

Brief morphological descriptions, based on all specimens examined, are provided for only those species with no recently published description. Conidial sizes for all accepted species are summarised in Fig. 7. Within a species, conidial sizes are reasonably consistent across isolates, independent of geographic origin or host. However, differences between species are often slight and size ranges often overlap (Fig. 7). The shape of appressoria is generally consistent within a species, some being simple in outline, others complex and highly lobed.

Several species are characterised in part by the development of perithecia in culture. These include four species in the Musae clade (*C. alienum*, C. *fructicola*, *C. queenslandicum*, and *C. salsolae*) and three in the Kahawae clade (*C. clidemiae*, *C. kahawae* subsp. *ciggaro*, and *C. ti*). Ascospore size and shape can be a useful species-level diagnostic feature (Fig. 8). In most species the ascospores are strongly curved and typically tapering towards the ends, but in *C. clidemiae* and *C. ti*, they are more or less elliptic with broadly rounded ends and not, or only slightly, curved. Individual isolates within any of these species may lose the ability to form perithecia, perhaps associated with cultural changes during storage.

Large, dark-walled stromatic structures are present in the cultures of some species not known to form perithecia. Often embedded in agar, less commonly on the surface or amongst the aerial mycelium, these structures differ from perithecia in comprising a compact tissue of tightly tangled hyphae rather than the pseudoparenchymatous, angular cells typical of perithecial walls. They have a soft, leathery texture compared to the more brittle perithecia. These stromatic structures sometimes develop a conidiogenous layer internally, and following the production of conidia they may split open irregularly, folding back to form a stromatic, acervulus-like structure. These kind of structures are also formed by some species in the *C. boninense* species complex (Damm *et al.* 2012b, this issue).

The macroscopic appearance of the cultures is often highly divergent within a species (*e.g. C. fructicola* and *C. theobromicola),* in most cases probably reflecting different storage histories of the isolates examined. Prolonged storage, especially with repeated subculturing, results in staling of the cultures, the aerial mycelium often becoming dense and uniform in appearance and colour, and a loss of conidial and perithecial production, and variable in growth rate (Fig. 9). In some species, individual single ascospore or single conidial isolates show two markedly different cultural types, see notes under *C. kahawae* subsp. *ciggaro*.

Some species appear to be host specialised, *e.g. C. horii, C. kahawae* subsp. *kahawae, C. nupharicola, C. salsolae, C. ti*, and *C. xanthorrhoeae*, but those most commonly isolated have broad host and geographic ranges, *e.g. C. fructicola, C. kahawae* subsp. *ciggaro, C. siamense,* and *C. theobromicola*. *Colletotrichum gloeosporioides s. str.* is commonly isolated from *Citrus* in many

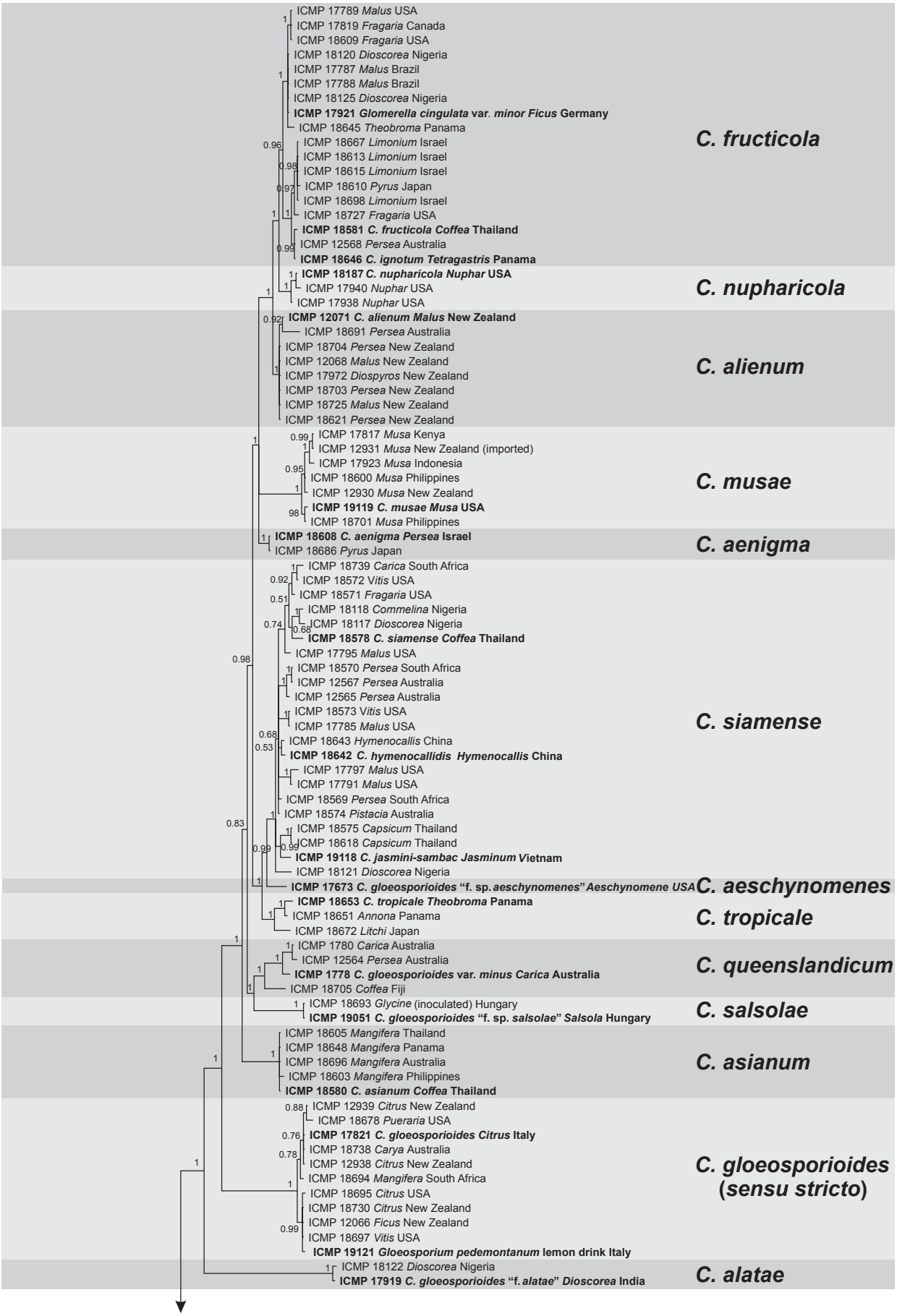


Fig. 1. A Bayesian inference phylogenetic tree of 156 isolates in the *Colletotrichum gloeosporioides* species complex. The tree was built using concatenated sequences of the ACT, CAL, CHS-1, GAPDH, and ITS genes each with a separate model of DNA evolution. Bayesian posterior probability values ≥ 0.5 are shown above nodes. Culture accession numbers are listed along with host plant genus and country of origin. Ex-type and authentic cultures are emphasised in bold font, and include the taxonomic name as originally described. Species delimitations are indicated with grey boxes. *Colletotrichum boninense* and *C. hippeastri* isolates are used as outgroups. The scale bar indicates the number of expected changes per site.

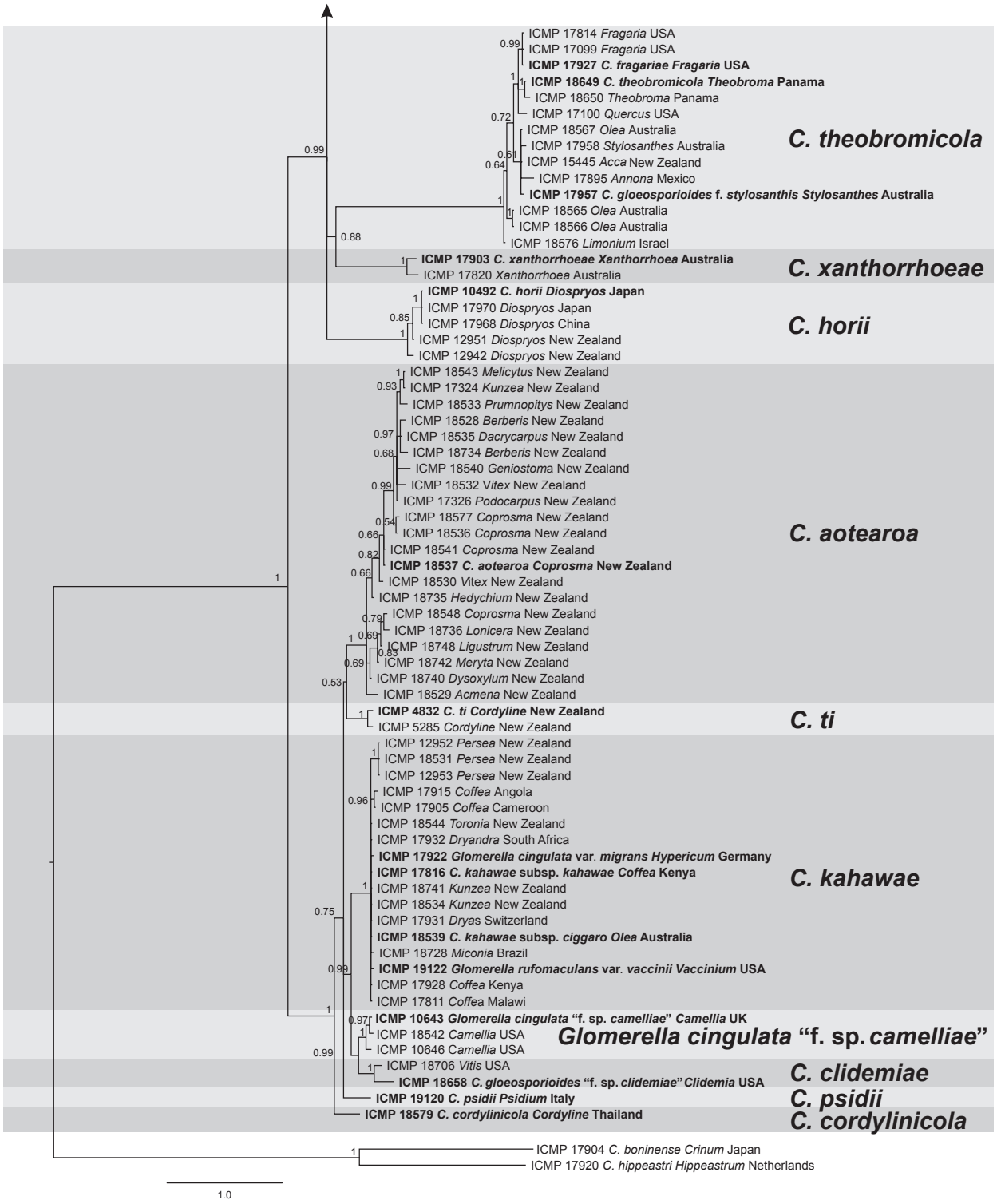


Fig. 1. (Continued).

parts of the world, but has been isolated from other hosts as well, such as *Ficus*, *Mangifera*, *Pueraria*, and *Vitis*. Not all of the species with a broad host range are found everywhere, for example in New Zealand *C. alienum* is commonly associated with cultivated fruits, whereas species such as *C. siamense* and *C. fructicola*, common on these same cultivated fruits in other parts of the world, have not been reported from New Zealand.

Taxonomy

Based on results of the multigene concatenated BI phylogenies, we accept 22 species plus one subspecies within the *C. gloeosporioides* complex. Isolates authentic for *G. cingulata* "f. sp. *camelliae*" form a genetically distinct group, but this is not formally named because of doubts over its relationship to *C. camelliae*. Based on DNA sequence comparisons, a few other isolates almost certainly represent additional unnamed species. We do not formally describe them because most are known from a single isolate, often stale, with little understanding of either their morphological or biological diversity. In the Musae clade these include ICMP 18614 and ICMP 18616, both from grape from Japan, and ICMP 18726 from pawpaw from the Cook Islands, and in the Kahawae clade ICMP 18699 from chestnut from Japan. These isolates are not included in the phylogenies in this study,

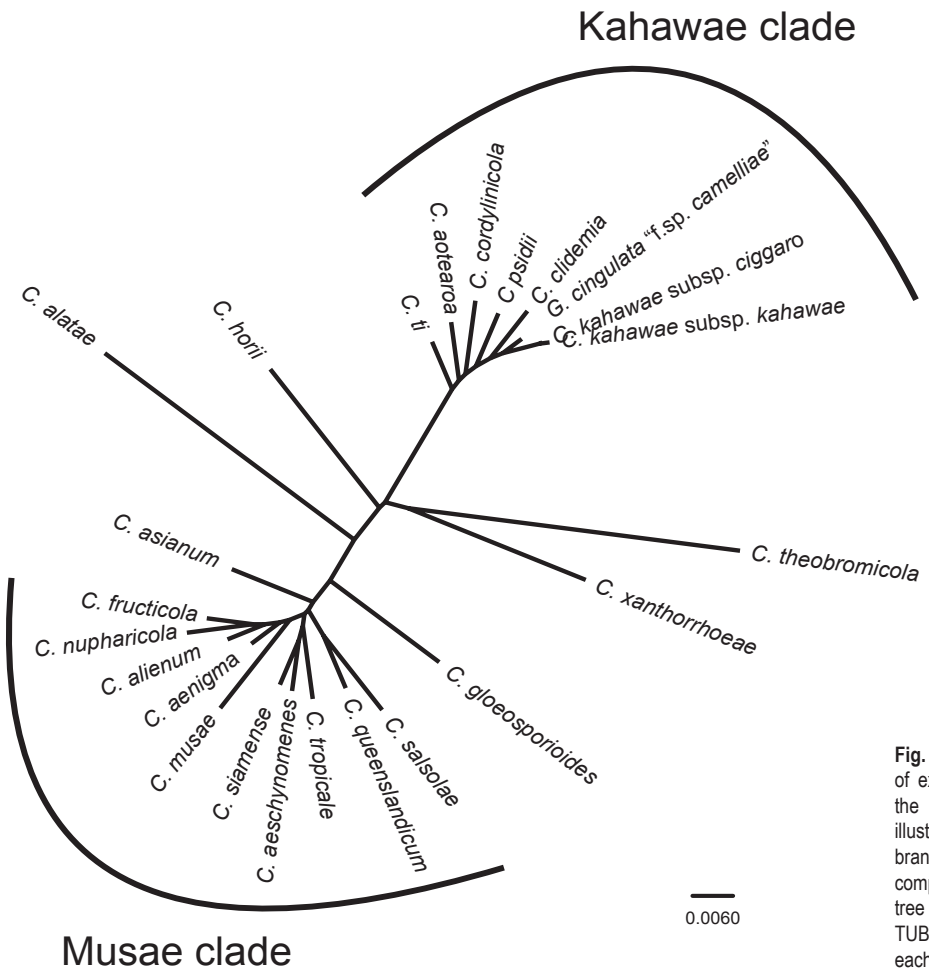


Fig. 2. An unrooted Bayesian inference phylogenetic tree of ex-type and authentic cultures of the 24 taxa within the *Colletotrichum gloeosporioides* species complex, illustrating their relative genetic distances, as indicated by branch lengths. There are two clusters within the species complex, the 'Musae clade' and the 'Kahawae clade'. The tree was build using concatenated sequences of the ACT, TUB2, CAL, CHS-1, GAPDH, GS, ITS, and SOD2 genes each with a separate model of DNA evolution.

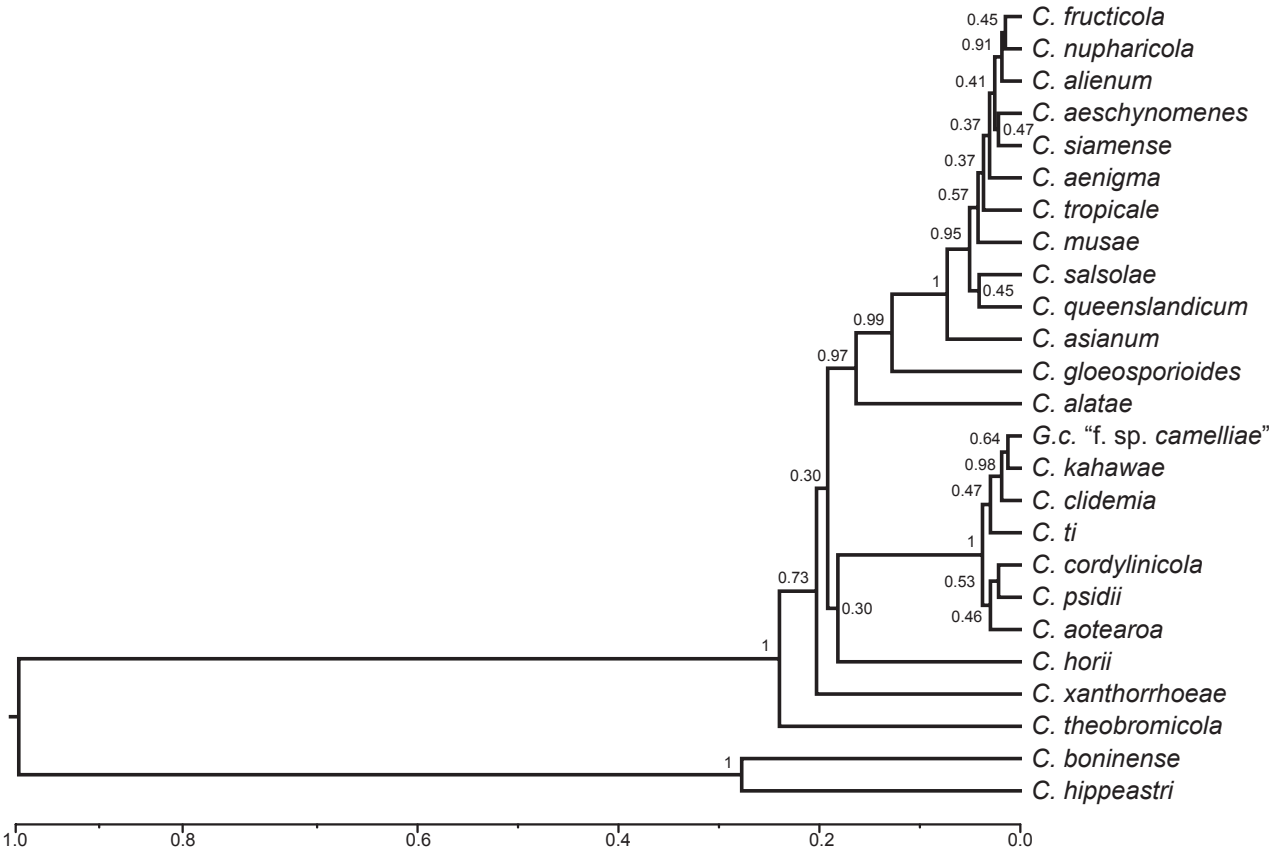


Fig. 3. A Bayesian inference species-tree of the *C. gloeosporioides* species complex. The tree was built by grouping all 158 isolates into species and simultaneously estimating the individual five gene trees (ACT, CAL, CHS-1, GAPDH, and ITS) and the summary species tree using BEAST. The scale is an uncalibrated clock set relative to the last common ancestor of the *C. gloeosporioides* and *C. boninense* species complexes.

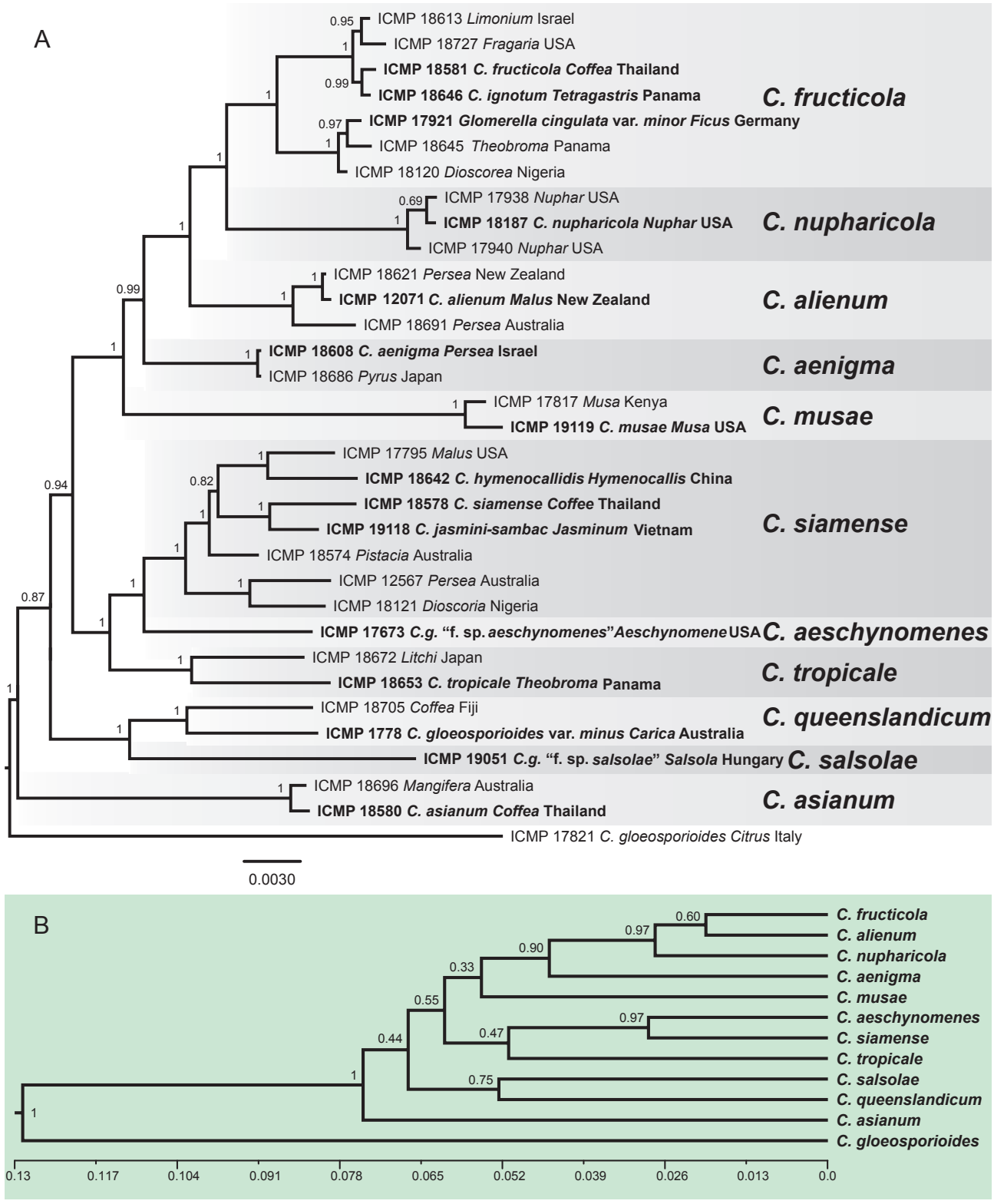


Fig. 4. A Bayesian inference phylogenetic tree of 32 selected isolates in the Musae clade of the *Colletotrichum gloeosporioides* species complex. The tree was build using concatenated sequences of the ACT, TUB2, CAL, CHS-1, GAPDH, GS, ITS, and SOD2 genes each with a separate model of DNA evolution. Other details as per Fig.1. B. A species-tree constructed from the same data, the scale is an clock set relative to the last common ancestor of the Musae clade and *C. gloeosporioides s. str.*, as calibrated in Fig. 3.

but DNA sequences from these isolates have been accessioned into GenBank (ITS: JX009423–JX009428, GAPDH: JX009416–JX009422, ACT: JX009404–JX009407, CAL: JX009408–JX009411, CHS-1: JX009412–JX009415).

Many of the species that we recognise fall into one of two clades, the informally named Musae clade and Kahawae clade (Fig. 2). Each clade contains several species that are phylogenetically well supported in multi-gene analyses, but within the clades branch lengths are short because of the small number of phylogenetically informative characters. This is reflected in the low support values in the gene tree analyses for the species we accept within that clade (Figs 3, 4). Both the Musae and Kahawae clades contain ex-type or authentic cultures from several long accepted species. In this work we have made a pragmatic decision to minimise taxonomic disruption, so that monophyletic subclades within the Kahawae and Musae clades are accepted as species where they include

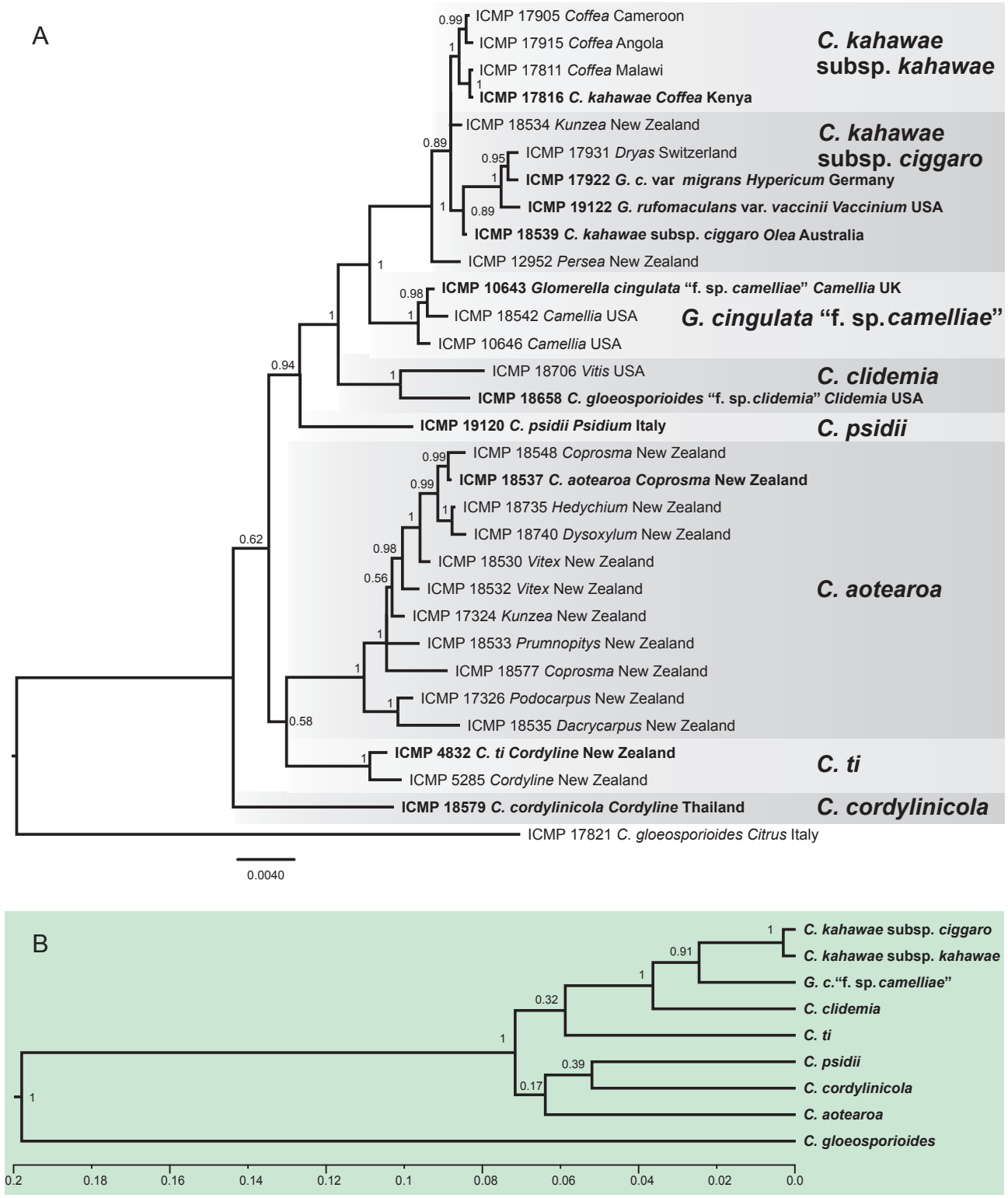


Fig. 5. A Bayesian inference phylogenetic tree of 30 selected isolates in the Kahawae clade of the *Colletotrichum gloeosporioides* species complex. The tree was build using concatenated sequences of the ACT, TUB2, CAL, CHS-1, GAPDH, GS, ITS, and SOD2 genes each with a separate model of DNA evolution. Other details as per Fig.1. B. A species-tree constructed from the same data, the scale is a clock set relative to the last common ancestor of the Kahawae clade and *C. gloeosporioides s. str.*, as calibrated in Fig. 3.

ex-type or authentic cultures. The Musae clade thus includes *C. fructicola*, *C. musae*, *C. nupharicola*, *C. siamense*, and *C. tropicale*; and the Kahawae clade includes *C. cordylinicola*, *C. psidii*, and *C. kahawae*. Also belonging in the latter is *Glomerella cingulata* "f. sp. *camelliae*". To provide a consistent taxonomic treatment of the subclades resolved within the Musae and Kahawae clades, several new species and one new subspecies are proposed. In the Musae clade these are *C. aenigma*, *C. aeschynomenes*, *C. alienum*, *C. queenslandicum*, and *C. salsolae*; in the Kahawae clade *C. aotearoa*, *C. clidemiae*, *C. kahawae* subsp. *ciggaro*, and *C. ti*. The other accepted species, well resolved in all of the gene trees, are *C. alatae, C. asianum*, *C. gloeosporioides*, *C. horii*, *C. theobromicola*, and *C. xanthorrhoeae*.

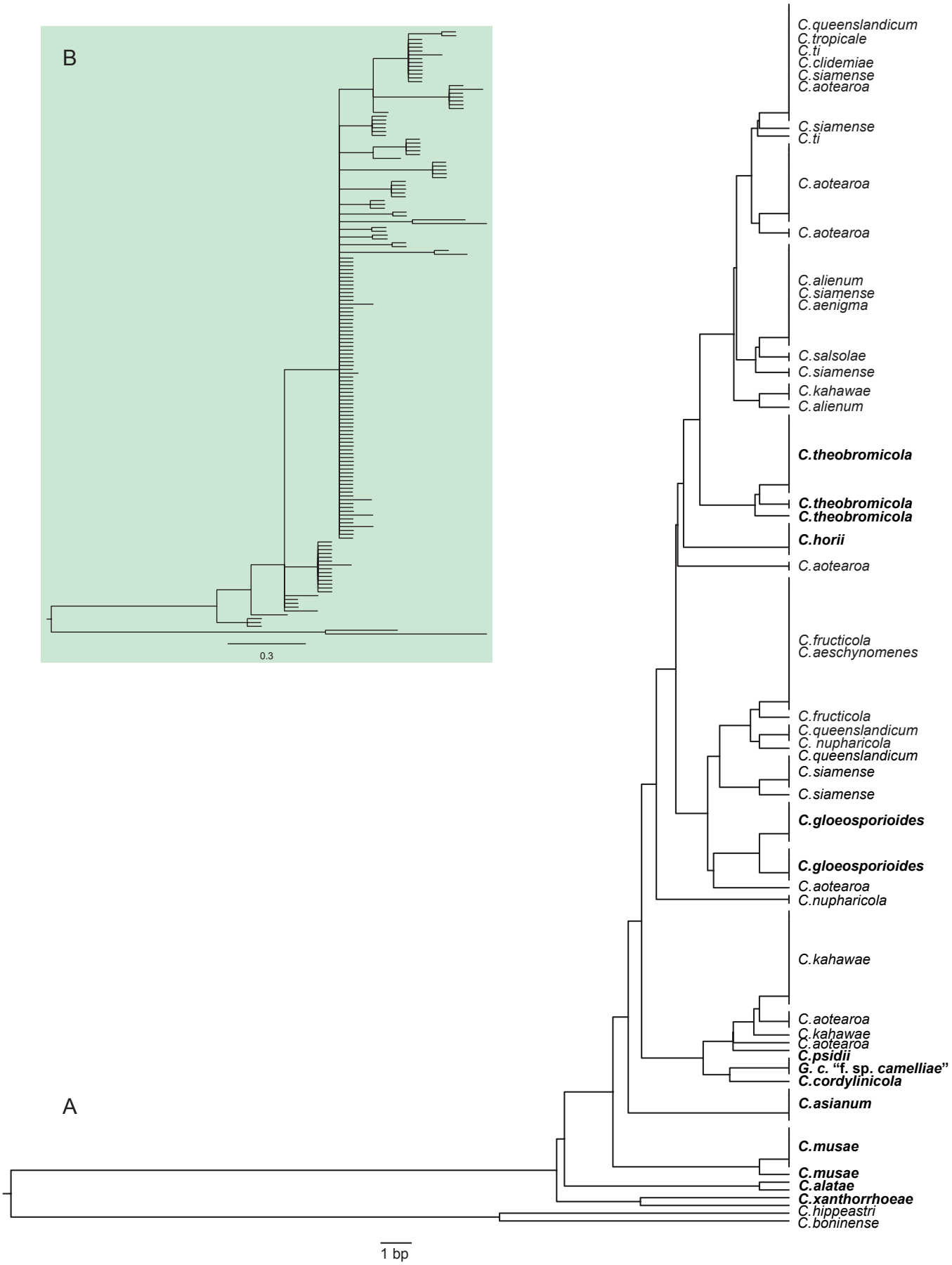
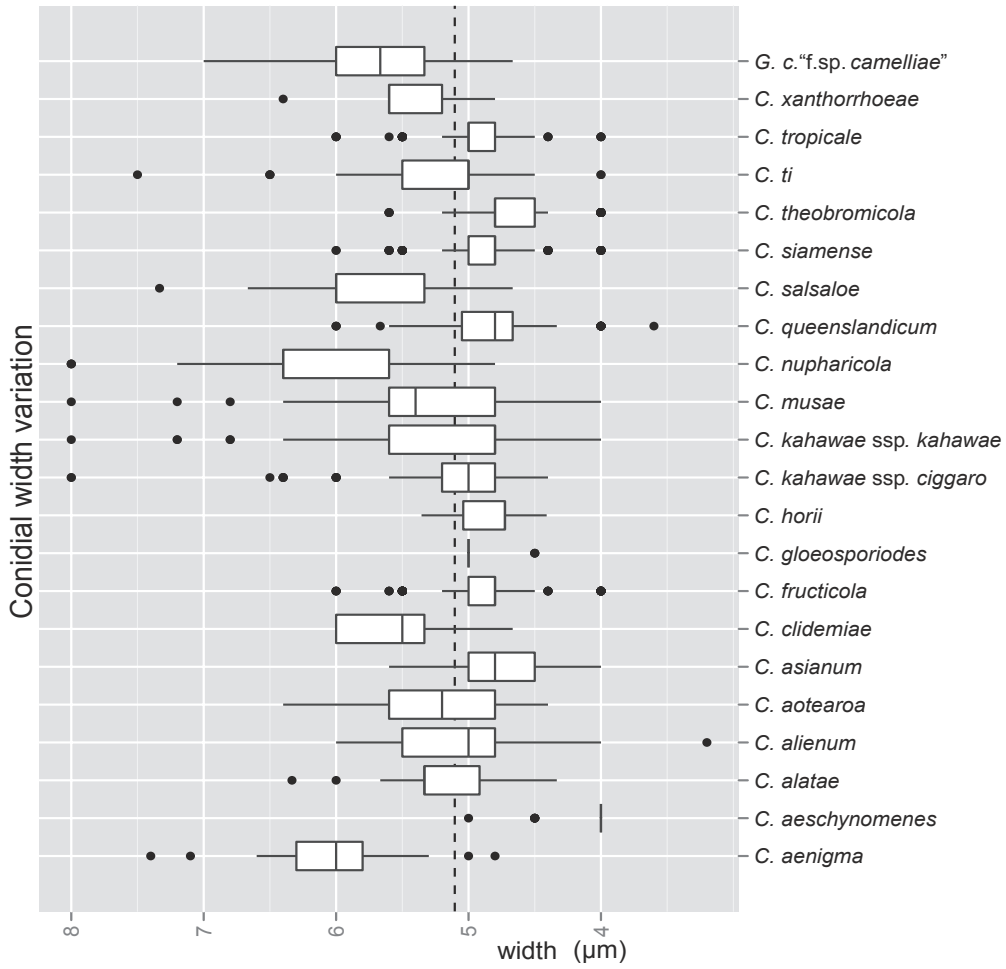


Fig. 6. An UPGMA tree of ITS sequences from 156 isolates in the *Colletotrichum gloeosporioides* species complex. Isolate names have been replaced with species present in each clade. Species that are in monophyletic clades are emphasised in bold font to indicate those for which ITS barcoding is likely to work well. B: A 50 % majority-rule consensus Bayesian inference tree of the same data, showing the collapse of structure when analysed with a more robust method.



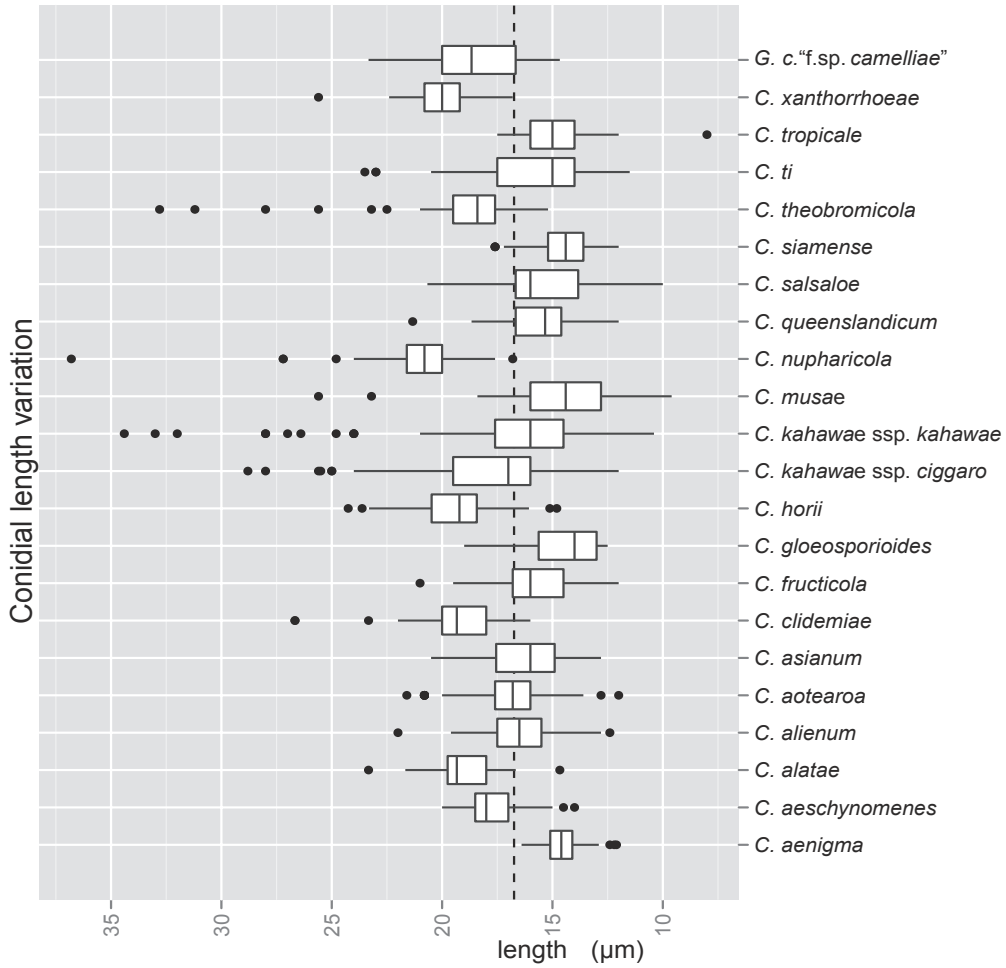
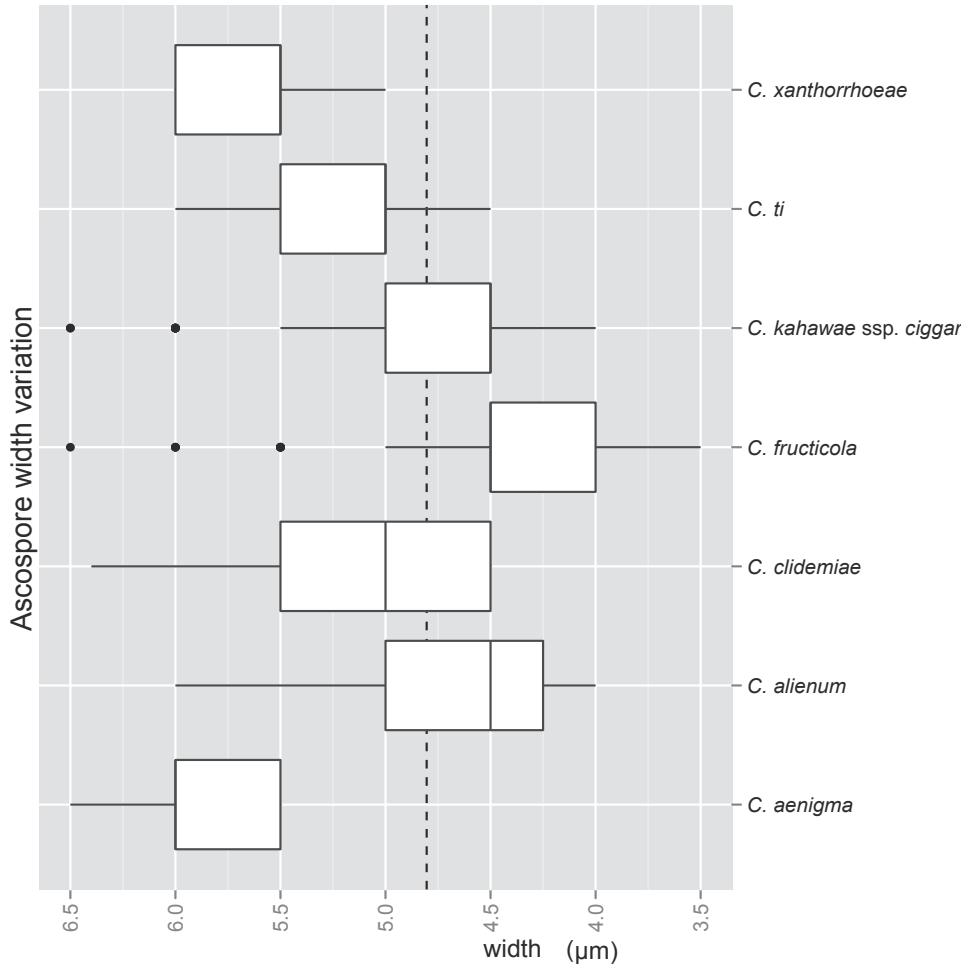


Fig. 7. Box plots showing the variation in length and width of conidia produced by the cultures examined in this study. The dashed lines show the mean length (16.74 µm) and width (5.1 µm) across the species complex (n = 1958).



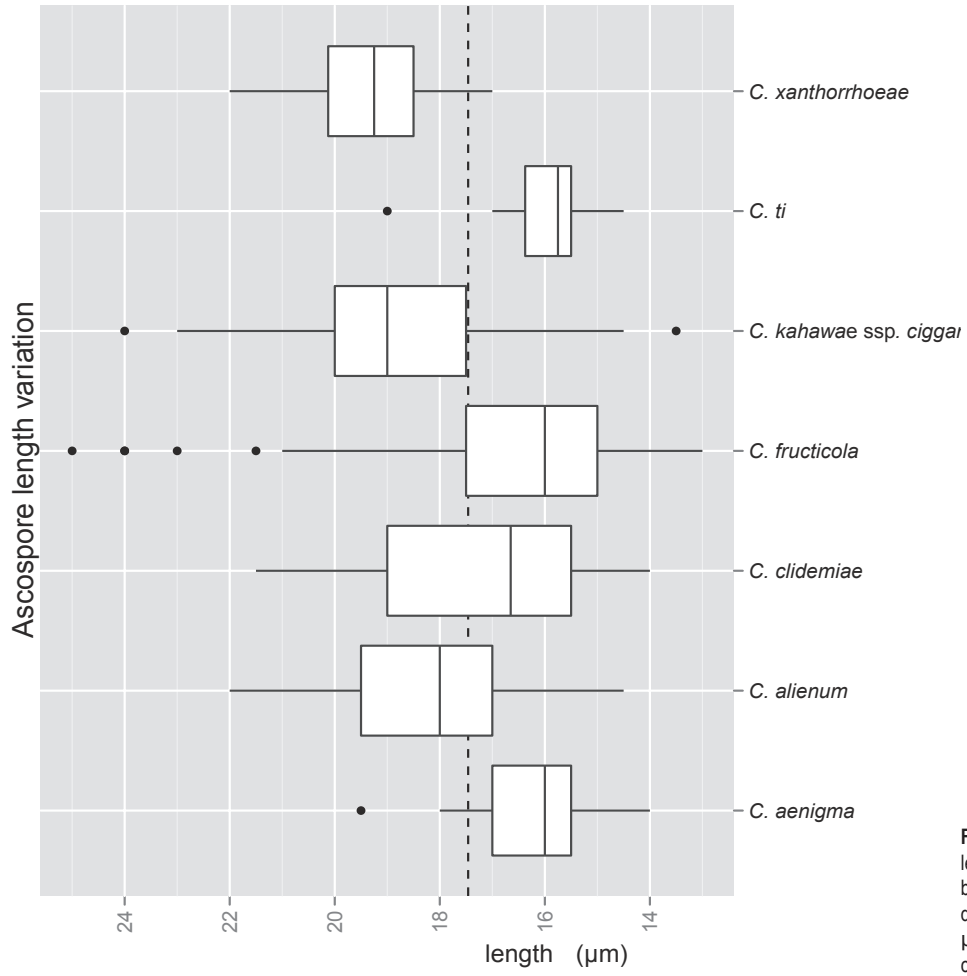


Fig. 8. Box plots showing the variation in length and width of ascospores produced by the cultures examined in this study. The dashed lines show the mean length (17.46 µm) and width (4.8 µm) across the species complex (n = 452).

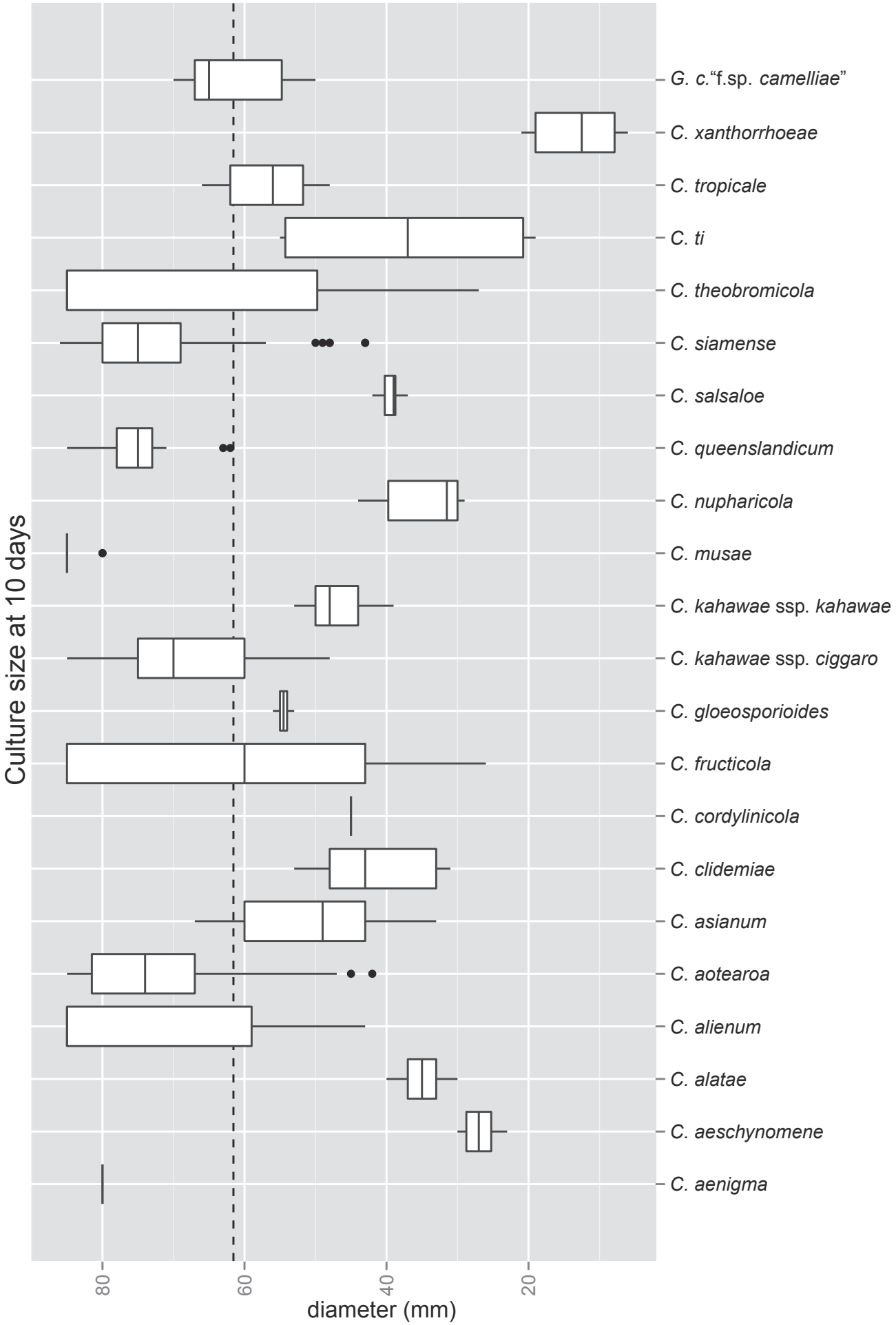


Fig. 9. A box plot of the diameter of cultures grown on PDA agar at 18 °C for 10 d. The dashed line shows the mean culture size (61.56 mm) across the species complex (n = 719). Note that the data is skewed by some fast growing cultures that reached the agar plate diam (85 mm) in under 10 d.

*** *Colletotrichum aenigma*** B. Weir & P.R. Johnst., **sp. nov.** MycoBank MB563759. Fig. 10.

Etymology: from the Latin *aenigma*, based on the enigmatic biological and geographic distribution of this species.

Holotype: **Israel**, on *Persea americana*, coll. S. Freeman Avo-37-4B, PDD 102233; ex-holotype culture ICMP 18608.

Colonies grown from single conidia on Difco PDA 30–35 mm diam after 10 d. Aerial mycelium sparse, cottony, white, surface of agar uniformly pale orange (7A5) towards centre, more or less colourless towards edge, conidia not associated with well differentiated acervuli and no masses of conidial ooze. In reverse pale orange towards centre. *Conidiogenous cells* arising haphazardly from dense, tangled hyphae across agar surface, short-cylindric with a poorly differentiated conidiogenous locus. *Conidia* often germinating soon after release, sometimes forming appressoria, so forming a thin, compact, layer of germinated, septate conidia, germ tubes, and appressoria across the central part of the colony surface. Conidia (12–)14–15(–16.5) × (5–)6–6.5(–7.5) µm (av. 14.5 × 6.1 µm, n = 53), cylindric with broadly rounded ends. *Appressoria* 6–10 µm diam, subglobose or with a few broad lobes.

Geographic distribution and host range: known from only two collections, one from *Pyrus pyrifolia* from Japan, the other from *Persea americana* from Israel.

Genetic identification: ITS sequences are insufficient to separate *C. aenigma* from *C. alienum* and some *C. siamense* isolates. These taxa are best distinguished using TUB2 or GS.

Notes: Although the biology of this species is more or less unknown, it has been found in two widely separate regions and is, therefore, likely to be found to be geographically widespread in the future. Genetically distinct within the Musae clade, this species has a distinctive appearance in culture with sparse, pale aerial mycelium and lacking differentiated acervuli.

Other specimen examined: **Japan**, on *Pyrus pyrifolia*, coll. H. Ishii Nashi-10 (ICMP 18686).

*** *Colletotrichum aeschynomenes*** B. Weir & P.R. Johnst., **sp. nov.** MycoBank MB563590. Fig. 11.

= *C. gloeosporioides* "f. sp. *aeschynomenes*" (Daniel *et al.* 1973, as *aeschynomene*).

Etymology: Based on *C. gloeosporioides* "f. sp. *aeschynomenes*", referring to the host from which this species was originally described.

Holotype: **USA**, Arkansas, on *Aeschynomene virginica* stem lesion, coll. D. TeBeest 3-1-3, PDD 101995; ex-type culture ICMP 17673 = ATCC 201874.

Colonies grown from single conidia on Difco PDA 25–35 mm diam after 10 d, aerial mycelium sparse, cottony, white, surface of colony with numerous acervuli, some with dark bases, with orange conidial ooze; in reverse more or less colourless apart from the dark acervuli and orange conidial masses showing through the agar. *Conidia* (14–)17–18.5(–20) × 4(–5) µm (av. 17.6 × 4.1 µm, n = 30), cylindric, straight, tapering slightly near both ends. *Appressoria* mostly elliptic to subfusoid, deeply lobed. Perithecia not seen.

Geographic distribution and host range: Reported only from USA, pathogenic to *Aeschynomeme.*

Genetic identification: ITS sequences do not distinguish *C. aeschynomenes* from *C. fructicola*. These taxa are best distinguished using TUB2, GAPDH, or GS.

Notes: *Colletotrichum gloeosporioides* "f. sp. *aeschynomenes*" has been used to refer to isolates pathogenic to *Aeschynomene virginica*, later developed as the weed biocontrol agent Collego (references in Ditmore *et al.* 2008). It has also been reported from a range of other hosts (TeBeest 1988). Our analyses, based on a single, authentic strain of *C. gloeosporioides* "f. sp. *aeschynomenes*" (TeBeest 3.1.3, apparently the source of the single spore isolate originally used in the development of Collego, Ditmore *et al.* (2008)) show it to be genetically distinct within the Musae clade of the *C. gloeosporioides* complex. Genetically close to the geographically and biologically diverse *C. siamense*, it differs morphologically from this species in having slightly longer and narrower conidia which taper slightly toward the ends, and in having larger, strongly lobed appressoria.

An isolate deposited as *C. gloeosporioides* f. sp. *aeschynomenes* in CBS (CBS 796.72) by G.E. Templeton, one of the early *C. gloeosporioides* f. sp. *aeschynomenes* researchers (Daniel *et al.* 1973), is genetically distinct to TeBeest 3.1.3 and has been identified by Damm *et al.* (2012a, this issue) as *C. godetiae*, a member of the *C. acutatum* complex. The strain that we examined (Te Beest 3.1.3) matches genetically another strain often cited in the *C. gloeosporioides* f. sp. *aeschynomenes* literature (Clar-5a = ATCC 96723) (GenBank JX131331). It is possible that two distinct species, both highly pathogenic to *Aeschynomene* in Arkansas, have been confused. A survey of additional isolates of *Colletotrichum* highly virulent to *Aeschynomene* in Arkansas would clarify the interpretation of the past literature on this pathogen. For example, *C. gloeosporioides* "f. sp. *aeschynomenes*" was initially reported as specific to *Aeschynomene virginica* (Daniel *et al.* 1973), while later studies reported isolates putatively of the same taxon, to have a wider host range (TeBeest 1988).

Cisar *et al.* (1994) reported fertile ascospores from crosses between isolates identified as *C. gloeosporioides* "f. sp. *aeschynomenes*" and isolates of *C. gloeosporioides* "f. sp. *jussiaeae*", a pathogen of *Jussiaea decurrens*. The position of *C. gloeosporioides* "f. sp. *jussiaeae*" within our phylogeny is not known, but these taxa could prove useful for better understanding of the biological differences between phylogenetically defined species of *Colletotrichum*.

Specimen examined: **USA**, Arkansas, on *Aeschynomene virginica* stem lesion, coll. D. TeBeest 3.1.3 (ICMP 17673 = ATCC 201874).

*** *Colletotrichum alatae*** B. Weir & P.R. Johnst., **sp. nov.** MycoBank MB563747. Fig. 12.

= *Colletotrichum gloeosporioides* "f. *alatae*" R.D. Singh, Prasad & R.L. Mathur, Indian Phytopathol. 19: 69. 1966. [nom. inval., no Latin description, no type designated].

Etymology: Based on the invalid name *C. gloeosporioides* "f. *alatae*" (Singh *et al.* 1966), referring to *Dioscorea alata*, the scientific name for yam.

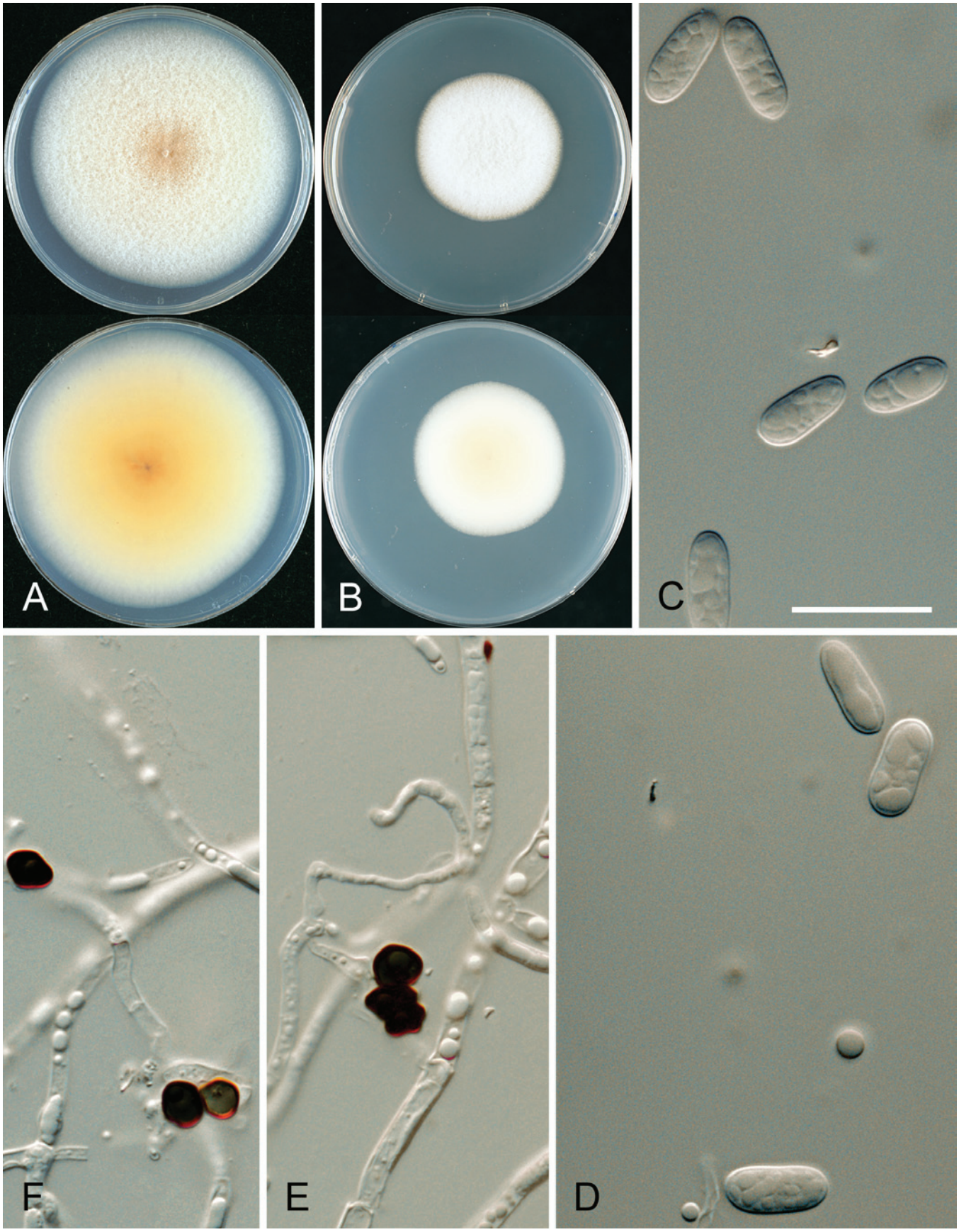


Fig. 10. *Colletotrichum aenigma*. A, C, D, E, F. ICMP 18608 – ex-holotype culture. B. ICMP 18616. A–B. Cultures on PDA, 10 d growth from single conidia, from above and below. C–D. Conidia. E–F. Appressoria. Scale bar C = 20 µm. Scale bar of C applies to C–F.

Holotype: **India**, Rajasthan, Udaipur, on *Dioscorea alata* leaves and stems, coll. K.L. Kothari & J. Abramham, 1959, CBS H-6939; ex-type culture and putatively authentic isolate of *C. gloeosporioides* f. *alatae* CBS 304.67 = ICMP 17919.

Colonies grown from single conidia on Difco PDA 30–40 mm diam after 10 d. Ex-holotype culture looks "stale", with low, felted, dense, pale grey aerial mycelium, orange agar surface showing through near the margin, scattered dark based acervuli with orange conidial

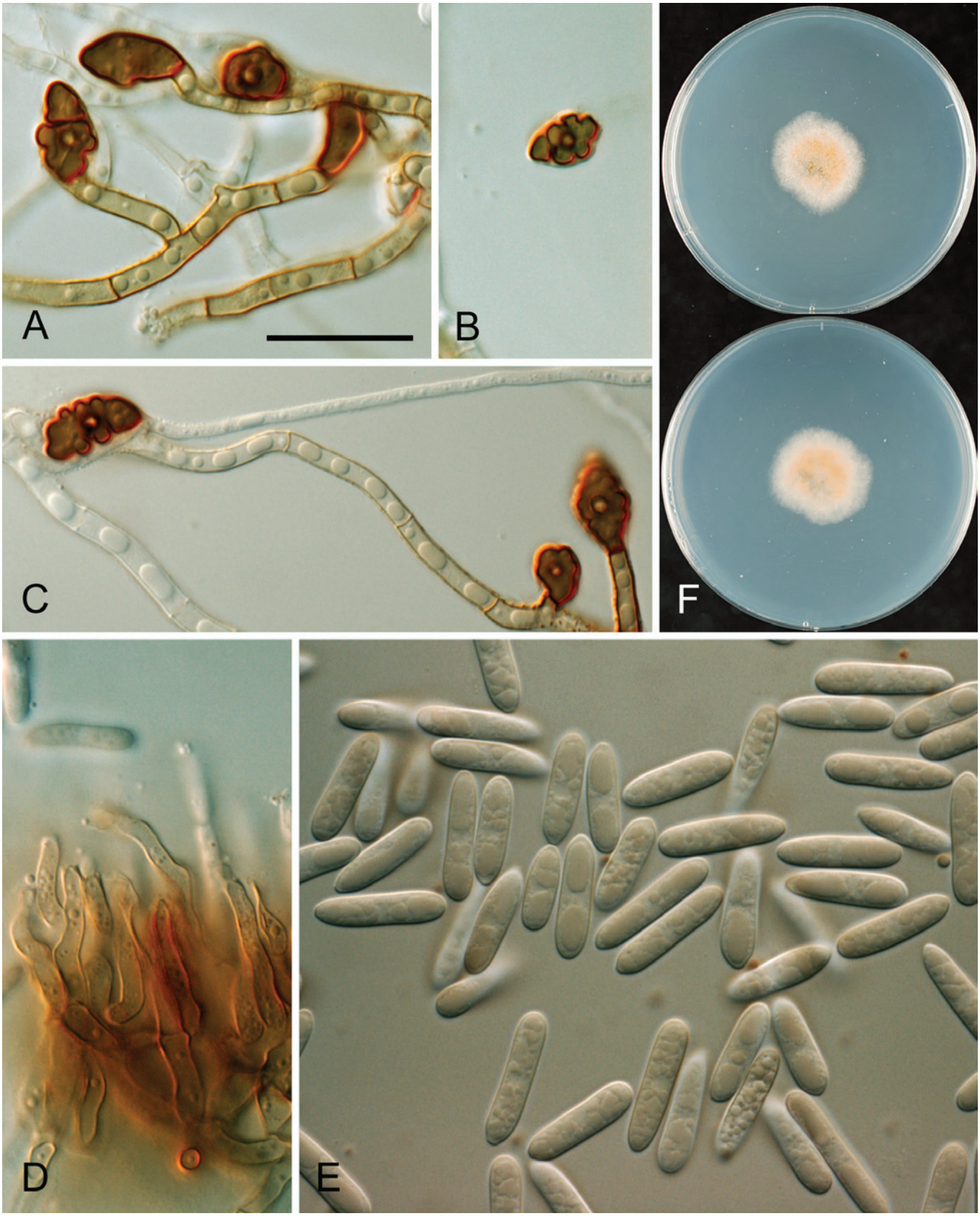


Fig. 11. *Colletotrichum aeschynomenes*. ICMP 17673 – ex-holotype culture. A–C. Appressoria. D. Conidiogenous cells. E. Conidia. F. Cultures on PDA, 10 d growth from single conidia, from above and below. Scale bar of A = 20 µm. Scale bar of A applies to A–E.

masses near centre; in reverse deep pinkish orange with patches of grey pigment near centre. ICMP 18122 with aerial mycelium sparse, colony surface with numerous discrete, dark-based acervuli with bright orange conidial ooze, margin of colony feathery; in reverse irregular sectors with pale grey pigment within the grey, otherwise colourless apart from the colour of the acervuli and conidial masses. *Conidia* (14.5−)18–19.5(−23.5) × (4.5−)5−5.5(−6.5) µm (av. 18.9 × 5.2 µm, n = 40), cylindric, straight, ends rounded, a few tapering towards the basal end. *Appressoria* mostly simple, elliptic to fusoid in shape, sometime developing broad, irregular lobes, about 7–13.5 × 5–10.5 µm. Perithecia not seen.

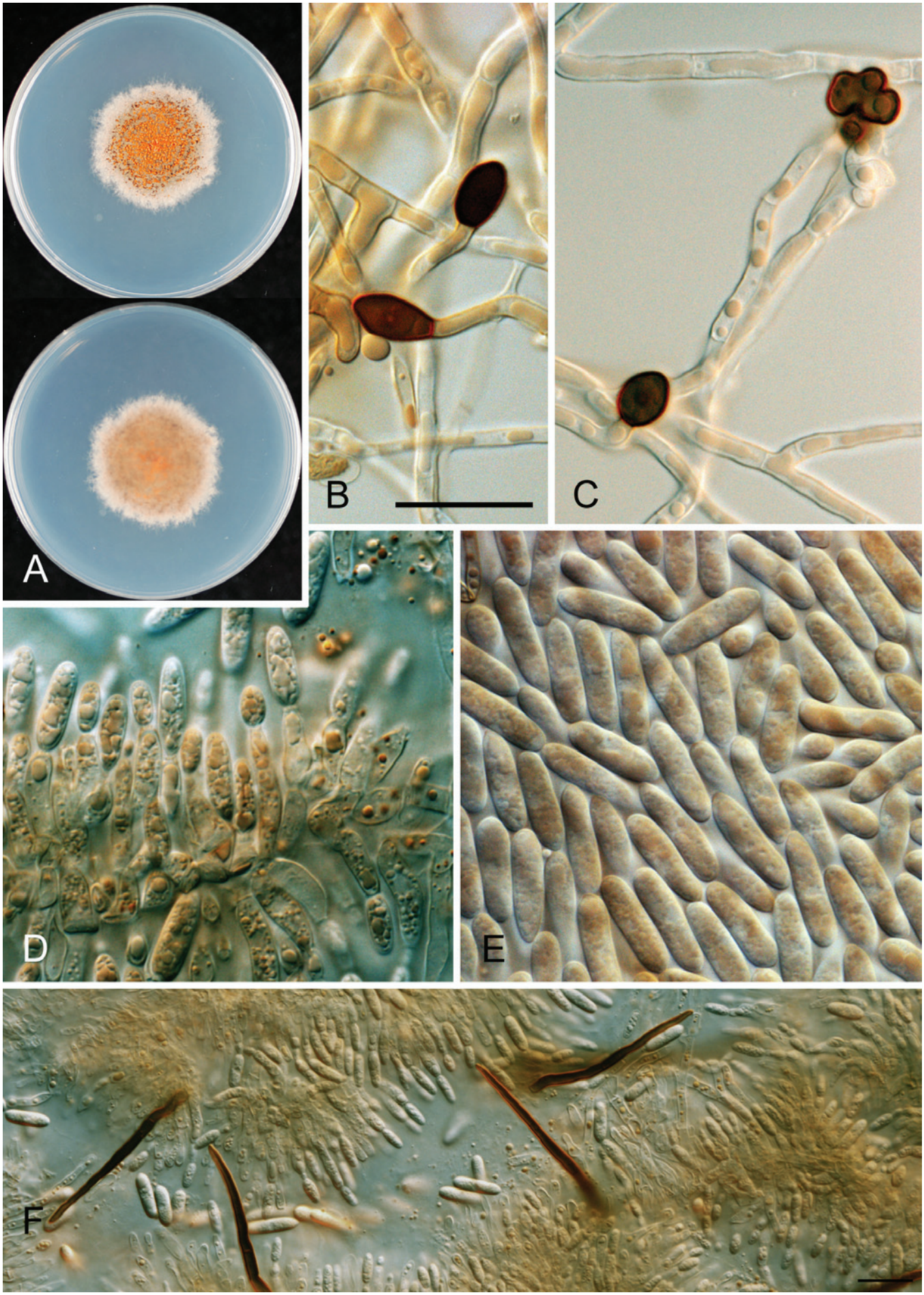


Fig. 12. *Colletotrichum alatae*. ICMP 18122. A. Cultures on PDA, 10 d growth from single conidia, from above and below. B–C. Appressoria. D. Conidiogenous cells and conidia. E. Conidia. F. Setae. Scale bars B, F = 20 µm. Scale bar of B applies to B–E.

Geographic distribution and host range: Known only from yam (*Dioscorea alata*), from Nigeria, Barbardos, India, Guadeloupe.

Genetic identification: ITS sequences distinguish *C. alatae* from all other taxa.

Notes: Anthracnose diseases of yam are found throughout the regions where the host is grown (*e.g.* Winch *et al.* 1984, Prasad & Singh 1960, Singh *et al.* 1966, Abang *et al.* 2002, 2003). Isolates from diseased yam leaves are morphologically (Winch *et al.* 1984) and genetically (Abang *et al.* 2002) diverse. Both of these authors used a broad species concept, grouping all isolates sourced from yam under the single name *C. gloeosporioides*. In this paper we accept part of that diversity to represent a distinct species, newly described here as *C. alatae*. The type specimen of *C. alatae* matches the SGG (slow growing grey) group of Abang *et al.* (2002), the group that these authors found to be more pathogenic to yam than the other morphological and genetic groups they recognised within *C. gloeosporioides*. In addition to the Nigerian isolates of Abang *et al.* (2002), isolates from yam from Barbados (isolates SAS8 and SAS9 from Sreenivasaprasad *et al.* 1996), Guadeloupe (GenBank accession GQ495617) and India (CBS 304.67 and GenBank accession FJ940734) belong in this clade, while no isolates from other hosts have been found.

Other isolates from yam that we sequenced included some representing the Abang *et al.* (2002) FGS group (Abang Cg22 = ICMP 18120, Abang Cg13 = ICMP 18125, Abang CgS6 = ICMP 18117, Abang CgS2 = ICMP 18121), a group distinguished from the highly pathogenic SGG isolates by faster growth in culture and shorter conidia (Abang *et al.* 2002). Two of these isolates (ICMP 18120, 18125) genetically match *C. fructicola*, the others match *C. siamense*.

Several names have been applied to *Colletotrichum* specimens from anthracnose of yam stems and leaves, including *Gloeosporium pestis* Massee, *G.* "*dioscoreae*" Sawada (nom. inval.; no Latin diagnosis), *Colletotrichum dioscoreae* Av.-Saccá 1917, and C. *dioscoreae* Tehon 1933. In addition, *Gloeosporium bomplandii* Speg. was described from a host doubtfully identified as *Dioscorea*. Because of the broad genetic diversity of *Colletotrichum* spp. associated with diseased yam, the lack of cultures from any of these early type specimens, and the uncertainty to which part of the yam-associated diversity they correspond, we have chosen not to use these names for our newly recognised, yam-specialised pathogen. Whether the post-harvest tuber rot referred to as dead skin disease of yam (Abang *et al.* 2003, Green & Simmons 1994) is caused by the same *Colletotrichum* population as associated with diseased foliage is not known.

Other specimen examined: **Nigeria**, Kpite, on *Dioscorea alata* leaf, coll. M.M. Abang Cg25, 2001 (ICMP 18122).

*** *Colletotrichum alienum*** B. Weir & P.R. Johnst., **sp. nov.** MycoBank MB563591. Figs 13, 14.

Etymology: Based on the biology of this species, confined to exotic hosts and presumed to be a recent introduction to Australasia.

Holotype: **New Zealand**, Auckland, Kumeu research orchard, *Malus domestica* fruit rot, coll. P.R. Johnston C824, 14 Aug. 1987, PDD 101996; ex-type culture ICMP 12071.

Colonies grown from single conidia on Difco PDA 85 mm diam after 10 d. Colonies often with distinct sectors; some with cottony, grey aerial mycelium with numerous dark-based acervuli and orange conidial ooze visible through the mycelium; others with dense, cottony to felted mycelium, fewer acervuli and these hidden by the dense mycelium. In reverse, irregular dark grey patches and sectors masking the pale orange coloured pigmentation. ICMP 18691 looks "stale" with slow growth, dense, pale aerial mycelium and sparse conidial production and no perithecia. *Conidia* (12.5–) 15.5–17.5(–22) × (3–)5–5.5(–6) µm (av. 16.5 × 5.0 µm, n = 70), cylindric with broadly rounded ends. *Appressoria* mostly simple, globose to short-cylindric, a few with broad, irregular lobes; ICMP 18691 has mostly lobed appressoria. *Perithecia* forming in most cultures after about 10 d, dark-walled, globose with short, narrow ostiolar neck. *Ascospores* (14.5–)17–19.5(–22) × 4–5(–6) µm (av. 18.1 × 4.6 µm, n = 55), cylindric, curved, tapering slightly to each end.

Geographic distribution and host range: Known only from Australia and New Zealand, common on a wide range of introduced fruit crops.

Genetic identification: ITS sequences do not separate *C. alienum* from some *C. siamense* isolates. These taxa are best distinguished using CAL or GS.

Notes: Common on commercial fruit crops, this fungus was referred to as *C. gloeosporioides* Group A by Johnston & Jones (1997) and Johnston *et al.* (2005).

Other specimens examined: **Australia**, New South Wales, Murwillumbah, on *Persea americana* (DAR 37820 = IMI 313842 = ICMP 18691). **New Zealand**, Auckland, Oratia, Shaw Rd, on *Malus domestica* fruit rot, coll. P.R. Johnston C938.5, 14 Apr. 1988 (ICMP 18725); Bay of Plenty, Katikati, on *Diospyros kaki* ripe fruit rot, coll. M.A. Manning, Jun. 1989 (ICMP 17972); Bay of Plenty, Te Puke, on *Persea americana* ripe fruit rot, coll. W.F.T. Hartill, 2 Feb. 1988 (ICMP 18704); Bay of Plenty, Te Puna, on *Persea americana* ripe fruit rot, coll. W.F.T. Hartill, 25 Jan. 1988 (ICMP 18703); Bay of Plenty, on *Persea americana* ripe fruit rot, coll. W.F.T. Hartill, Feb. 1991 (ICMP 18621); Waikato, Hamilton, on *Malus domestica* fruit rot, coll. G.I. Robertson, May 1988 (ICMP 12068).

*** *Colletotrichum aotearoa*** B. Weir & P.R. Johnst., **sp. nov.** MycoBank MB800213. Figs 15, 16.

Etymology: Based on the Maori name for New Zealand; most isolates from native New Zealand plants belong here.

Holotype: **New Zealand**, Auckland, Glen Innes, Auckland University campus, on *Coprosma* sp. incubated berries, coll. B. Weir C1282.4, 30 Apr 2009, PDD 101076; ex-type culture ICMP 18537.

Colonies grown from single conidia on Difco PDA 70–85 mm diam after 10 d, several isolates with restricted growth, 50–55 mm diam with an irregularly scalloped margin. Aerial mycelium cottony to dense cottony, tufted near centre, grey to dark grey, scattered, small, dark-based acervuli and large, globose, stromatic structures partially embedded in agar, these sometimes splitting apart and forming conidia. In reverse typically with pinkish-orange pigments, variable in intensity, in some isolates this colour partially hidden by more or less concentric bands of dark grey pigment. *Conidia* (12–)16–17.5(–21.5) × (4.5–)5–5.5(–6.5) µm (av. 16.9 × 5.2 µm, n = 216), cylindric, straight, apex broadly rounded, often tapering slightly towards subtruncate base, 0-septate, hyaline. *Appressoria*

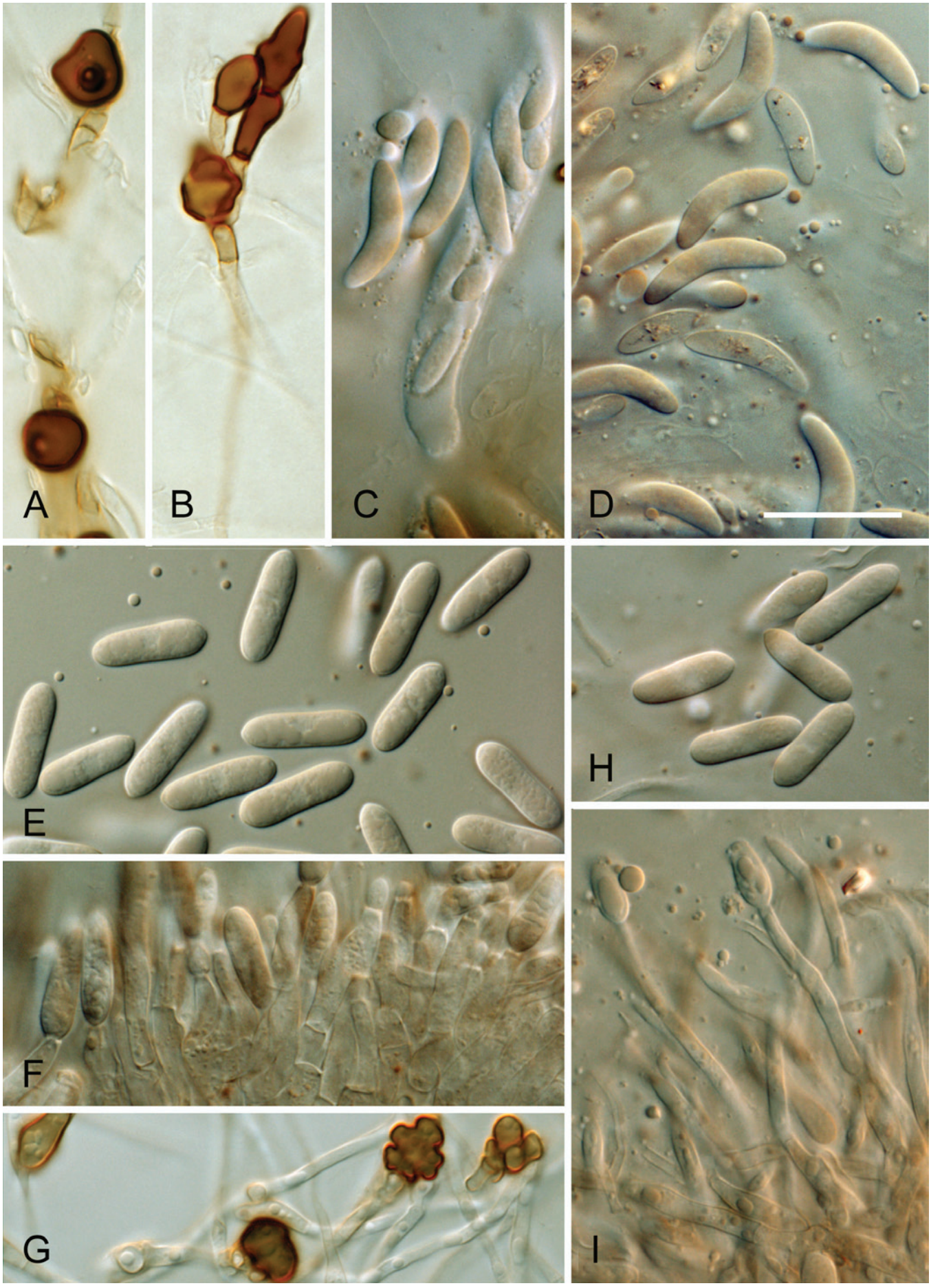


Fig. 13. *Colletotrichum alienum*. A, E, F. ICMP 12071 – ex-holotype culture. B. ICMP 18703. C–D. ICMP 12068. G–I. ICMP 18691 (ex DAR 37820). A–B. Appressoria. C–D. Asci and ascospores. E. Conidia. F. Conidiogenous cells. G. Appressoria. H. Conidia. I. Conidiogenous cells. Scale bar D = 20 µm. Scale bar of D applies to A–I.

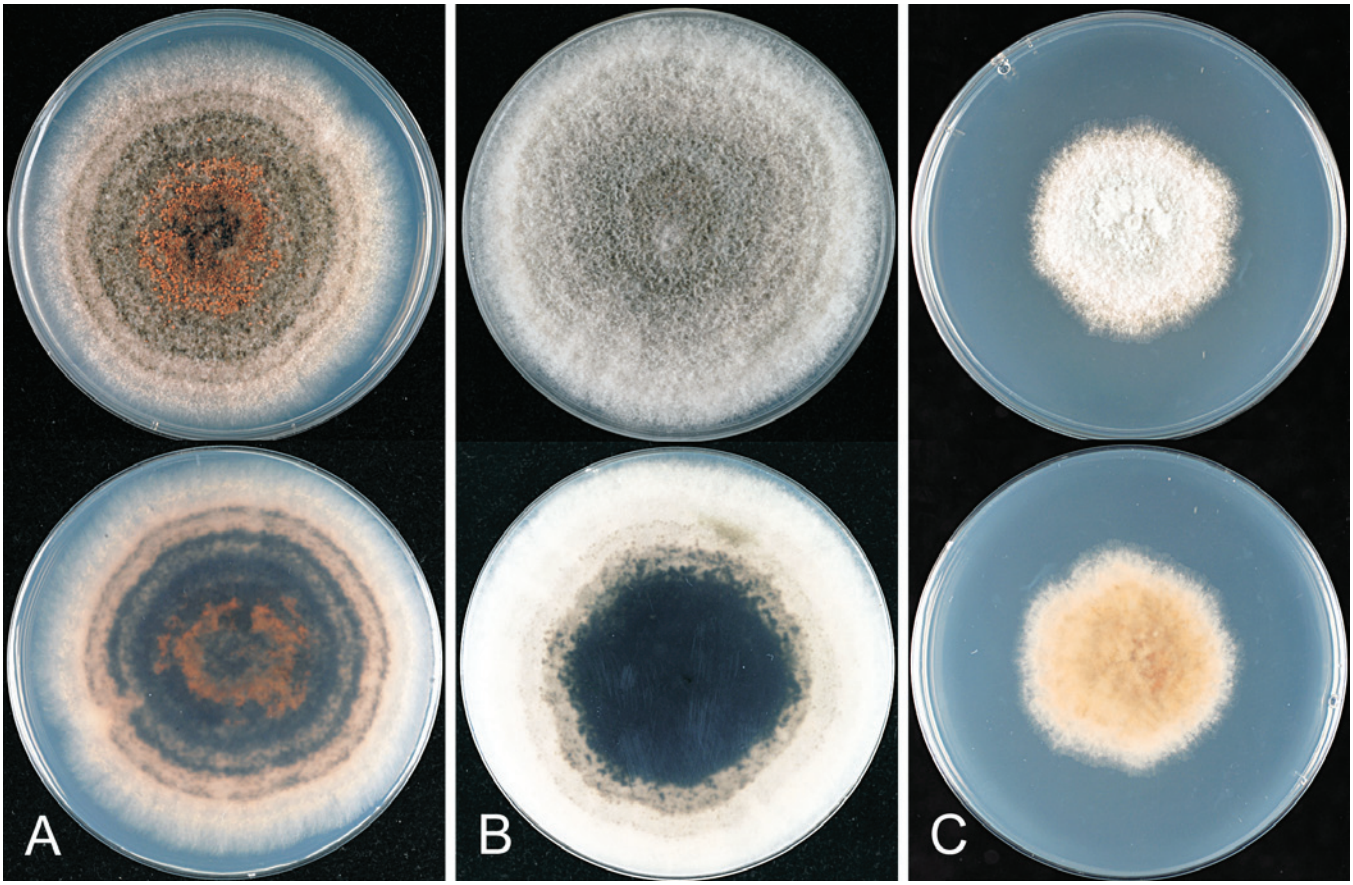


Fig. 14. *Colletotrichum alienum*. A. ICMP 12071 – ex-holotype culture. B. ICMP 12068. C. ICMP 18691 (ex DAR 37820). A–C. Cultures on PDA, 10 days growth from single conidia, from above and below.

variable in shape, simple to broadly lobed, sometimes in groups, sometimes intercalary, about 7–17 × 4–9.5 µm. *Perithecia* not seen in culture.

Geographic distribution and host range: Confirmed only from New Zealand, but GenBank records suggest *C. aotearoa* also occurs in China (see below). In New Zealand this species is common on a taxonomically diverse set of native plants, as both a fruit rot and a leaf endophyte, and has also been isolated from leaves of several species of naturalised weeds.

Genetic identification: ITS sequences do not separate *C. aotearoa* from several taxa in the Kahawae and Musae clades. This species can be distinguished using several other genes, including TUB2, CAL, GS, and GAPDH.

Notes: All isolates in the *C. gloeosporioides* complex from New Zealand native plants studied here belong in the Kahawae clade, and most of these are *C. aotearoa*; a small number of leaf endophyte isolates from New Zealand native trees are *C. kahawae* subsp. *ciggaro*. The *C. aotearoa* isolates have been isolated as endophytes from symptomless leaves as well as from rotting fruit from native trees. Morphologically indistinguishable from isolates of *C. kahawae* subsp. *ciggaro*, this species is distinguished genetically with all genes sampled, except ITS. The GAPDH gene tree splits *C. aotearoa* into two well supported clades, but these do not correlate to any other features, either geographic or biological. Isolates associated with distinctive and common leaf spots on *Meryta sinclairii*, first recorded by Beever (1984), belong in this species. Whether isolates of *C. aotearoa* from other hosts are able to cause the same disease on *Meryta* is not known.

Also in *C. aotearoa* are a range of isolates from weeds that have become naturalised in New Zealand. We assume that *C. aotearoa* is a New Zealand native species. It has a broad host range amongst native plants and has apparently jumped host to some weeds. It has never been found associated with cultivated plants or as a rot of cultivated fruit.

Colletotrichum aotearoa may also occur in China. ITS sequences from isolates from *Boehmeria* from China (GenBank records GQ120479 and GQ120480) from Wang *et al.* (2010) match exactly a set of *C. aotearoa* isolates. ITS between-species differences within the *C. gloeosporioides* complex are very small, so this match needs confirming with additional genes. *C. aotearoa* was referred to as Undescribed Group 2 by Silva et al. (2012b).

Other specimens examined: **New Zealand**, Auckland, Freemans Bay, on *Vitex lucens* fruit, coll. P.R. Johnston C1252.1, 26 Aug. 2007 (ICMP 18532; PDD 92930). on *Berberis* sp. leaf spot, coll. N. Waipara C69 (ICMP 18734); Auckland, Mangere, on *Berberis glaucocarpa* leaf spot, coll. N. Waipara C7, Jun. 2007 (ICMP 18528); Auckland, Waitakere Ranges, on *Kunzea ericoides* leaf endophyte, coll. S. Joshee 7Kun3.5, Jan. 2004 (ICMP 17324); Auckland, Waitakere Ranges, on *Prumnopitys ferruginea* leaf endophyte, coll. S. Joshee 8Mb5.1, Jan. 2004 (ICMP 18533); Auckland, Waitakere Ranges, on *Dacrycarpus dacrydioides* leaf endophyte, coll. S. Joshee 5K5.9, Jan. 2004 (ICMP 18535); Auckland, St Johns, Auckland University campus, on *Coprosma* sp. incubated berries, coll. B. Weir C1282.1, 30 Apr. 2009 (ICMP 18577); Auckland, Mt Albert, on *Acmena smithii* lesions fruit, coll. P.R. Johnston C847, 9 Sep. 1987 (ICMP 18529); Auckland, Glen Innes, Auckland University campus, on *Coprosma* sp. incubated berries, coll. B. Weir C1282.3, 30 Apr. 2009 (ICMP 18536); Auckland, Orakei, on *Ligustrum lucidum* leaf spot, coll. C. Winks & D. Than M136.3 (ICMP 18748); Auckland, Waitakere Ranges, on *Podocarpus totara* leaf endophyte, coll. S. Joshee 3T5.6, Jan. 2004 (ICMP 17326); Auckland, Waitakere Ranges, Huia, on *Geniostoma ligustrifolium* leaf endophyte, coll. S. Bellgard M128, 8 Jul. 2010 (ICMP 18540); Auckland, Waitakere Ranges, Huia, on *Coprosma* sp. rotten berry, coll. S. Bellgard M130-2, 8 Jul. 2010 (ICMP 18541); Auckland, Waiheke Island, Palm Beach, on *Meryta sinclairii* leaf spot, coll. P.R. Johnston C1310.1, 21 Mar. 2010 (PDD 99186; ICMP 18742); Auckland, Tiritiri Island, on *Dysoxylum spectabile* fruit rot, coll. P.R.

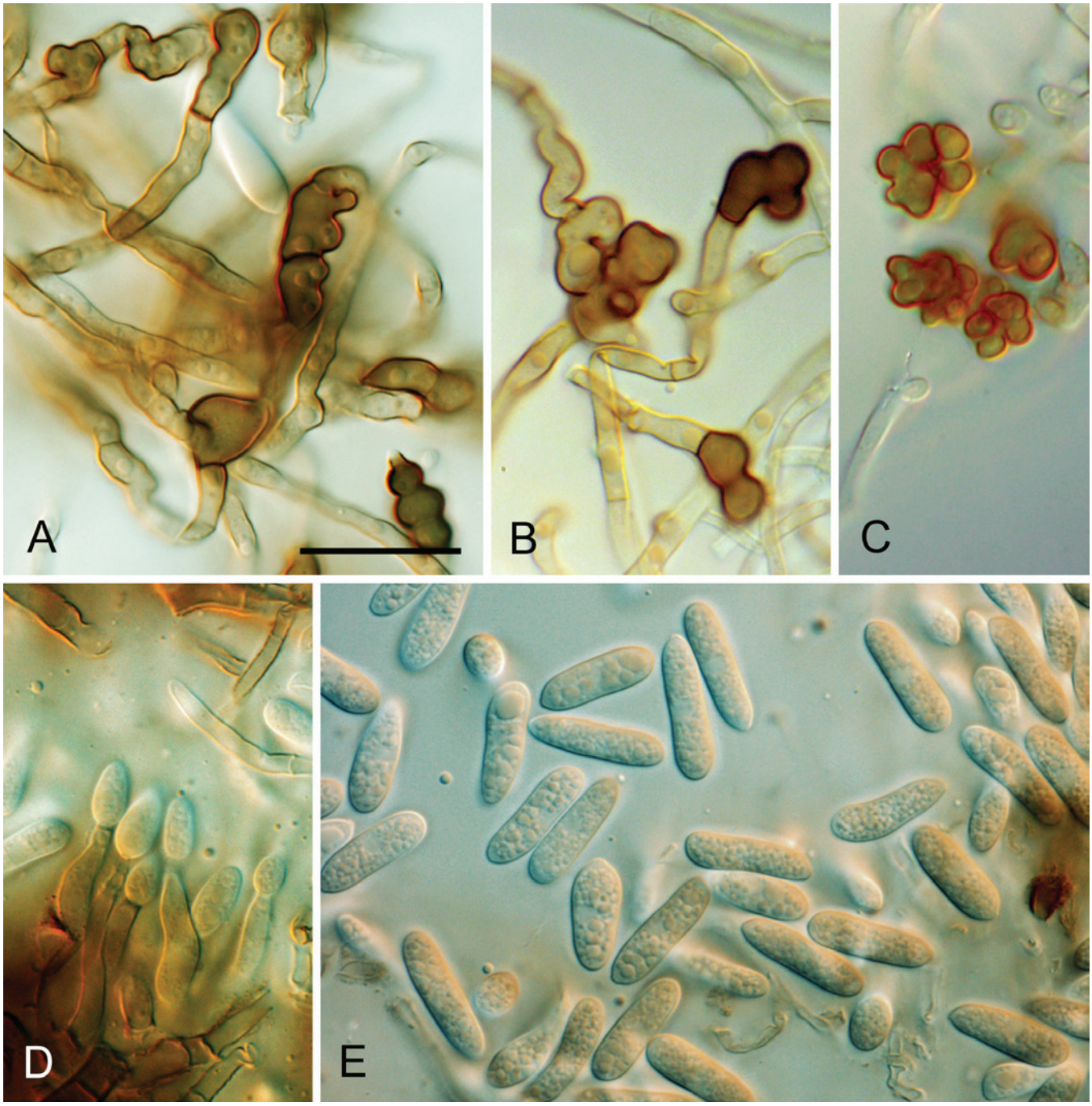


Fig. 15. *Colletotrichum aotearoa*. A. ICMP 17324. B. ICMP 18529. C. ICMP 18548. D. 18532. E. ICMP 18540. A–C. Appressoria. D. Conidiogenous cells. E. Conidia. Scale bar A = 20 µm. Scale bar of A applies to A–E.

Johnston C1220, 12 Feb. 1997 (PDD 67042; ICMP 18740); Northland, Whangaruru, on *Vitex lucens* fruit rot, coll. P.R. Johnston C880.1, L. Brako, P. Berry, 28 Jan. 1988 (PDD 48408; ICMP 18530); on *Berberis* sp. leaf spot, coll. N. Waipara C77 (ICMP 18735), on *Lonicera japonica* leaf spot, coll. N. Waipara J3 (ICMP 18736); Wellington, Waikanae, on *Coprosma* sp. leaf, coll. B. Weir C1285, 14 May 2009 (ICMP 18548); Auckland, Wenderholm Regional Park, on *Melicytus ramiflorus* leaf endophyte, coll. G.C. Carroll MELRA, 16 Sep. 2009 (ICMP 18543).

*** *Colletotrichum asianum*** Prihastuti, L. Cai & K.D. Hyde, Fungal Diversity 39: 96. 2009. Fig. 17.

Prihastuti *et al.* (2009) provide a description of this species.

Geographic distribution and host range: Known on *Mangifera indica* from Australia, Colombia, Japan, Panama, Philippines, and Thailand; also reported on *Coffea arabica* from Thailand.

Genetic identification: *Colletotrichum asianum* is distinguished from all other taxa using any of the genes tested, including ITS.

Notes: Although the type specimen is from coffee, this fungus is isolated commonly from mango (*Mangifera indica*) (*e.g.* Morphological Group 1 from Than *et al.* 2008; IMI 313839 from Australia; MAFF 306627 from Japan). Isolates referred to *Colletotrichum* indet. sp. 1 by Rojas *et al.* (2010), also associated with mango fruit rots, again match *C. asianum*. Based on ITS sequences, isolates Man-63 and Man-69 cited by Afanador-Kafuri *et al.* (2003) from mango from Colombia, are probably also *C. asianum*. Several papers have reported genetically uniform populations of *C. gloeosporioides* associated with *M. indica* around the world (*e.g.* Hodson *et al.* 1993, Alahakoon *et al.* 1994, Sanders & Korsten 2003) and these perhaps also represent *C. asianum*, although DNA sequences are not available to confirm this.

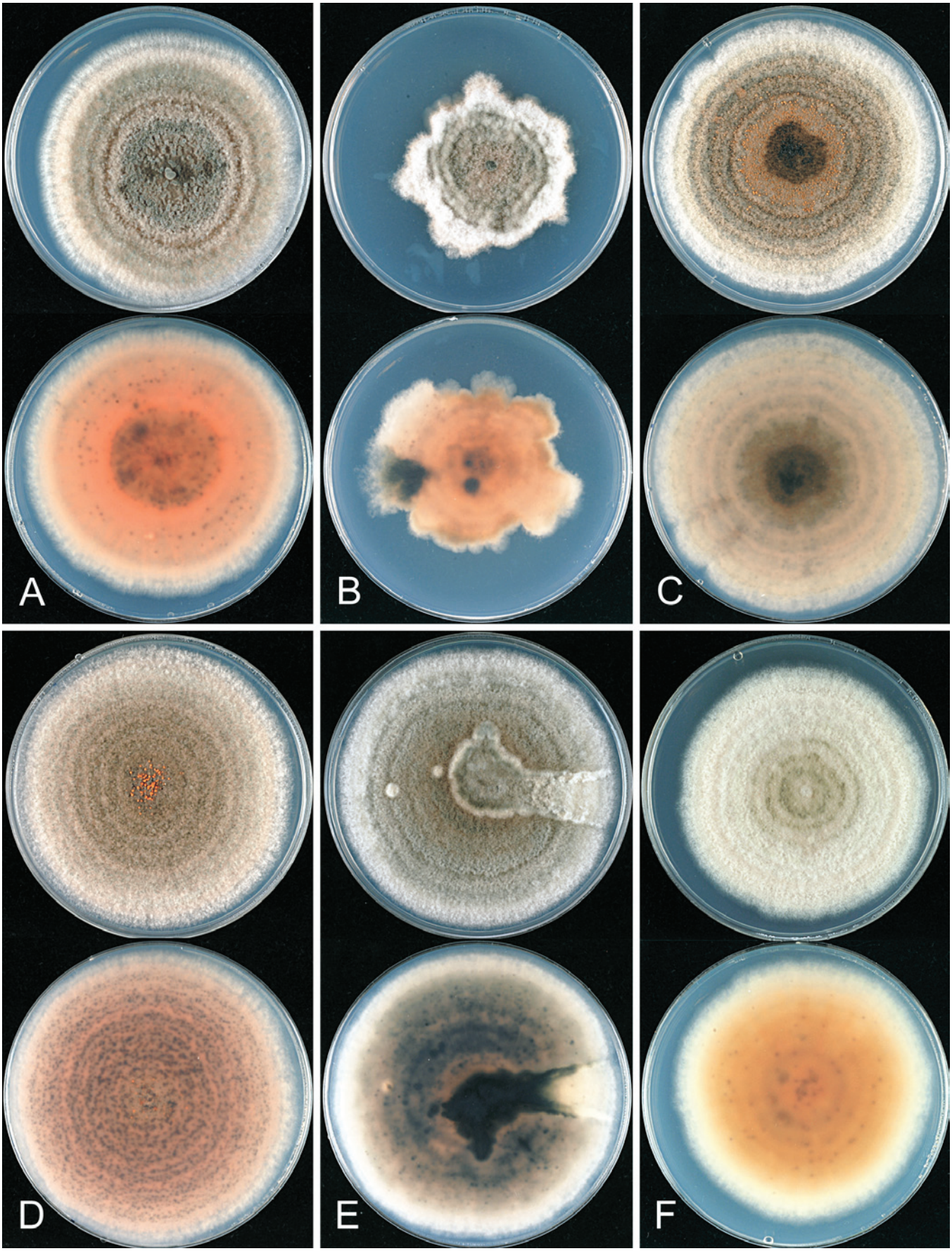


Fig. 16. *Colletotrichum aotearoa*. A. ICMP 18537 – ex-holotype culture. B. ICMP 18548. C. ICMP 18532. D. ICMP 18740. E. ICMP 18533. F. ICMP 18530. A–F. Cultures on PDA, 10 d growth from single conidia, from above and below.

Three earlier species, originally described from leaves rather than fruit of *Mangifera*, may provide earlier names for *C. asianum* but type material for these species has not been examined in this study; *C. mangiferae* Kelkar, *Gloeosporium mangiferae* Henn. 1898, and *G. mangiferae* Racib. 1900. As with most substrates, several different species of *Colletotrichum* often occur on the same host.

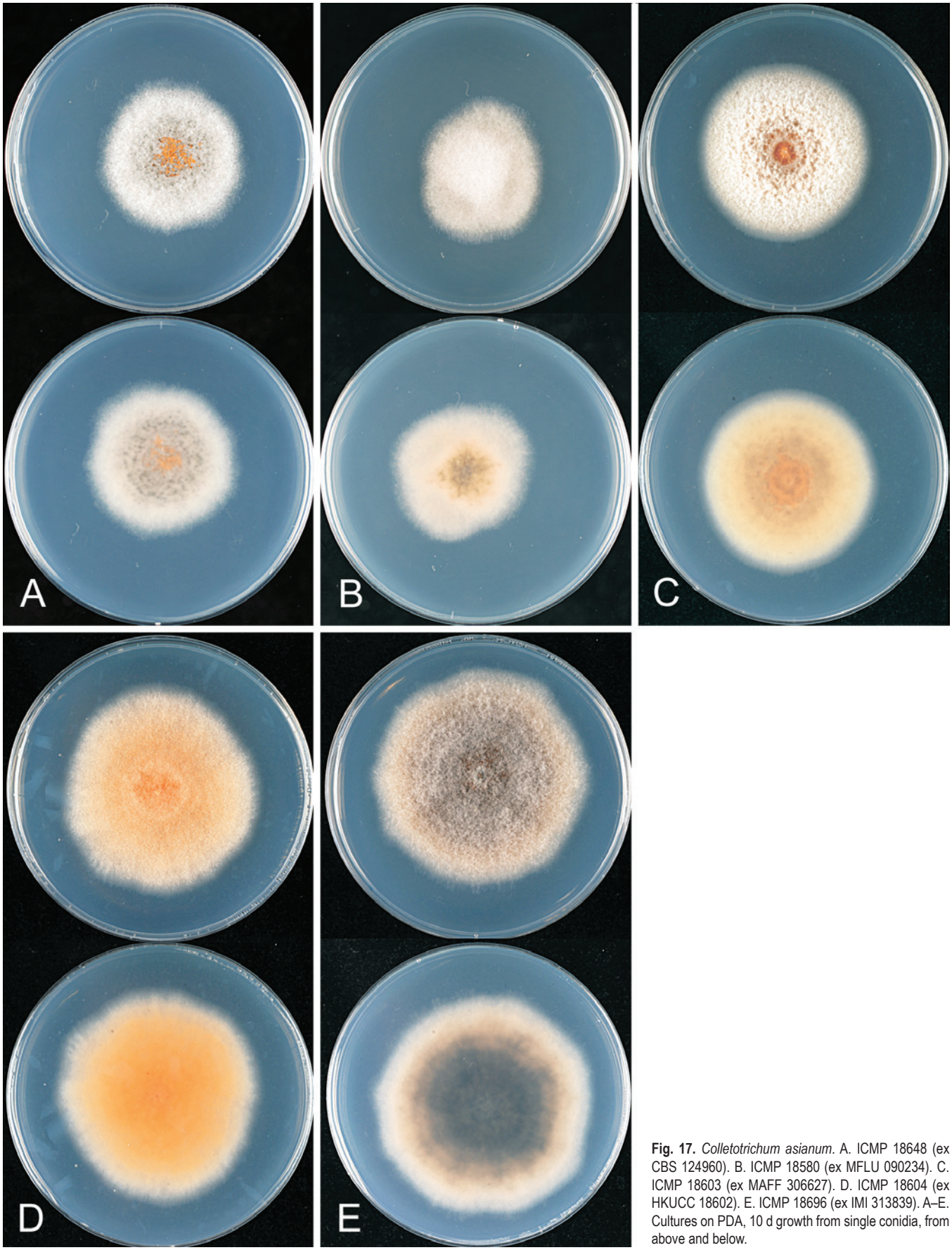


Fig. 17. *Colletotrichum asianum*. A. ICMP 18648 (ex CBS 124960). B. ICMP 18580 (ex MFLU 090234). C. ICMP 18603 (ex MAFF 306627). D. ICMP 18604 (ex HKUCC 18602). E. ICMP 18696 (ex IMI 313839). A–E. Cultures on PDA, 10 d growth from single conidia, from above and below.

For example, Damm *et al.* (2012a, b, this issue) report members of the *C. acutatum* and *C. boninense* species complexes, *C. simmondsii*, *C. fioriniae*, and *C. karstii*, from mango from Australia.

Isolates from *Capsicum* reported by Than *et al.* (2008) as *C. gloeosporioides* Morphological Group 2 (*e.g.* isolates Ku4 = ICMP 18575 and Ku8 = ICMP 18618), were referred to as *C. asianum* by Hyde *et al.* (2009), however they are genetically distinct from *C. asianum* and belong to *C. siamense* based on our analyses.

The *C. asianum* protologue designates the holotype as MFLU 090234, and the culture derived from the holotype as "BCC" with

no strain number. The ex-holotype culture is listed as BDP-I4 in the Prihastuti *et al.* (2009) Table 1, but this number is not mentioned in the description. Culture BDP-I4 was obtained from the authors (Prihastuti *et al.* 2009) for this study.

Specimens examined: **Australia**, New South Wales, Sextonville, on *Mangifera indica*, 1987 (IMI 313839 = ICMP 18696). **Philippines**, on *Mangifera indica* (MAFF 306627 = ICMP 18603). **Thailand**, Chiang Mai, on *Mangifera indica* fruit, coll. P.P. Than M3 (HKUCC 10862 = ICMP 18605); Chiang Mai, on *Mangifera indica* fruit, coll. P.P. Than M4 (HKUCC 10863 = ICMP 18604); Mae Lod Village, Mae Taeng District, Chiang Mai, on *Coffea arabica* berries, coll. H. Prihastuti BPD-I4, 16 Jan. 2008 (**ex-holotype culture** of *C. asianum* from specimen MFLU 090234 = ICMP 18580 = CBS 130418). **Panama**, Gamboa, on *Mangifera indica* fruit rot, coll. S. Van Bael GJS 08-144, Jul 2008 (CBS 124960 = ICMP 18648).

Colletotrichum boehmeriae Sawada, Hakubutsu Gakkwai Kwaihô (Trans. Nat. Hist. Soc. Formosa) 17: 2. 1914.

Notes: Sawada (1922) provided an English translation of his original description. This species was described as a stem pathogen of *Boehmeria nivea*, and remains in use in this sense (*e.g.* Li & Ma 1993). Wang *et al.* (2010) cite several GenBank accessions from isolates they identify as *C. gloeosporioides* that cause severe disease of *Boehmeria*. Based on a comparison of the GenBank data with our ITS gene tree, these and other isolates from the same host deposited by the same authors (GQ120479–GQ120499), appear to represent three different taxa within the *C. gloeosporioides* complex — *C. gloeosporioides s. str.*, *C. aotearoa*, and *C. fructicola*. Isolates representative of all three taxa are reportedly pathogenic on *Boehmeria* (Wang *et al.* 2010). The genetic relationship of these fungi needs to be confirmed using additional genes.

Colletotrichum camelliae Massee, Bull. Misc. Inform. Kew. 1899: 91. 1899.

Notes: *Colletotrichum camelliae* was described by Massee (in Willis 1899) from the living leaves of tea (*Camellia sinensis*) from Sri Lanka. It was placed in synonymy with *C. gloeosporioides* by von Arx (1957). Although not listed by Hyde *et al.* (2009), the name is widely used in the trade and semi-popular literature as the causal agent of the brown blight disease of tea (*e.g.* Sosa de Castro *et al.* 2001, Muraleedharan & Baby 2007).

We have been unable to sample *Colletotrichum* isolates from tea with typical brown blight symptoms. There are four GenBank accessions of *Colletotrichum* from tea, two from China (EU732732, FJ515007), one from Japan (AB218993), and another from Iran (AB548281), referred variously to *C. camelliae*, *C. crassipes* and *C. gloeosporioides*. Although ITS sequences only are available for these geographically widespread isolates, the DNA sequence of the Iranian isolate appears to match *C. gloeosporioides s. str.*, while those from the other three isolates are all very similar to each other. The ITS sequence from these isolates matches that of CBS 232.79, from tea shoots from Java (GenBank JX009429). GAPDH and ITS sequences from CBS 232.79 (GenBank JX009417, JX009429) place this isolate in *C. fructicola*. Note that CBS 571.88, isolated from tea from China and deposited as *Glomerella cingulata*, is a *Colletotrichum* sp. outside *C. gloeosporioides s. lat.*, based on ITS sequences (GenBank JX009424).

We tested the pathogenicity of CBS 232.79 and isolates of *G. cingulata* "f. sp. *camelliae*" (see below) using detached tea leaves and found that only the *G. cingulata* "f. sp. *camelliae*" isolates were strong pathogens (unpubl. data).

The genetic relationship between the pathogen of ornamental *Camellia* (here referred to *G. cingulata* "f. sp. *camelliae*"), isolates from tea with DNA sequence data in GenBank, and isolates associated with brown blight symptoms of tea remain unresolved. Additional isolates with known pathogenicity, collected from typical brown blight symptoms from the field, are required to determine whether or not there are two distinct pathogens of *Camellia*, one of tea, the other of ornamental varieties.

Other *Colletotrichum* species reported from tea include *C.* "*theae-sinensis*", an invalid recombination of *Gloeosporium theae-sinensis* I. Miyake, proposed by Yamamoto (1960). Moriwaki and Sato (2009) summarised the taxonomic history of this name and transferred *G. theae-sinensis* to *Discula* on the basis of DNA sequences. *Sphaerella camelliae* Cooke and its recombination *Laestadia camelliae* (Cooke) Berl. & Voglino were listed by von Arx & Müller (1954) as synonyms of *Glomerella cingulata*. This species is now accepted as *Guignardia camelliae* (Cooke) E.J. Butler ex Petch and is regarded as the causal agent of copper blight disease of tea (Spaulding 1958).

Thang (2008) placed *C. camelliae* in synonymy with *C. coccodes*, presumably on the basis of the Species Fungorum synonymy (www.speciesfungorum.org, website viewed 6 Oct 2010). Thang (2008) questioned the synonymy, noting differences between the descriptions of the two species provided by Massee (in Willis 1899) and Sutton (1980) respectively.

Colletotrichum caricae F. Stevens & J.G. Hall, Z. Pflanzenkrankh., 19: 68. 1909.

Notes: Placed in synonymy with *C. gloeosporioides* by von Arx (1957), *C. caricae* was listed as a separate species by Sutton (1992). It was described from fruits and leaves of *Ficus carica* from the USA (Stevens & Hall 1909) but is poorly understood both morphologically and biologically. Its genetic relationship to and within the *C. gloeosporioides* species complex, and to other *Ficus*-associated species such as *Colletotrichum ficus* Koord. and *Glomerella cingulata* var. *minor* (here placed in synonymy with *C. fructicola*) is unknown.

Glomerella cingulata (Stonem.) Spauld. & H. Schrenk, Science, n.s. 17: 751. 1903.

Basionym: *Gnomoniopsis cingulata* Stonem., Bot. Gaz. 26: 101. 1898.

= *Gloeosporium cingulatum* G.F. Atk., Bull. Cornell Univ. Agric. Exp. Sta. 49: 306. 1892. [fide Stoneman 1898]

Notes: Stoneman (1898) described *Glomerella cingulata* from diseased stems of *Ligustrum vulgare* from the USA and reported the development of perithecia in cultures initiated from conidia of what she considered its asexual morph, *Gloeosporium cingulatum*. There are recent reports of anthracnose diseases of *Ligustrum* (*e.g.* Alfieri *et al.* 1984, Vajna & Bagyinka 2002) but the relationship of isolates causing this disease to the *C. gloeosporioides* complex is not known.

Glomerella cingulata is often linked taxonomically to the anamorph *Colletotrichum gloeosporioides*, and the name has in the past been applied in an equally broad sense to *C. gloeosporioides s. lat.* (*e.g.* Small 1926, von Arx & Müller 1954). However, it is unlikely that the type specimen of *G. cingulata* represents the same species as *C. gloeosporioides s. str.* (see notes under *C. gloeosporioides*). *Colletotrichum gloeosporioides s. str.* is not known to form perithecia in culture, and there are no isolates of *C. gloeosporioides s. str.* known to us that are associated with a *Glomerella* state on diseased stems of *Ligustrum,* An isolate of *C.*

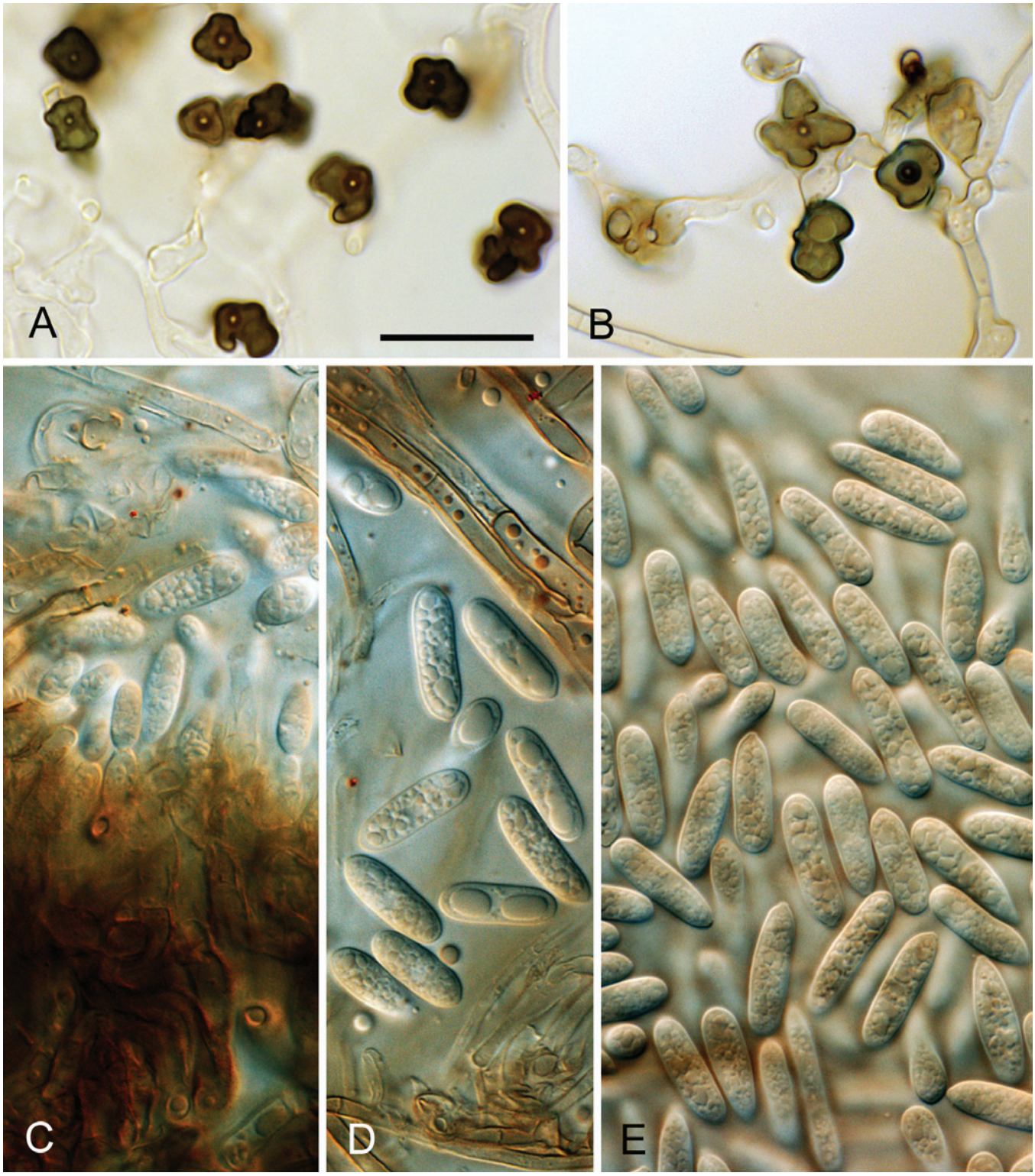


Fig. 18. *Glomerella cingulata* "f. sp. *camelliae*". A, C, D. ICMP 10643. B, E. ICMP 10646. A–B. Appressoria. C. Conidiogenous cells. D–E. Conidia. Scale bar A = 20 µm. Scale bar of A applies to A–E.

aotearoa (ICMP 18748) was isolated from *Ligustrum lucidum* in New Zealand, but it was not associated with a stem lesion and no *C. aotearoa* isolates were observed forming perithecia.

Glomerella cingulata* var. *brevispora Wollenw., Z. Parasitenk. (Berlin) 14: 260. 1949.

Notes: Described from fruit rots from Germany, this name has not been used since. No cultures are available and its relationship to and within the *C. gloeosporioides* complex is not known.

*** *Glomerella cingulata*** "**f. sp. *camelliae***" (Dickens & Cook 1989). Figs 18, 19.

Notes: Dickens & Cook (1989) proposed the name *Glomerella cingulata* "f. sp. *camelliae*" for isolates morphologically typical of *C. gloeosporioides s. lat.* that were highly pathogenic to leaves and shoots of ornamental *Camellia saluenensis* hybrids, causing the disease *Camellia* twig blight. These authors reported the fungus from plants imported into the UK from New Zealand and noted that a similar disease had been reported from plants grown in the UK,

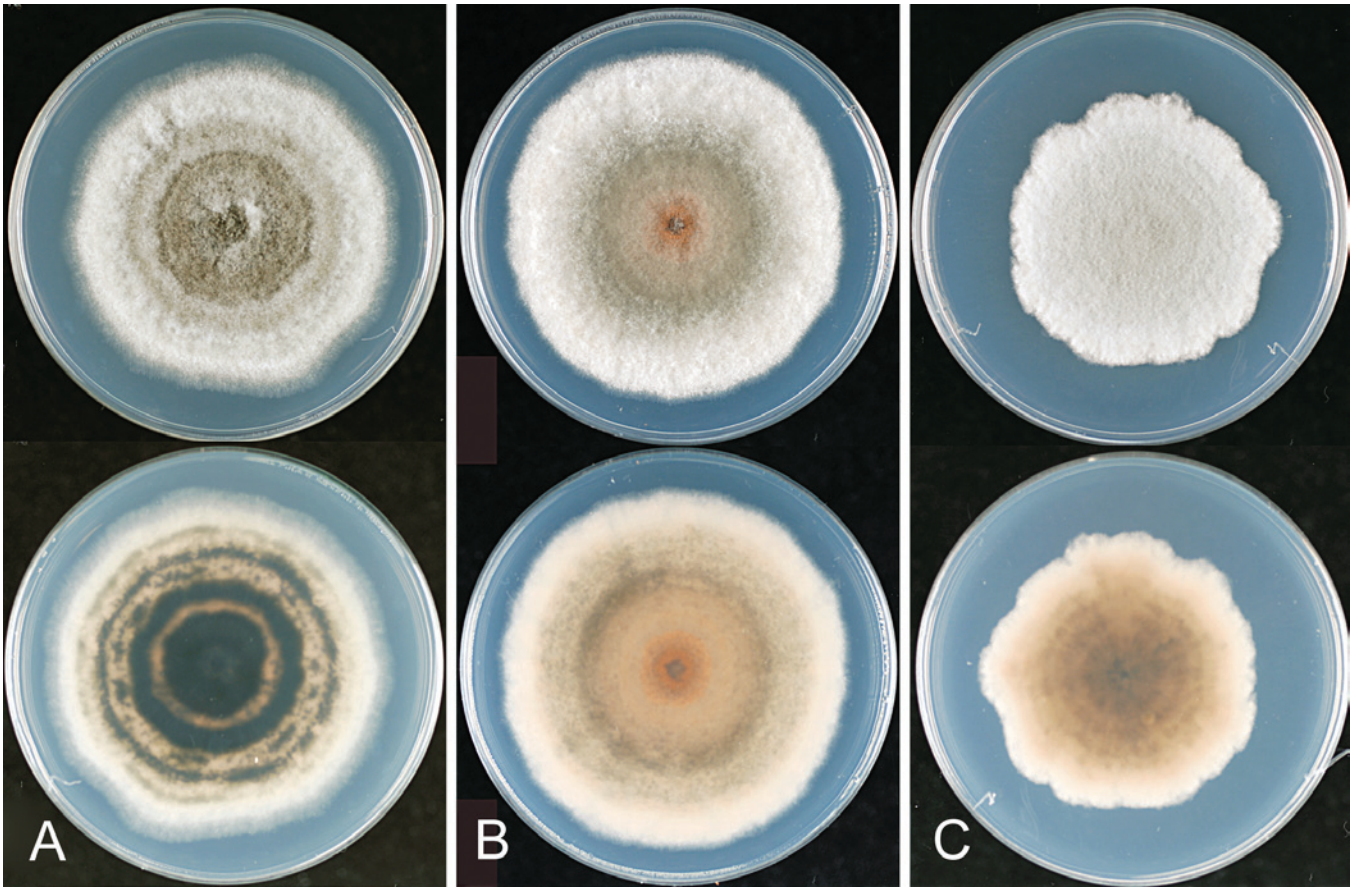


Fig. 19. *Glomerella cingulata* "f. sp. *camelliae*". A. ICMP 18542. B. ICMP 10643. C. ICMP 10646. A–C. Cultures on PDA, 10 d growth from single conidia, from above and below.

USA, Australia, France, and Italy. The disease has been reported from *Camellia japonica*, *C. reticulata*, and *C. sasanqua*. Although isolated in the UK from plants imported from New Zealand, this pathogen has not yet been found on *Camellia* plants growing in New Zealand.

We have sequenced authentic isolates cited by Dickens & Cook (1989) as well as isolates pathogenic to *Camellia saluenensis* collected from the USA. They are similar to each other genetically as well as biologically and morphologically. ITS sequences alone distinguish *G. cingulata* "f. sp. *camelliae*" from all other taxa in the *C. gloeosporioides* complex, and there is good genetic evidence to consider these isolates to be representative of a distinct species within the *C. kahawae* clade. A new species is not proposed here because the relationship between the *G. cingulata* "f. sp. *camelliae*" isolates and *C. camelliae*, the fungus causing brown blight of tea, remains uncertain.

Dickens & Cook (1989) also reported two *C. acutatum* strains from ornamental *Camellia* species that were avirulent in tests with detached *Camellia* cv. Donation leaves. Strain IMI 351261, deposited 1992 in IMI by R. Cook, is likely to be one of them. This strain was confirmed as belonging to the *C. acutatum* species complex and identified as *C. lupini*, which causes lupin anthracnose and is occasionally found on other hosts (Damm *et al.* 2012a, this issue). Another strain from *Camellia reticulata* from China belongs to *C. fioriniae*, also a species in the *C. acutatum* complex, while a strain from New Zealand (ICMP 10338) is *C. boninense s. str.* (Damm *et al.* 2012a, b, this issue).

See notes under *C. camelliae*.

Specimens examined: **UK**, plants imported from New Zealand, on *Camellia* × *williamsii*, coll. Dickens & Cook 82/437, 1982 (**authentic culture** of *Glomerella cingulata* "f. sp. *camelliae*" – ICMP 10643; dried culture PDD 56488). **USA**, Mississippi, on *Camellia sasanqua* twig blight, coll. W.E. Copes CG02g, May 2002 (ICMP 18542); South Carolina, on *Camellia* sp., coll. G. Laundon 20369, 1 Jan. 1982 (ICMP 10646).

Glomerella cingulata* var. *crassispora Wollenw., Z. Parasitenk. (Berlin) 14: 260. 1949.

Notes: Described from *Coffea arabica* from a glasshouse in Germany, this name has not been used since. No cultures are available and its relationship to and within the *C. gloeosporioides* complex is not known.

***Glomerella cingulata* "f. sp. *manihotis*"** (Chevaugeon 1956)

Notes: See notes under *Colletotrichum manihotis*.

Glomerella cingulata* var. *minor Wollenw., Z. Parasitenk. (Berlin) 14: 261. 1949.

= *Gloeosporium elasticae* Cooke & Massee, Grevillea 18: 74. 1890. [fide Wollenweber & Hochapfel 1949]

Notes: Placed here in synonymy with *C. fructicola*.

Glomerella cingulata var. *minor* was described from *Ficus* from Germany, but Wollenweber & Hochapfel (1949) noted that the same fungus occurred also on other hosts in Europe, Africa, and America, including *Malus* and *Coffea*. Genetically the ex-holotype culture of *G. cingulata* var. *minor* (CBS 238.49) matches the type specimen of *C. fructicola*, although the culture itself appears to be stale, with slow growth and an irregularly scalloped margin (see

images under *C. fructicola*). Wollenweber & Hochapfel (1949) used the name *Gloeosporium elasticae* Cooke & Massee for the conidial state of *G. cingulata* var. *minor*, the type specimens for both names being from *Ficus*.

See also notes under *C. queenslandicum*.

Specimen examined: **Germany,** Berlin-Dahlem, from *Ficus edulis* leaf spot, May 1936 (**ex-holotype culture** of *G. cingulata* var. *minor* – CBS 238.49 = ICMP 17921).

Glomerella cingulata* var. *migrans Wollenw., Z. Parasitenk. (Berlin) 14: 262. 1949.

Notes: Placed here in synonymy with *C. kahawae* subsp. *ciggaro*, see notes under this species.

Specimen examined: **Germany**, Berlin-Dahlem, on stem of *Hypericum perforatum*, Jun. 1937 (**ex-holotype culture** of *Glomerella cingulata* var. *migrans* – CBS 237.49 = ICMP 17922).

Glomerella cingulata "**var. *orbiculare***" Jenkins & Winstead, *Phytopathology* 52: 15. 1962.

Notes: Listed in Index Fungorum, this name was mentioned in an abstract, but is invalid (no Latin description) and never formally published. It was being used to refer to the teleomorph of *Colletotrichum orbiculare*, not part of the *C. gloeosporioides* complex (Cannon *et al.* 2012, this issue). *Glomerella lagenaria* (Pass.) F. Stevens, a recombination of the anamorphic name *Fusarium lagenarium* Pass., has also been used to refer to this teleomorph. Correll *et al.* (1993) comment on the pathogenicity of cucurbit-associated strains that form a *Glomerella* state in culture, suggesting a degree of confusion around the application of these names.

Glomerella cingulata "**f. sp. *phaseoli***" (Kimati & Galli 1970).

Notes: Both *G. cingulata* "f. sp. *phaseoli*" (*e.g.* Castro *et al.* 2006) and *Glomerella lindemuthiana* (*e.g.* Rodríguez-Guerra *et al.* 2005, as *G. lindemuthianum*) have been used for the teleomorph of *Colletotrichum lindemuthianum* in the recent literature, the two names placed in synonymy by Sutton (1992). This fungus is not part of the *C. gloeosporioides* complex (Cannon *et al*. 2012, this issue).

Glomerella cingulata* var. *sorghicola Saccas, Agron. Trop. (Maracay). 9: 171. 1954.

Notes: Not a member of the *C. gloeosporioides* complex. Sutton (1992) suggested using this name to refer to the teleomorph of *Colletotrichum sublineola*, although Crouch *et al.* (2006) note that *C. sublineola* has no known teleomorph.

*** *Colletotrichum clidemiae*** B. Weir & P.R. Johnst. **sp. nov.** MycoBank MB563592. Figs 20, 21.

= *Colletotrichum gloeosporioides* "f. sp. *clidemiae*" (Trujillo *et al.* 1986).

Etymology: Based on the host reportedly susceptible to this species.

Holotype: **USA**, Hawai'i, Aiea, on *Clidemia hirta* leaf spot, coll. S.A. Ferreira & K. Pitz, 14 May 2010, PDD 101997; ex-type culture ICMP 18658.

Colonies grown from single conidia on Difco PDA 25 mm diam after 10 d, aerial mycelium grey, cottony, sparse, surface of colony with numerous small, dark-based acervuli with deep orange conidial ooze and scattered setae, in reverse more or less colourless except for the acervuli and masses of conidial ooze showing through. After 18 d numerous globose, pale walled protoperithecia developing near centre of colony. *Conidia* (16−)18−20(−26.5) × (4.5−)5.5−6 µm (av. 19.3 × 5.5 µm, n = 48), broad-cylindric, ends broadly rounded, longer conidia sometimes tapering slightly towards the base. *Appressoria* variable in shape, some simple, subglobose, but often with a small number of broad, irregular lobes. *Perithecia* mature after about 21 d, dark-walled, about 200–250 µm diam with short ostiolar neck, perithecial wall of 3–4 layers of angular cells 10–15 µm diam with walls thin, pale brown to brown. *Asci* 8-spored 60–67 × 10–14 µm. *Ascospores* (14–)15.5–19(–21.5) × 4.5–5.5(–6.5) µm (av. 17.2 × 5.0 µm, n = 46), oblong-elliptic, tapering to rounded ends, widest point toward one end, in side view flat on one side, rarely curved and if so, then slightly.

Geographic distribution and host range: First reported from *Clidemia*, native to Panama, and subsequently introduced to Hawai'i as a pathogen of that host. Genetically matching isolates occur on native *Vitis* and *Quercus* spp. in Florida (see notes below).

Genetic identification: ITS sequences do not separate *C. clidemiae* from *C. aotearoa*. The two species are best distinguished using ACT, GAPDH, or GS.

Notes: Isolates referred to *C. gloeosporioides* "f. sp. *clidemiae*" by Trujillo *et al.* (1986) were highly pathogenic to *Clidemia*, but not to the other species of *Melastomataceae* tested. No voucher cultures of the original isolates collected from Panama were kept, but recent specimens isolated from naturalised *Clidemia hirta* plants in Hawai'i with typical disease symptoms are genetically uniform and distinct within the Kahawae clade. Phylogenetic, biological, and morphological evidence support this fungus being described as a new species within the *C. gloeosporioides* complex.

A fungus isolated from a *Vitis* sp. in Florida and referred to as "*Glomerella cingulata* native host" by MacKenzie *et al.* (2007), is genetically close to our isolates from *Clidemia* and is here referred to the same species. Data in MacKenzie *et al.* (2007) shows the same fungus occurs on both *Vitis* and *Quercus* in Florida. Micro-morphologically the isolates from *Clidemia* and from *Vitis* that we examined are similar with respect to the size and shape of appressoria, conidia, and ascospores. They are distinct in cultural appearance, the cultures of the *Vitis*-associated fungus having aerial mycelium darker and more dense, and a faster growth rate. Similar variation in cultural appearance is present in several of the phylogenetically defined species that we recognise. Whether or not the *Clidemia*-associated isolates are biologically distinct from the *Vitis*- and *Quercus*-associated isolates from Florida requires pathogenicity tests to determine.

Other specimens examined: **USA,** Florida, Sarasota, on *Vitis* sp. leaf, coll. S. MacKenzie SS-Grape-12, 2002 (ICMP 18706); Hawai'i, Aiea, on *Clidemia hirta* leaf spot, coll. S.A. Ferreira & K. Pitz, 14 May 2010 (ICMP 18659, ICMP 18660, ICMP 18661, ICMP 18662, ICMP 18663).

Colletotrichum coffeanum F. Noak, Z. Pflanzenkrankh. 11: 202. 1901.

Notes: Waller *et al.* (1993) discussed the use of the names *Colletotrichum coffeanum* and *Gloeosporium coffeanum* Delacr. and the geographic and biological differences between these

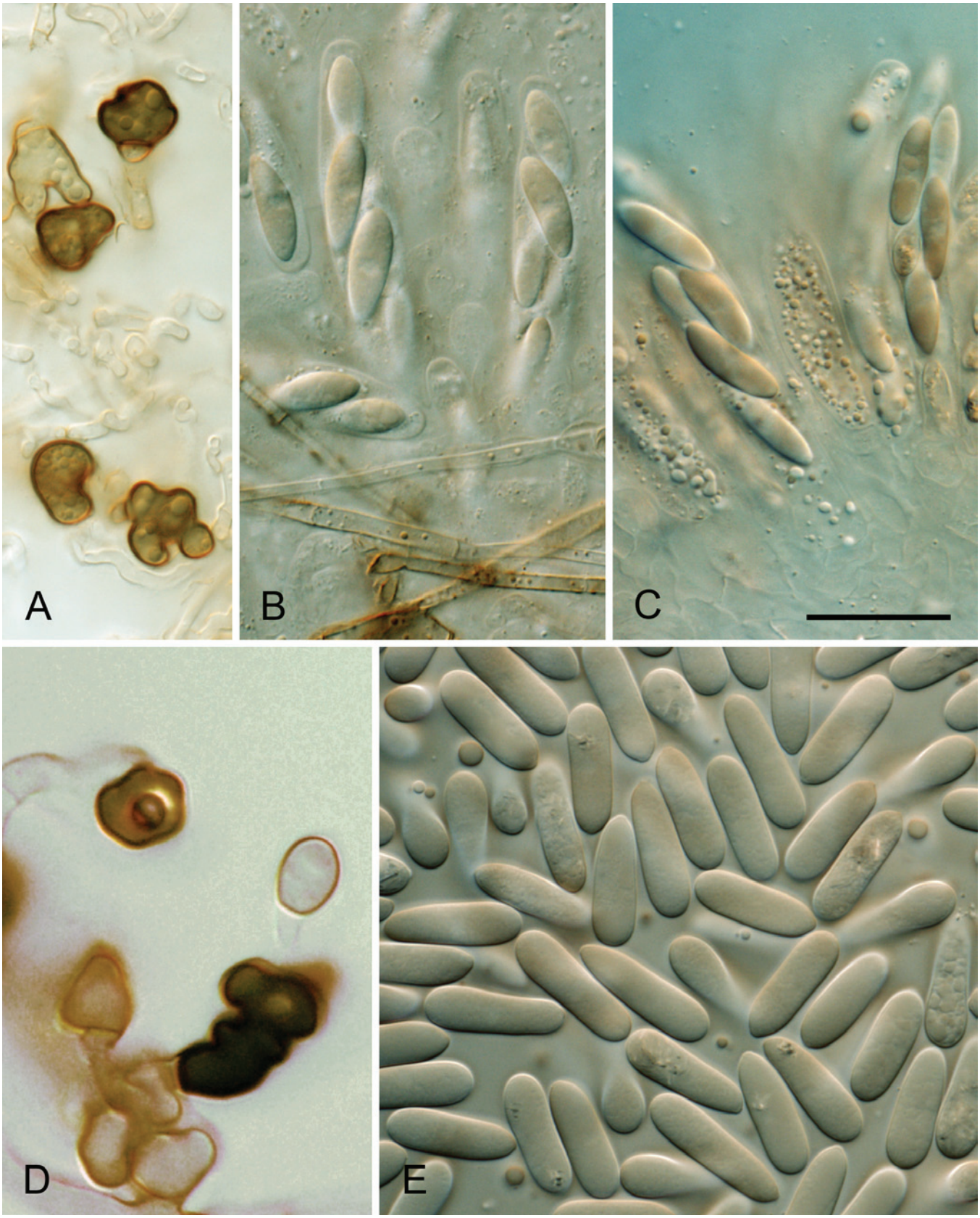


Fig. 20. *Colletotrichum clidemiae*. A, B, E. ICMP 18658 – ex-holotype culture. C, D. ICMP 18706. A, D. Appressoria. B, C. Asci and ascospores. E. Conidia. Scale bar C = 20 µm. Scale bar of C applies to A–E.

species and the pathogen of coffee berries, *C. kahawae*. Both *C. coffeanum* and *G. coffeanum* were described from leaves of coffee, the two species distinguished by Noak (1901) by the presence or absence of setae in the acervuli. There is a wide range of *C. gloeosporioides*-like species on coffee plants (see Waller *et al.* 1993 and notes under *C. kahawae*) and the relationships of *C. coffeanum* and *G. coffeanum* within the *C. gloeosporioides* species complex remain uncertain.

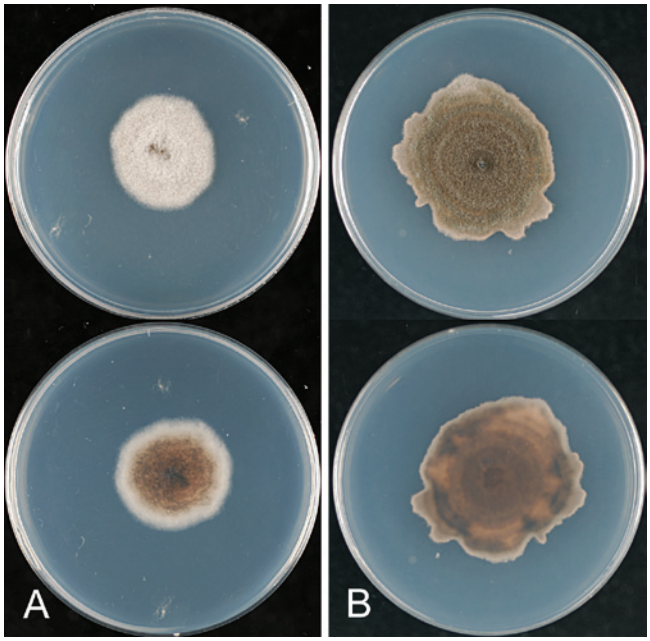


Fig. 21. *Colletotrichum clidemiae*. A. ICMP 18658 – ex-holotype culture. ICMP 18706. Cultures on PDA, 10 d growth from single conidia, from above and below.

Colletotrichum cordylines Pollacci, Atti Ist. Bot. Univ. Pavia, Serie 2, 5: 44. 1899.

Notes: Described from leaves of *Cordyline indivisa* from a botanical garden in Italy, the genetic and biological status of this species is not known. Two *Cordyline*-associated species are accepted in this study, *C. cordylinicola* from Thailand and the newly described *C. ti* from New Zealand. The original description of *C. cordylines* is brief (Pollacci 1899) but it specifically mentions setae more than 100 µm long. *Colletotrichum cordylinicola* is described as lacking setae (Phoulivong *et al.* 2011) and in *C. ti* they are rare and when present much less than 100 µm long. The phylogenetic significance of this apparent difference and confirmation that these names represent different fungi requires DNA sequences to be generated from type material of *C. cordylines.*

*** *Colletotrichum cordylinicola*** Phoulivong, L. Cai & K.D. Hyde, Mycotaxon 114: 251. 2011 ["2010"]. Fig. 22.

Phoulivong *et al.* (2011) provide a description.

Geographic distribution and host range: Known only from *Cordyline* from Thailand and *Eugenia* from Laos.

Genetic identification: ITS sequences separate *C. cordylinicola* from all other species.

Notes: Phoulivong *et al.* (2011) report *C. cordylinicola* from *Cordyline* (*Agavaceae*) and *Eugenia* (*Myrtaceae*). They noted that the isolate from *Eugenia* was not pathogenic to *Cordyline* and vice versa, and they also showed that the specimens from the two hosts are genetically somewhat distinct, although forming a sister relationship amongst the taxa included in their analysis. The calmodulin gene tree generated from our sequence data together with the sequences provided by Phoulivong *et al.* (2011) (GenBank accession HM470236) supports placing the isolates from *Eugenia* and from *Cordyline* in the same species (unpubl. data).

Colletotrichum cordylinicola is genetically distinct from a species associated with *Cordyline* leaf spots from New Zealand, described here as *C. ti*. See also notes under *C. cordylines*.

Specimen examined: **Thailand,** Chiang Mai, Sam Sai District, Maejo Village, on *Cordyline fruticosa*, coll. S. Phoulivong, 15 Mar. 2009 (**ex-holotype culture** – MFLUCC 090551 = ICMP 18579). Note that the ex-holotype culture was mistakenly cited as MFUCC 090551 by Phoulivong *et al.* (2011).

Colletotrichum crassipes (Speg.) Arx, Verh. Kon. Ned. Akad. Wetensch., Afd. Natuurk., Sect. 2, 51(3): 77. 1957.
Basionym: *Gloeosporium crassipes* Speg., Rivista Vitic. Enol. 2: 405. 1878.

Notes: Several isolates identified as *Colletotrichum crassipes* that have sequences accessioned to GenBank belong in *C. gloeosporioides s. lat*. GenBank accessions identified as *C. crassipes* that have a publically available culture include *C. kahawae* subsp. *ciggaro* (STE-U 5302 = CBS 112988 – AY376529, AY376577, FN557348, FN557538, and FN599821; STE-U 4445 = CBS 112984 – AY376530, AY376578, – FN557347, FN557537, and FN599820), along with several other species outside of the *C. gloeosporioides* complex (CBS 169.59 = IMI 309371 – AJ536230, FN557344, and FN599817; CBS 159.75 – FN557345 and FN599818; CBS 109355 – FN557346 and FN599819). Those with no isolates in a public collection include *C. kahawae* subsp. *ciggaro* (CORCS3 cited in Yang *et al.* (2011), HM584410, HM582002, HM585412), *C. fructicola* (strain 080912009 Jining, unpubl. data, FJ515007), and a possibly undescribed species within the Kahawae clade (strain SYJM02, unpubl. data, JF923835). Originally described from the berries of *Vitis vinifera* from Italy (Spegazzini 1878), the identity of *C. crassipes* remains unresolved. There is confusion regarding its morphology. Von Arx (1970) uses the name *C. crassipes* for fungi in which setae are rare, conidia are 22–34 × 6–8 µm (more or less matching the original description), and the lobed appressoria are distinctively globose in shape. Sutton (1980) uses a different morphological concept – setae common (according to Sutton these are rare in the otherwise morphologically similar *C. musae*), conidia 10–15 × 4.5–6.5 µm (Sutton's concept of *C. gloeosporioides* is characterised by narrower conidia), and the appressoria deeply lobed. The conidial width cited for *C. gloeosporioides* by Sutton (1980), 3–4.5 µm, is narrower than we have found for all the taxa we accept within *C. gloeosporioides s. lat.*, whereas his *C. crassipes* measurement of 4.5–6.5 µm matches many of the taxa we recognise. Several of these taxa also have deeply lobed appressoria.

Colletotrichum dracaenae Allesch., *Rabenhorst's Kryptogamen-Flora von Deutschland, Oesterreich und der Schweiz*, Ed. 2, 1(7): 560. 1902.

Notes: Farr *et al.* (2006) examined the type specimen of this species and concluded it was a member of *C. gloeosporioides s. lat.*, based on conidial size and shape. Genetic data is not available to confirm this. See also discussion under *C. petchii* in Damm *et al.* (2012b, this issue)

Colletotrichum fragariae A.N. Brooks, Phytopathology 21: 113. 1931.

Notes: Placed here in synonymy with *C. theobromicola*. See notes and additional specimens examined under *C. theobromicola*.

The name *C. fragariae* was originally applied to isolates associated with a disease of strawberry (*Fragaria* × *ananassa*) runners (stolons) and petioles in Florida (Brooks 1931). Although the name was placed in synonymy with *C. gloeosporioides* by

Fig. 22. *Colletotrichum cordylinicola*. ICMP 18579 (ex MFLUCC 090551 – ex-holotype culture). A. Cultures on PDA, 10 d growth from single conidia, from above and below.

von Arx (1957), it has continued to be used in the literature for strawberry-associated *Colletotrichum* isolates. It was accepted as distinct by Sutton (1992), although he noted confusion surrounding application of the name. Designation of one of Brook's cultures (CBS 142.31 = IMI 346325) as the epitype of *C. fragariae* by Buddie *et al.* (1999) has allowed a modern, genetic basis for this name to be fixed. The ex-epitype culture of *C. fragariae* sits in a strongly supported clade containing isolates from a wide range of hosts from many parts of the world, including the ex-epitype culture of *C. theobromicola*, an earlier name for *C. fragariae* in the sense that we accept these species in this paper.

There are several species from the *C. gloeosporioides* complex which inhabit diseased strawberry plants, and as shown by MacKenzie *et al.* (2007, 2008) isolates that genetically match the epitype of *C. fragariae* have a wide host range. Despite its name MacKenzie *et al.* (2007, 2008) regarded this fungus as simply one of a group of several species sometimes found on strawberry. Our study confirms that members of the *C. fragariae*/*theobromicola* clade occur throughout the world on a wide range of hosts. Within the diversity of the *C. fragariae*/*theobromicola* clade, there is a subclade consisting of the *C. fragariae* epitype and two contemporary ex-strawberry isolates from the USA (Fig. 1), further work will be needed to establish if the strawberry stolon disease is restricted to this subclade. Despite regular surveys this disease has not been found on strawberries in New Zealand.

Xie *et al.* (2010b) provides a good example of the confusion that continues to surround the application of *Colletotrichum* names to isolates from strawberry. These authors noted that putative *C. gloeosporioides* and *C. fragariae* isolates were difficult to distinguish using ITS sequences, the only sequences that they generated. Xie *et al.* (2010b) found 4 groups of isolates, each with a slightly different ITS sequence, two of those groups they considered to be *C. fragariae* and two to be *C. gloeosporioides*. To classify their isolates as either *C. fragariae* of *C. gloeosporioides* they used a restriction enzyme method based on Martinez-Culebras *et al.* (2000). Incorporating their ITS sequences into our ITS alignment, one of their groups genetically matches *C. tropicale*, one matches *C. gloeosporioides s. str.*, one matches *C. fructicola*, and one matches *C. siamense*. These relationships are based on ITS sequences only — the genetic differences between some of these species are small and are indicative only of possible relationships. However, it is clear that none of the Xie *et al.* (2010b) sequences match those of the epitype of *C. fragariae*. There are also several species within the *C. acutatum* species complex associated with *Fragaria* (Damm *et al.* 2012, this issue).

Specimen examined: **USA**, Florida, on *Fragaria* × *ananassa*, coll. A.N. Brooks, 1931 (**ex-epitype culture** – CBS 142.31 = ICMP 17927).

*** *Colletotrichum fructicola*** Prihastuti, L. Cai & K.D. Hyde, Fungal Diversity 39: 158. 2009. Fig. 23.

= *Colletotrichum ignotum* E.I. Rojas, S. A. Rehner & Samuels, Mycologia 102: 1331. 2010.

= *Glomerella cingulata* var. *minor* Wollenw., Z. Parasitenk. (Berlin) 14: 261. 1949.

Prihastuti *et al.* (2009) and Rojas *et al.* (2010) provide descriptions.

Geographic distribution and host range: Originally reported from coffee berries from Thailand (as *C. fructicola*) and as a leaf endophyte from several plants in Central America (as *C. ignotum*), isolates that we accept as *C. fructicola* are biologically and geographically diverse. Known from *Coffea* from Thailand, *Pyrus pyrifolia* from Japan, *Limonium* from Israel, *Malus domestica* and *Fragaria* × *ananassa* from the USA, *Persea americana* from Australia, *Ficus* from Germany, *Malus domestica* from Brazil, *Dioscorea* from Nigeria, and *Theobroma* and *Tetragastris* from Panama.

Genetic identification: ITS sequences do not separate *C. fructicola* from *C. aeschynomenes* and some *C. siamense* isolates. These taxa are best distinguished using GS or SOD2.

Notes: Rojas *et al.* (2010) noted the occurrence of two distinct haplotype subgroups (A4-3 and A5-4) within their concept of *C. ignotum*. Our genetic analyses resolve the two clades representative of these two subgroups. However, together they are monophyletic within the Musae clade of the *C. gloeosporioides* complex, and we retain them here as a single species. Both clades include isolates from a wide range of hosts from many countries, and both are similar in morphology and cultural appearance. The types of both *C. fructicola* and *C. ignotum* are in the same haplotype subgroup.

The *C. fructicola* protologue designates the holotype as MFLU 090228, but the culture derived from holotype as "BCC" with no specimen number. The ex-holotype culture is listed as BDP-I16 in Table 1 of Prihastuti *et al.* (2009) but this number is not mentioned in the description. Culture BDP-I16 was obtained from the authors (Prihastuti *et al.* 2009) for this study and deposited as ICMP 18581.

See also notes under *G. cingulata* var. *minor*.

Specimens examined: **Australia,** Queensland, Bli-Bli, on *Persea americana* fruit rot, coll. L. Coates 24154 (ICMP 12568). **Brazil,** Rio Grande do Sul State, on *Malus domestica* leaf, coll. T. Sutton BR 8 2001, Jan. 2001 (ICMP 17787); Santa Catarina State, on *Malus domestica* leaf, coll. T. Sutton BR 21 2001, Jan. 2001 (ICMP 17788).

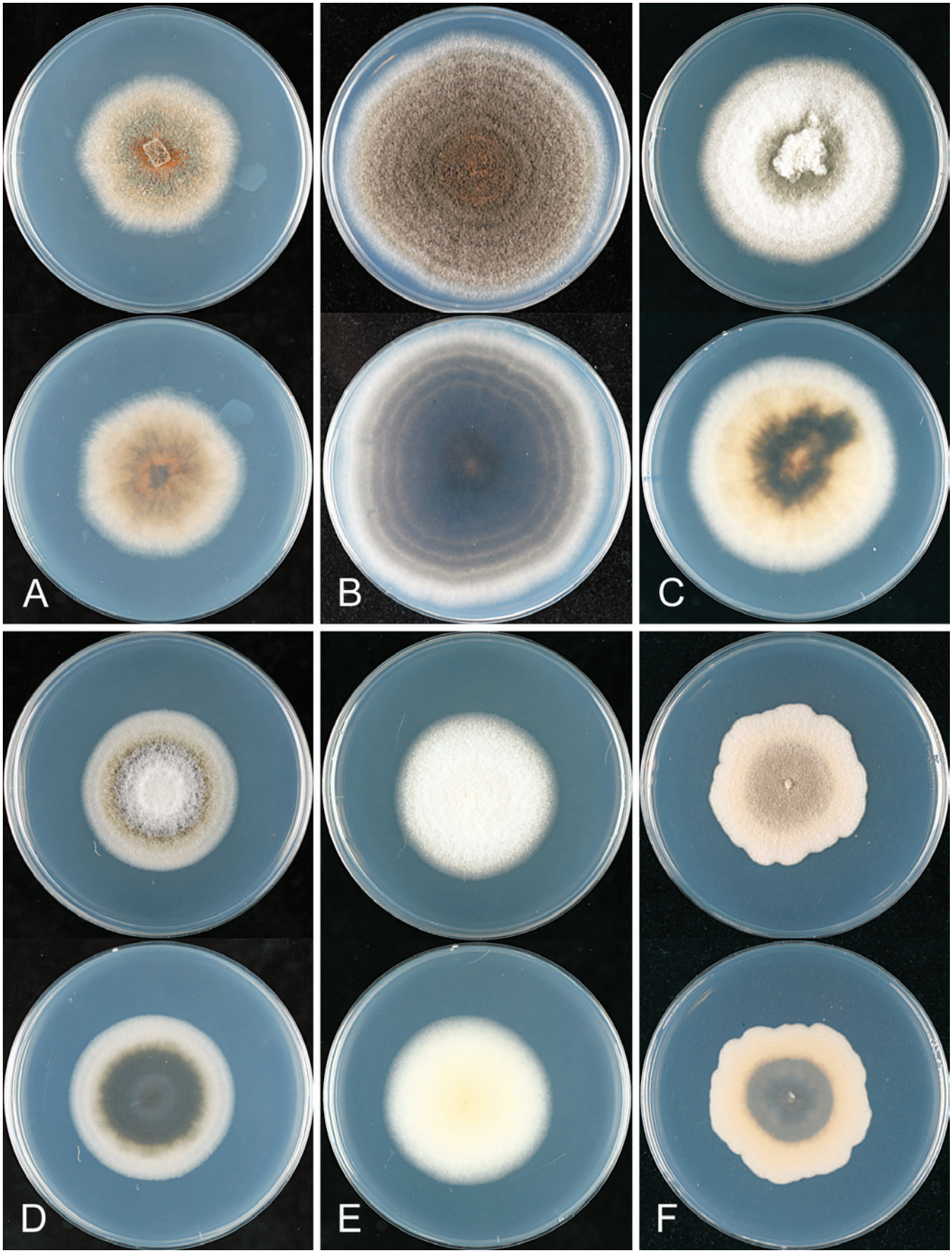


Fig. 23. *Colletotrichum fructicola*. A. ICMP 12568. B. ICMP 18615. C. ICMP 18581 (ex MFLU 090228 – ex-holotype culture of *C. fructicola*). D. ICMP 18610. E. ICMP 18646 (ex CBS 125379 – ex-holotype culture of *C. ignotum*). F. ICMP 17921 (ex CBS 238.49 – ex-holotype culture of *G. cingulata* var. *minor*). A–F. Cultures on PDA, 10 d growth from single conidia, from above and below.

Canada, Ontario, on *Fragaria* × *ananassa*, Jan. 1991 (IMI 345051 = ICMP 17819). **Germany**, Berlin-Dahlem Botanical Garden, on *Ficus edulis* leaf spot, (**ex-holotype culture** of *Glomerella cingulata* var. *minor* – CBS 238.49 = ICMP 17921). **Indonesia,** Java, Bandung, Pangheotan Estate, on *Camellia sinensis* shoots, coll. H. Semangun, Apr. 1979 (CBS 232.79 = ICMP 18656). **Israel**, on *Limonium sinuatum* leaf lesion, coll. S. Freeman L32 (cited in Moriwaki *et al.* 2006) (ICMP 18613); on *Limonium* sp. leaf

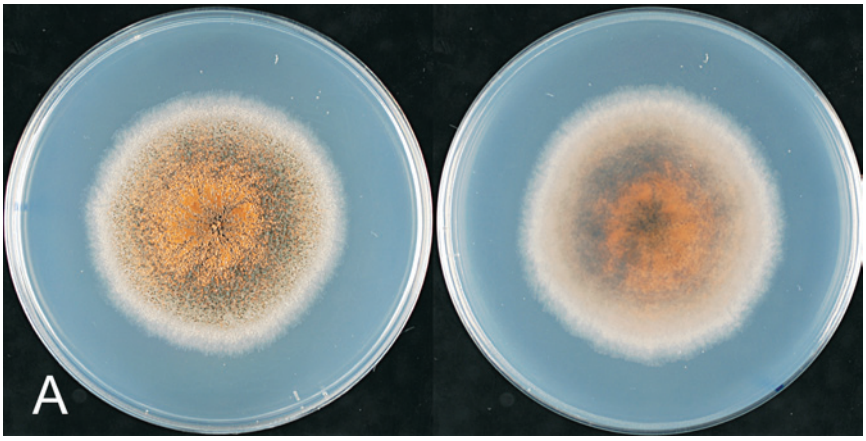


Fig. 24. *Colletotrichum gloeosporioides*. A. ICMP 17821 (ex IMI 356878 – ex-epitype culture). A. Cultures on PDA, 10 d growth from single conidia, from above and below.

lesion, coll. S. Freeman L50 (cited in Maymon *et al.* 2006) (ICMP 18698); on *Limonium* sp. leaf lesion, coll. S. Freeman Cg2 (cited in Maymon *et al.* 2006) (ICMP 18667); on *Limonium sinuatum*, coll. S. Freeman L11 (cited in Maymon *et al.* 2006) (ICMP 18615). **Japan**, Saga, on *Pyrus pyrifolia*, coll. H. Ishii sA02-5-1 (cited in Chung *et al.* 2006) (ICMP 18610). **Nigeria**, Ibadan, on *Dioscorea alata* leaf spot, M. Abang Cg13 (cited in Abang *et al.* 2002) (ICMP 18125); Ilesha, *Dioscorea rotundata* leaf spots, coll. M. Abang Cg22 (cited in Abang *et al.* 2002) (ICMP 18120). **Panama**, Barro Colorado Monument, *Tetragastris panamensis* leaf endophyte, coll. E.I. Rojas E886, 1 Jun. 2004 (**ex-holotype culture** of *C. ignotum* – CBS 125397 = ICMP 18646); *Theobroma cacao* leaf endophyte, coll. E. Rojas E183 (CBS 125395 = ICMP 18645). **Thailand**, Chiang Mai, Pa Daeng Village, on *Coffea arabica* berry, coll. H. Prihastuti BPD-I16, 12 Dec. 2007 (**ex-holotype culture** of *C. fructicola*, from specimen MFLU 090228 – ICMP 18581 = CBS 130416). **USA**, on *Fragaria* × *ananassa* crown, F. Louws 9, (ICMP 18727); Florida, on *Fragaria* × *ananassa*, coll. F.A. Ueckes FAU552 (CBS 120005 = BPI 747977 = ICMP 18609); North Carolina, Lincoln County, on *Malus domestica* fruit, coll. T. Sutton CROTTS 13 2001, Jan. 2001 (ICMP 17789).

**** Colletotrichum gloeosporioides*** (Penz.) Penz. & Sacc., Atti Reale Ist. Veneto Sci. Lett. Arti., Serie 6, 2: 670. 1884. Fig. 24.

Basionym: *Vermicularia gloeosporioides* Penz., Michelia 2: 450. 1882.

= *Gloeosporium pedemontanum* Pupillo, Ann. Sperim. Agrar. n.s. 6: 57. 1952.

Cannon *et al.* (2008) provide a description of the species.

Geographic distribution and host range: Most isolates of *C. gloeosporioides* are associated with *Citrus*, and in many parts of the world this fungus is common on *Citrus*, but it also occurs on other hosts including *Ficus*, *Mangifera*, *Pueraria*, and *Vitis*. The isolate reported as a pathogen of paper mulberry (*Broussonetia papyrifera*) by Yan *et al.* (2011) matches *C. gloeosporioides s. str.* genetically.

Genetic identification: ITS separates *C. gloeosporioides* from all other species.

Notes: The name *Colletotrichum gloeosporioides* is currently in common use in two senses, one a genetically and biologically broad sense more or less following von Arx (1957, 1970) and Sutton (1992), including the whole species complex, the other a strict sense, encompassing only those specimens genetically matching the epitype selected for this name by Cannon *et al.* (2008). Depending on the context, use of the name in either sense can be useful. When used in a broad sense in this paper, it is referred to as the *C. gloeosporioides* species complex or *C. gloeosporioides s. lat*.

Colletotrichum gloeosporioides is often linked taxonomically to the teleomorph *Glomerella cingulata*, see notes under *G. cingulata*.

Specimens examined: **Australia**, New South Wales, Tamworth, on *Carya illinoinensis* (DAR 76936; ICMP 18738). **Italy**, Calabria, on *Citrus sinensis*, (**ex-epitype culture** of *C. gloeosporioides* – IMI 356878 = CBS 112999 = ICMP 17821); on *Citrus limon* juice, coll. G. Goidánich, 1951 (**ex-holotype culture** of *Gloeosporium pedemontanum* – CBS 273.51 = ICMP 19121). **New Zealand**, Auckland, Sandringham, on *Citrus* sp. fruit, coll. P.R. Johnston C1014.6, 2 May 1988 (ICMP 12939); Auckland, Sandringham, on *Ficus* sp. fruit, coll. P.R. Johnston C945.2, 9 May 1988 (ICMP 12066); Auckland, on Citrus sp. fruit, coll. G. Caroll, Feb 2010 (ICMP 18730); Northland, Kerikeri, Kapiro Rd, on *Citrus sinensis* fruit, coll. P.R. Johnston C1009.2, 10 Aug. 1988 (ICMP 12938). **South Africa**, on *Mangifera indica*, coll. L. Korsten Cg68 (ICMP 18694). **USA**, Georgia, on *Pueraria lobata* (AR2799 = CBS 119204 = BPI 871837 = ICMP 18678); Florida, on *Citrus* sp. leaf lesion, coll. N. Peres SRL-FTP-9 (ICMP 18695); Florida, on *Vitis vinifera* leaf lesion, coll. N. Peres LAGrape8 (ICMP 18697).

Colletotrichum gloeosporioides "**f. sp. *aeschynomenes***" (Daniel *et al.* 1973, as *aeschynomene*).

Notes: See *Colletotrichum aeschynomenes*.

Colletotrichum gloeosporioides "**f. *alatae***" R.D. Singh, Prasad & R.L. Mathur, Indian Phytopathol. 19: 69. 1966. [nom. inval., no Latin description, no type designated]

Notes: See *Colletotrichum alatae*.

Colletotrichum gloeosporioides* var. *aleuritis Saccas & Drouillon [as "aleuritidis"], Agron. Trop. (Nogent-sur-Marne) 6: 249. 1951.

≡ *Glomerella cingulata* var. *aleuritis* Saccas & Drouillon [as "aleuritidis"], Agron. Trop. (Nogent-sur-Marne) 6: 251. 1951.

Notes: Originally described from *Aleurites fordii* and *A. montaba* from French Equatorial Africa, these names have not been used since being described and the genetic relationship of this fungus to and within the *C. gloeosporioides* species complex is unknown. Although the original publications have not been seen, both names were tagged as invalid in the Index of Fungi 2: 53, 57 (1952).

Colletotrichum gloeosporioides "**f. sp. *clidemiae***" (Trujillo *et al.* 1986).

Notes: See *Colletotrichum clidemiae*.

Colletotrichum gloeosporioides "**f. sp. *cucurbitae***" (Menten *et al.* 1980).

Notes: First described from cucumber, this fungus is widely regarded as a synonym of *C. orbiculare* in the plant pathology literature (*e.g.* Snowdon 1991, da Silva *et al.* 2011).

Colletotrichum gloeosporioides "**f. sp. *cuscutae***" (Zhang 1985).

Notes: A strain identified by this name was developed as a mycoherbicide against dodder (*Cuscuta chinensis* in China (Zhang 1985). This strain referred to as "Lu Bao No.1" is apparently included in the study of Guerber *et al.* (2003) as strain 783 and belongs to the *C. acutatum* species complex. Other strains from dodder in the USA included in the same study were revealed to be *C. fioriniae*, while a strain from Dominica was found to represent a new species, both belonging to the *C. acutatum* species complex as well (Damm *et al.* 2012, this issue).

Colletotrichum gloeosporioides **var. *gomphrenae*** Perera, Revista Fac. Agron. Univ. Nac. La Plata 41: 12. 1965.

Notes: Originally described from *Gomphrena globosa*, the name has not been used since it was described and its genetic relationship to and within the *C. gloeosporioides* species complex is unknown.

Colletotrichum gloeosporioides **var. *hederae*** Pass., Atti Reale Accad. Italia, Rendiconti., Serie 4, 6: 469. 1889.

Notes: The original description of this *Hedera*-inhabiting species, with fusiform, straight to curved conidia suggests that it is a synonym of the *Hedera* pathogen *C. trichellum*.

Colletotrichum gloeosporioides **f. *heveae*** (Petch) Saccas, Agron. Trop. (Nogent-sur-Marne) 14: 430. 1959.
Basionym: *Colletotrichum heveae* Petch, Ann. Roy. Bot. Gard. Peradeniya 3(1): 8. 1906.

Notes: Originally described from the leaves of seedlings of *Hevea brasiliensis* from Sri Lanka, this fungus was described with very broad conidia, 18–24 × 7.5–8 µm. Carpenter & Stevenson (1954) considered this, and several other *Colletotrichum*, *Gloeosporium* and *Glomerella* species described from rubber, to be synonyms of *C. gloeosporioides*. The genetic relationship of these species to and within the *C. gloeosporioides* species complex is unknown. See also notes in Damm *et al.* (2012b, this issue) under *Colletotrichum annelatum*.

Colletotrichum gloeosporioides "**f. sp. *hyperici***" (Harris 1993).

Notes: This name was first used by Harris (1993) for strains of *C. gloeosporioides* pathogenic to *Hypericum perforatum*. Earlier studies by Hildebrand & Jensen (1991) had found the *Hypericum* pathogen to be pathogenic also on several other plants. The genetic relationship of the *Hypericum* pathogen to and within the *C. gloeosporioides* species complex is unknown. Note that the ex-holotype culture of *G. cingulata* var. *migrans*, a variety here placed in synonymy with *C. kahawae* subsp. *ciggaro*, was also isolated from *Hypericum*.

Colletotrichum gloeosporioides "**f. sp. *jussiaeae***" (Boyette *et al*. 1979).

Notes: Strains identified as *C. gloeosporioides* "f. sp. *jussiaeae*" are highly pathogenic, specialised pathogens of *Jussiaea decurrens* (Boyette *et al.* 1979). The genetic relationship of this taxon to and within the *C. gloeosporioides* species complex, or to *Colletotrichum jussiaeae* Earle, is unknown. Isolates pathogenic to *Jussiaea* have a similar conidial germination self-inhibitor profile to another isolate identified as *C. fragariae* (Tsurushima *et al.* 1995). The authentic isolate of *C. gloeosporioides* "f. sp. *jussiaeae*" deposited as ATCC 52634, is not included in this study.

Colletotrichum gloeosporioides "**f. sp. *malvae***" (Makowski & Mortensen 1989).

Notes: Strains identified as *C. gloeosporioides* "f. sp. *malvae*" were registered as a bioherbicide against round leafed mallow in Canada (Makowski & Mortensen 1989). The fungus was subsequently recognised as belonging to the *C. orbiculare* species complex (Bailey *et al.* 1996).

Colletotrichum gloeosporioides "**f. sp. *manihotis***" (Chevaugeon 1956).

Notes: See *Colletotrichum manihotis*.

Colletotrichum gloeosporioides **f. *melongenae*** Fournet, Ann. Mus. Civico Storia Nat. Genova 5: 13. 1973.

Notes: In addition to *C. gloeosporioides* f. *melongenae*, the names *C. gloeosporioides* "f. sp. *melongenae*", *C. melongenae* Av.-Saccá 1917, and *C. melongenae* Lobik 1928 have been used to refer to fungi associated with anthracnose diseases of *Solanum melongena* (*e.g.* Sherf & McNab 1986, Kaan 1973). Other names used for isolates from the same host have included *Gloeosporium melongenae* Ellis & Halst. 1891 and *G. melongenae* Sacc. 1916. The genetic relationships of these eggplant-associated taxa to and within the *C. gloeosporioides* species complex remain unknown. *Solanum melongena* associated species are known also from the *C. boninense* species complex (Damm *et al*. 2012b, this issue).

Colletotrichum gloeosporioides "**f. sp. *miconiae***" (Killgore *et al.* 1999).

Notes: Killgore *et al.* (1999) reported that the isolates they recognised as *C. gloeosporioides* "f. sp. *miconiae*" were highly specialised pathogens of *Miconia calvescens*, unable to infect the closely related *Clidemia hirta*. The original voucher cultures are no longer available (pers. comm., Robert Barreto). Recently collected isolates from *Miconia* from the type locality in Brazil have proved to be genetically diverse across the *C. gloeosporioides* species complex, with isolates in both the Kahawae and Musae clades (unpubl. data). For now the genetic position of this pathogen remains unresolved.

Colletotrichum gloeosporioides **var. *minus*** Simmonds, Queensland J. Agric. Anim. Sci. 25: 178A. 1968.

Notes: See *Colletotrichum queenslandicum*.

Colletotrichum gloeosporioides* var. *nectrioidea Gonz. Frag., Bol. Soc. Brot., 2: 52. 1924.

Notes: Originally described from *Citrus aurantium* from Portugal, the name has not been used since it was described and its genetic relationship to and within the *C. gloeosporioides* species complex is unknown.

Colletotrichum gloeosporioides "**f. sp. *ortheziidae***" (Marcelino *et al.* 2008).

Notes: Marcelino *et al.* (2008) clearly show that the *Orthezia praelonga* pathogen belongs in the *C. acutatum* species complex, despite referring to the fungus only as *C. gloeosporioides* "f. sp. *ortheziidae*". See also notes under *C. nymphaeae* in Damm *et al.* (2012a, this issue).

Colletotrichum gloeosporioides "**f. sp. *pilosae***" (Singh 1974).

Notes: First described from leaves of *Bidens pilosa*, this name has not been used since it was described and its genetic relationship to and within the *C. gloeosporioides* species complex is unknown.

Colletotrichum gloeosporioides* f. *stylosanthis Munaut, Mycol. Res. 106: 591. 2002.

Notes: Placed here in synonymy with *C. theobromicola*; see notes under *C. theobromicola*.

Irwin & Cameron (1978) and Munaut *et al.* (2002) described different diseases of *Stylosanthes* associated with Type A and Type B isolates of *C. gloeosporioides* f. *stylosanthis*, the two groups of isolates distinguished morphologically by growth rate in culture and by conidial morphology. Compared with Type A, the Type B isolates had a slower growth rate on PDA, and conidia more variable in size and shape (Irwin & Cameron 1978). They were also distinguished genetically using RFLP and similar methods (*e.g.* Munaut *et al.* 1998, 2002). Munaut *et al.* (2002) used ITS1 sequences to show the *C. gloeosporioides* f. *stylosanthis* to be related to an isolate they identified as *C. fragariae*. We regard *C. fragariae* to be a synonym of *C. theobromicola*, with putatively authentic Type A (HM335, *C. gloeosporioides* f. *stylosanthis* "f. sp. *guianensis*") and Type B (HM 336, *C. gloeosporioides* f. *stylosanthis* "f. sp. *stylosanthis*") isolates both also belonging to this species. From the ITS1 sequence data available, isolates regarded as typical of Type A (RAPD cluster I) and of Type B (RAPD cluster II) by Munaut *et al.* (1998) all belong in *C. theobromicola* in the sense that we are using the name; their RAPD cluster III isolate could be *C. tropicale*, and their RAPD cluster IV isolates are probably *C. fructicola*.

The cultures of *C. gloeosporioides* f. *stylosanthis* that we used were originally studied by Irwin & Cameron (1978), and selected as the "types" of "f. sp. *guianensis*" and "f. sp. *stylosanthis*" by Munaut *et al.* (2002). Both isolates have a 'stale' growth form, no longer forming conidia in culture and with aerial mycelium closely appressed to the agar surface, resulting in an almost slimy colony surface. Both isolates had a slow growth rate, similar to that reported for Type B isolates by Irwin & Cameron (1978). Genetically both isolates were identical for all the genes we sequenced. This identity should be checked against additional isolates, especially some matching Type A *sensu* Irwin & Cameron (1978) with respect to both pathogenicity and growth form.

Sherriff *et al.* (1994), using ITS2 and partial 28S rDNA sequences, found isolates they considered to represent *C. gloeosporioides* f. *stylosanthis* Type A and Type B respectively to be genetically distinct. However, their ITS2 sequences show that the putative Type B isolate in their study was in fact a member of the *C. boninense* species complex.

Specimens examined: **Australia**, Queensland, Townsville, on *Stylosanthes viscosa*, coll. J.A.G. Irwin 21365 (HM335), 1976 (**ex-holotype culture** of *C. gloeosporioides* f. *stylosanthis* – MUCL 42294 = ICMP 17957 = CBS 124251); Samford, on *Stylosanthes guianensis*, coll. J.A.G. Irwin 21398 (HM336), 1979 (MUCL 42295 = ICMP 17958 = CBS 124250).

Colletotrichum gloeosporioides* f. *stylosanthis "**f. sp. *guianensis***" (Munaut *et al.* 2002)

≡ *Colletotrichum gloeosporioides* "f. sp. *guianensis*" (Vinijsanum *et al.* 1987).

Notes: See notes and specimens examined under *C. gloeosporioides* f. *stylosanthis*.

Colletotrichum gloeosporioides* f. *stylosanthis "**f. sp. *stylosanthis***" (Munaut *et al.* 2002).

Notes: See notes and specimens examined under *C. gloeosporioides* f. *stylosanthis*.

Colletotrichum gloeosporioides "**f. sp. *uredinicola***" (Singh 1975).

Notes: Described from uredinia and telia of *Ravenelia sessilis* on pods of *Albizia lebbek*, this name has not been used since it was described and its genetic relationship to and within the *C. gloeosporioides* species complex is unknown.

Colletotrichum gossypii Southw., J. Mycol. 6: 100. 1891.

= *Glomerella gossypii* Edgerton, Mycologia 1: 119. 1909.

Notes: This species was originally described from the USA and was reported to cause disease symptoms on all parts of cotton plants, but especially the bolls (Southworth 1891, Edgerton 1909). Isolates identified as *C. gossypii* by Shear & Wood (1907) were reportedly associated with a *Glomerella* state in culture, and Edgerton (1909) described *Glomerella gossypii* from diseased, mature cotton plants in the USA Edgerton (1909) discussed differences in ascospore shape between *G. gossypii* and fruit-rotting isolates of *G. cingulata*, with *G. gossypii* having elliptic, not curved ascospores. Von Arx (1957) considered *C. gossypii* to be a synonym of *C. gloeosporioides* and von Arx & Müller (1954) regarded *G. gossypii* to be a synonym of *G. cingulata*.

Modern authors have recognised two pathogens of cotton, *C. gossypii* and *C. gossypii* var. *cephalosporioides*. *Colletotrichum gossypii* is reportedly the cause of cotton anthracnose, a damping-off disease of cotton seedlings, and *C. gossypii* var. *cephalosporioides* the cause of ramulosis, a disease causing abnormal branching of mature plants (Bailey *et al.* 1996, Silva-Mann *et al.* 2005). In a study based on ITS2 sequences, Bailey *et al.* (1996) found *C. gossypii* and *C. gossypii* var. *cephalosporioides* to be genetically distinct but with both belonging to the *C. gloeosporioides* species complex. Silva-Mann *et al.* (2005) also distinguished the two taxa genetically, based on an AFLP analysis. The only DNA sequences available for isolates identified as *C. gossypii* and *C.*

gossypii var. *cephalosporioides* are ITS2 and the D2 region of the rDNA LSU, neither of which resolves their relationships within the *C. gloeosporioides* complex. Whether the seedling pathogen regarded by Silva-Mann *et al.* (2005) and Bailey *et al.* (1996) to be *C. gossypii* represents the species first described from cotton in the USA is not known. The genetic relationship of these apparently biologically specialised fungi requires additional sequences to be generated from authentic isolates with known pathogenicity.

Colletotrichum gossypii* var. *cephalosporioides A.S. Costa, Bragantia 6: 5. 1946.

≡ *Colletotrichum gloeosporioides* "var. *cephalosporioides*" (A.S. Costa) Follin & Mangano, Coton et fibres tropicales 37: 209. 1983. [comb. inval., no full reference to basionym]

Notes: See notes under *Colletotrichum gossypii*.

*** *Colletotrichum horii*** B. Weir & P.R. Johnst., Mycotaxon 111: 21. 2010.

Weir & Johnston (2010) and Xie *et al.* (2010a) provide descriptions.

Geographic distribution and host range: Associated with fruit and stem disease of *Diospyros kaki* from China, Japan, and New Zealand. Xie *et al.* (2010a) noted minor symptoms on inoculated fruit of *Capsicum annuum*, *Musa acuminata*, and *Cucurbita pepo*, but noted that the fungus had never been associated with disease symptoms on these hosts from the field.

Genetic identification: ITS distinguishes *C. horii* from all other species.

Specimens examined: See Weir & Johnston (2010).

Colletotrichum hymenocallidis Yan L. Yang, Zuo Y. Liu, K.D. Hyde & L. Cai, Fungal Diversity 39: 138. 2009.

Notes: Placed here in synonymy with *Colletotrichum siamense*. See notes and additional specimens examined under *C. siamense*. Yang *et al.* (2009) reported this species as a leaf pathogen of *Hymenocallis americana*. They distinguished *C. hymenocallidis* from *C. siamense*, also described from *Hymenocallis*, primarily on the basis of a multi-gene phylogeny and differences in colony colour. Although gene selection was appropriate for resolving genetic relationships within the *C. gloeosporioides* group, Yang *et al.* (2009) included only five isolates of the *C. gloeosporioides* complex in their phylogeny. Based on this isolate selection, the *C. hymenocallidis* isolates were genetically distinct from the *C. siamense* isolates. However, in our analysis, in which the *C. siamense*/*C. hymenocallidis* group is represented by 30 isolates from a wide range of hosts from all over the world, authentic isolates of the two species fall within a monophyletic clade that cannot be further subdivided phylogenetically.

The Latin part of the *C. hymenocallidis* protologue designates a culture ("Holotypus: Cultura (CSSN2)") as the holotype but the English citation of the type specimen corrects this apparent mistake, citing CSSN2 as an ex-holotype culture, with the herbarium specimen GZAAS 080001 as the holotype.

Specimen examined: **China**, Guangxi, Nanning, on *Hymenocallis americana* leaf spot, coll. Y.L. Yang GZAAS 080001, 19 Jun 2008 (**ex-holotype culture** of *C. hymenocallidis* − CBS 125378 = ICMP 18642).

Colletotrichum ignotum E.I Rojas, S.A. Rehner & Samuels, Mycologia 102: 1331. 2010.

Notes: Placed here in synonymy with *Colletotrichum fructicola*. See notes and additional specimens examined under *C. fructicola*.

Specimen examined: **Panama**: Barro Colorado Monument, *Tetragastris panamensis* leaf endophyte, coll. E.I. Rojas E886, 1 Jun 2004 (**ex-holotype culture** of *C. ignotum* − CBS 125397 = ICMP 18646).

Colletotrichum jasmini-sambac Wikee, K.D. Hyde, L. Cai & McKenzie, Fungal Diversity 46: 174. 2011.

Notes: Placed here in synonymy with *Colletotrichum siamense* based on the ITS, GAPDH, CAL, TUB2, and ACT gene sequences from the ex-holotype culture, deposited in GenBank by Wikee *et al.* (2011).

Wikee *et al.* (2011) discussed similarities between *C. jasmini-sambac*, *C. siamense* and *C. hymenocallidis*, three species genetically close in their phylogenetic analysis. The broader range of isolates representing *C. siamense* in our analysis shows that these species form a single, monophyletic clade that cannot be sensibly subdivided (see notes under *C. siamense*).

Specimen examined: **Vietnam**, Cu Chi District, Trung An Ward, on living leaves of *Jasminum sambac*, Jan. 2009, coll. Hoa Nguyen Thi LLTA–01 (**ex-holotype culture** of C. *jasmini-sambac* – CBS 130420 = ICMP 19118).

*** *Colletotrichum kahawae*** J.M. Waller & Bridge subsp. ***kahawae***, Mycol. Res. 97: 993. 1993. Fig. 25.

Waller *et al.* (1993) provide a description.

Geographic distribution and host range: Known only from *Coffea* from Africa.

Genetic identification: ACT, CAL, CHS-1, GAPDH, TUB2, SOD2, and ITS sequences are the same as those from *C. kahawae* subsp. *ciggaro*. The two subspecies can be distinguished by GS sequences; *C. kahawae* subsp. *kahawae* has a 22 bp deletion and a single C to T transition. Collectively, the two subspecies can be distinguished from all other species using ITS sequences alone.

Notes: *Colletotrichum kahawae* was proposed by Waller *et al.* (1993) as a name to refer specifically to *Colletotrichum* isolates causing Coffee Berry Disease (CBD), to taxonomically distinguish these disease-causing isolates from the several other *Colletotrichum* spp. that can be isolated from coffee plants, including *C. coffeanum* (see notes under *C. coffeanum*). *Colletotrichum kahawae* is an apparently clonal population (Varzea *et al.* 2002), widespread on coffee in Africa, and with a distinctive growth form and biology (Waller *et al.* 1993).

In this paper *C. kahawae sensu* Waller *et al.* (1993) is reduced to subspecies. Based on ACT, CAL, CHS-1, GAPDH, TUB2, SOD2, and ITS gene sequences the coffee berry pathogen cannot be distinguished from isolates from a wide range of other hosts that are not pathogenic to coffee. Those other isolates are referred to here as *C. kahawae* subsp. *ciggaro*. We retain a distinct taxonomic label for the coffee berry pathogen to reflect its biosecurity importance. In addition to its biology, *C. kahawae* subsp. *kahawae* can be distinguished metabolically, and genetically using GS gene sequences. Waller *et al.* (1993) used a metabolic test, an inability

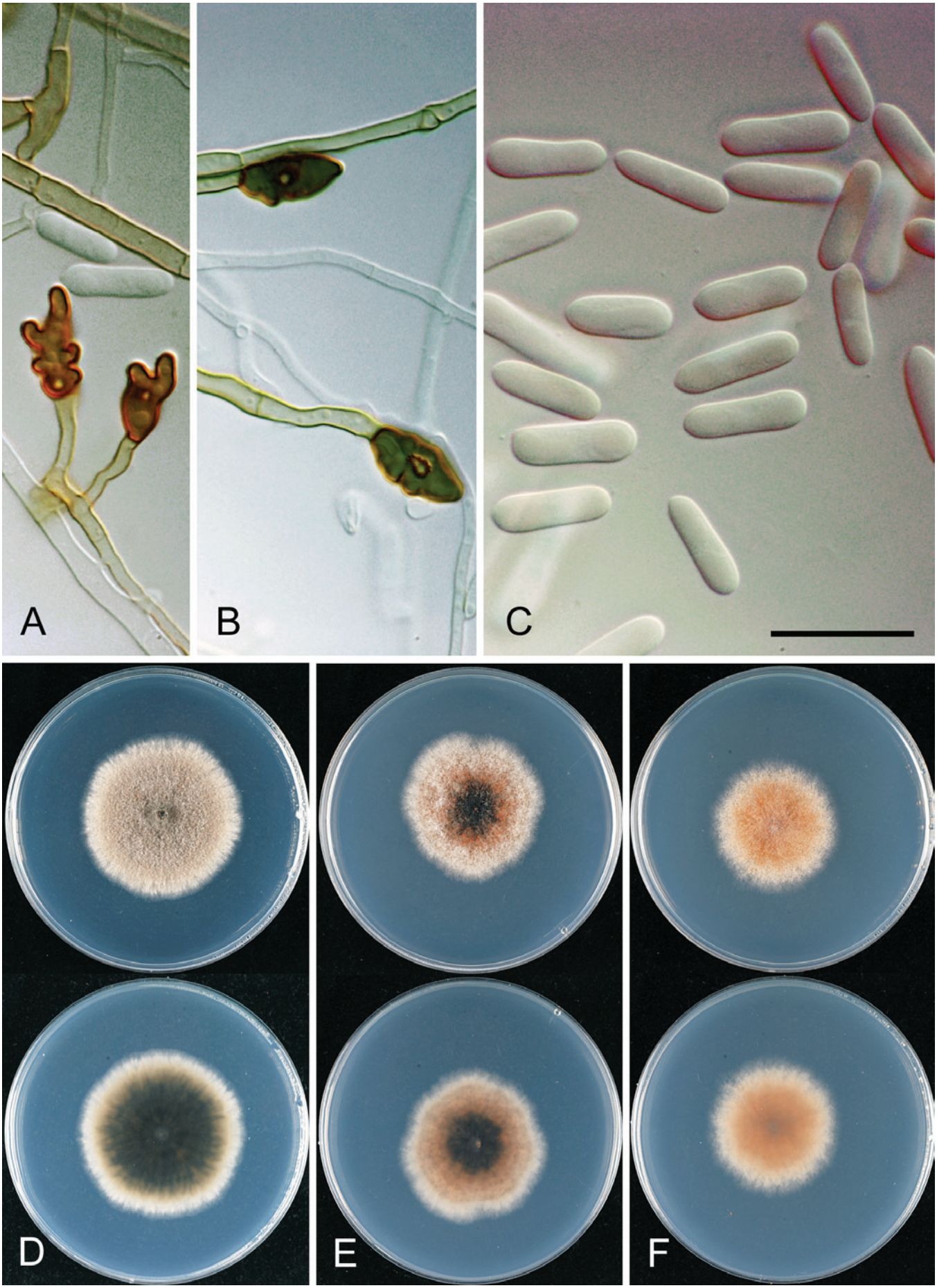


Fig. 25. *Colletotrichum kahawae* subsp. *kahawae*. A, E. ICMP 17905 (ex IMI 361501). B–C. ICMP 17816 (ex IMI 319418 – ex-holotype culture). C. ICMP 17915 (ex CBS 982.69). A–B. Appressoria. C. Conidia. D–E. Cultures on PDA, 10 d growth from single conidia, from above and below. Scale bar C = 20 µm. Scale bar of C applies to A–C.

to utilise either citrate or tartrate as a sole carbon source, to help characterise isolates as *C. kahawae*. None of our *C. kahawae* subsp. *kahawae* isolates were able to utilise either citrate or tartrate, whereas all of the *C. kahawae* subsp. *ciggaro* isolates were able to utilise one or both of these carbon sources (Weir & Johnston 2009). All of the *C. kahawae* subsp. *kahawae* isolates share a 22 bp deletion in the glutamine synthetase gene, lacking in the *C. kahawae* subsp. *ciggaro* isolates. Note that one of the isolates metabolically and genetically typical *C. kahawae* subsp. *kahawae* (CBS 982.69) was reported by Gielink & Vermeulen (1983) to be non-pathogenic to coffee, but we have not independently checked this result.

The isolates we accept as *C. kahawae* subsp. *kahawae* show two cultural types, one matching the description of Waller *et al.* (1993), slow growing, darkly pigmented cultures with conidia developing mostly in the aerial mycelium. The second cultural type grew even more slowly, had little or no pigmentation within the agar, and the colony surface was covered with numerous acervuli and orange conidial masses. Metabolically and genetically both cultural types were the same, and pathogenicity tests showed that the non-pigmented isolates caused CBD (unpubl. data, D. Silva, Centro de Investigação das Ferrugens do Cafeeiro). Rodriguez *et al.* (1991) reported further variation in cultural appearance amongst CBD causing isolates.

Waller *et al.* 1993 stated that *C. kahawae* was not known to form ascospores. However, Gielink & Vermeulen (1983) observed the production of perithecia on coffee berries that had been inoculated with CBD-causing isolates, many months after inoculation and death of the berries. At least one of the isolates that they cited with this biology, CBS 135.30, has the GS sequence typical of *C. kahawae* subsp. *kahawae*. Vermeulen *et al.* (1984) grew cultures from the perithecia that developed on the previously inoculated berries, and found that none were pathogenic to coffee. It is possible that the perithecia developing on inoculated berries reported by Gielink & Vermeulen (1983) were from other *Colletotrichum* spp. present on the berries before they were inoculated, and represented species distinct from *C. kahawae* subsp. *kahawae*. A similar situation has been noted with some of our inoculations, where species present on tissues prior to inoculation, either endophytic or latent, started to sporulate on the dead tissue following inoculation (unpubl. data, B.S. Weir).

Based on ITS sequences, most of the accessions in GenBank identified as *C. kahawae* and isolated from coffee, match our concept of *C. kahawae* subsp. *kahawae*. There are two exceptions, AF534468 (from Malawi) and AY376540 (STE-U 5295 = IMI 319424 = CBS 112985, from Kenya). The Kenyan isolate was cited as *C. kahawae* in Lubbe *et al.* (2004). Based on the ITS sequences, and the TUB2 sequence from isolate STE-U 5295 (AY376588), these isolates represent *C. siamense*.

Specimens examined: **Angola**, Ganada, on *Coffea arabica* berry, coll. J.N.M. Pedro 16/65, 2 Jun. 1965 (IMI 310524 = CBS 982.69 = ICMP 17915). **Cameroon**, on *Coffea arabica* (IMI 361501 = ICMP 17905). **Kenya**, Ruiru, Kakuzi Estate, on *Coffea arabica* young shoots, coll. D.M. Masaba 22/87, 29 Jan. 1987 (**ex-holotype culture** of *C. kahawae* – IMI 319418 = ICMP 17816); on *Coffea* sp., coll. E.C. Edwards, May 1930 (CBS 135.30 = ICMP 17982). **Malawi**, on *Coffea arabica* (IMI 301220 = ICMP 17811).

*** *Colletotrichum kahawae* subsp. *ciggaro*** B. Weir & P.R. Johnst., **subsp. nov.** MycoBank MB563758. Figs 26, 27.

= *Glomerella cingulata* var. *migrans* Wollenw., Z. Parasitenk. (Berlin) 14: 262. 1949.

= *Glomerella rufomaculans* var. *vaccinii* Shear, Bull. Torrey Bot. Club. 34: 314. 1907.

Etymology: Based on the title of the Jim Jarmusch movie "Coffee and Cigarettes", referring to the close genetic relationship between *C. kahawae* subsp. *ciggaro* and the coffee pathogen *C. kahawae* subsp. *kahawae*; ciggaro is Portuguese for cigarette.

Holotype: **Australia**, on *Olea europaea*, coll. V. Sergeeva UWS124, 1989, PDD 102232; ex-type culture ICMP 18539.

Colonies grown from single conidia on Difco PDA 75–85 mm diam after 10 d for most isolates, the ex-holotype culture of *G. cingulata* var. *migrans* 48–49 mm diam. Aerial mycelium cottony, grey, dense, or in some isolates with dark stromatic masses and associated orange conidial ooze showing through mycelium from agar surface; in reverse agar with pinkish-orange pigments (6B4–7B4), irregular scattered black spots, and variable levels of development of overlying dark grey to green-grey pigments (4C2–5D4), these sometimes in discrete sectors. See notes below about a divergent growth form single ascospore cultures from perithecia in culture. *Conidia* form on dark-based acervuli, (12–)16–19.5(–29) × (4.5–)5(–8) µm (av. 17.8 × 5.1 µm, n = 214), cylindric, straight, apex rounded, often tapering slightly towards the base. *Appressoria* typically cylindric to fusoid in shape, deeply lobed. *Perithecia* numerous, forming tightly packed clumps, individual perithecia globose, small, about 250 µm diam, with a short ostiolar neck. *Asci* 55–100 × 10–12 µm, 8–spored. *Ascospores* (13.5–)17.5–20(–24) × (4–)4.5–5(–6.5) µm (av. 18.8 × 4.8 µm, n = 121), gently curved, tapering to quite narrow, rounded ends, widest point usually towards one end of the spore.

Geographic distribution and host range: Known from Australia, Germany, New Zealand, and South Africa. Both host and geographic range of the isolates we accept in *C. kahawae* subsp. *ciggaro* are broad. *Genetic identification*: ACT, CAL, CHS-1, GAPDH, TUB2, SOD2, and ITS sequences match those from *C. kahawae* subsp. *kahawae*. The two subspecies can be distinguished by GS sequences. Collectively, the two subspecies can be distinguished from all other species using ITS sequences alone.

Notes: The authentic isolate of *G. cingulata* var. *migrans* (CBS 237.49) differed from all other isolates we accept in *C. kahawae* subsp. *ciggaro* by its slower growth rate. Wollenweber & Hochapfel (1949) distinguished *Glomerella cingulata* var. *migrans* from *G. cingulata* var. *cingulata* on the basis of pathogenicity (*G. cingulata* var. *migrans* was pathogenic to *Hypericum* and not to apple) and because of its slightly longer ascospores and shorter conidia — ascospores average 21 × 4.2 µm versus 18 × 4.6 µm, conidia average 14 × 5.2 µm versus 18 × 5 µm (Wollenweber & Hochapfel 1949). We were unable to produce ascospores from CBS 237.49, the conidia were similar in size to that reported by Wollenweber & Hochapfel (1949), averaging 16.6 × 5.3 µm. However, the average ascospore and conidial lengths of our *C. kahawae* subsp. *ciggaro* isolates varied across the range cited by Wollenweber & Hochapfel (1949) for both *G. cingulata* var. *cingulata* and *G. cingulata* var. *migrans*, the average ascospore length from individual isolates ranging from 16.6 to 20 µm, the average conidial length ranging from 14.9 to 21.2 µm.

Glomerella rufomaculans var. *vaccinii* was described by Shear (1907) for a fungus isolated from cranberry that was morphologically identical to isolates from apple and other hosts but which appeared to be biologically distinct (Shear 1907, Shear & Wood 1913). A putatively authentic isolate of this species, deposited by Shear in CBS in 1922, matches *C. kahawae* subsp. *ciggaro* genetically. Polashock *et al.* (2009) discussed the diversity of *Colletotrichum*

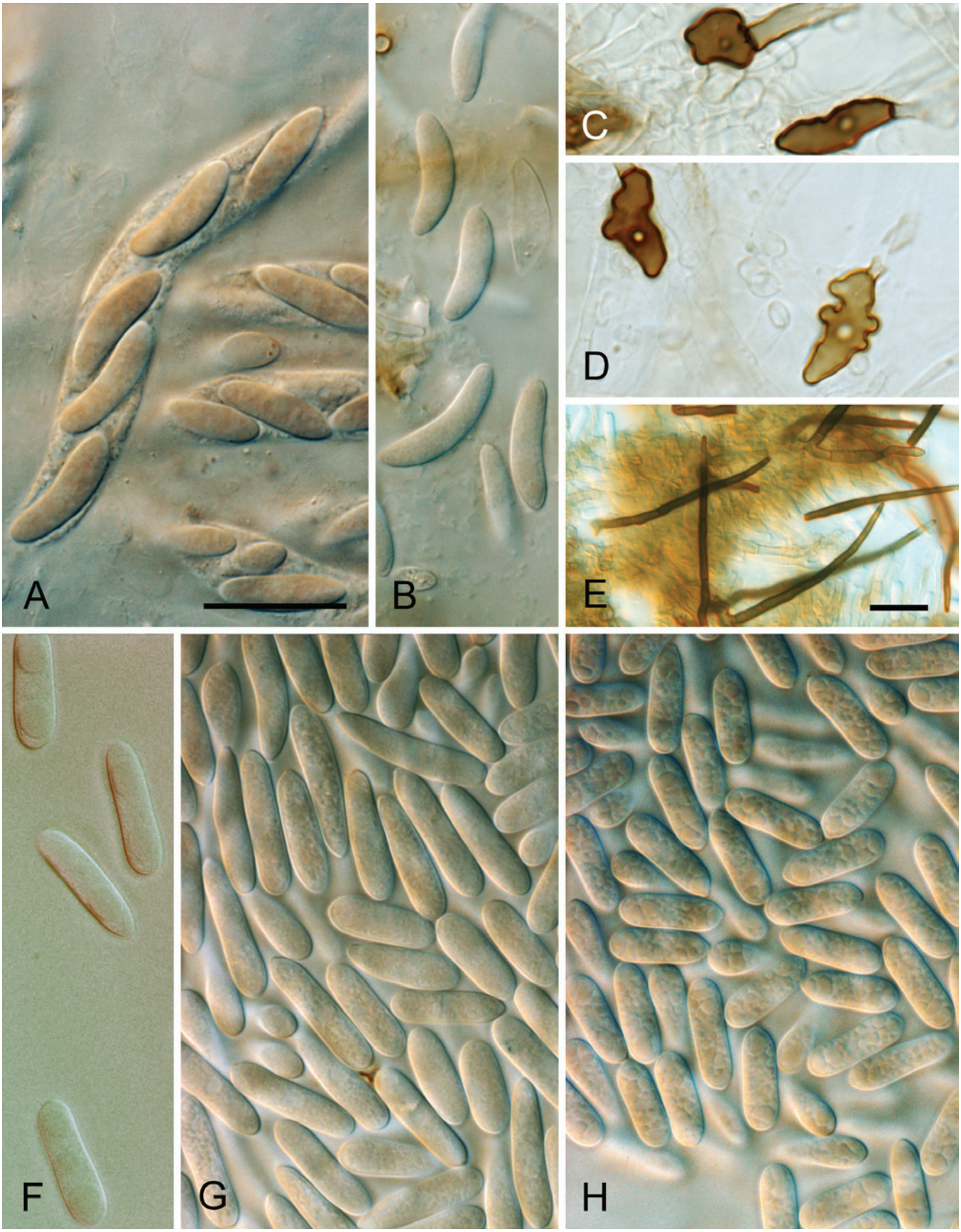


Fig. 26. *Colletotrichum kahawae* subsp. *ciggaro*. A. ICMP 12952. B, D. ICMP 17932 (ex CBS 112984). E, H. ICMP 17931 (ex IMI 359911). C, F. ICMP 18539 – ex-holotype culture. G. ICMP 18531. A–B. Asci and ascospores. C–D. Appressoria. E. Setae. F–H. Conidia. Scale bars A, E = 20 µm. Scale bar of A applies to A–D, F–H.

spp. associated with North American cranberry fruit rots, reporting a close match between their isolates and *C. kahawae*. Incorporation of their ITS sequences into our alignment confirms this. Whether or not there is a genetically distinct, cranberry specialised taxon within *C. kahawae* requires additional genes to be sequenced from the cranberry-associated isolates.

Colletotrichum kahawae subsp. *ciggaro* was referred to as *C. gloeosporioides* Group B by Johnston & Jones (1997) and Johnston

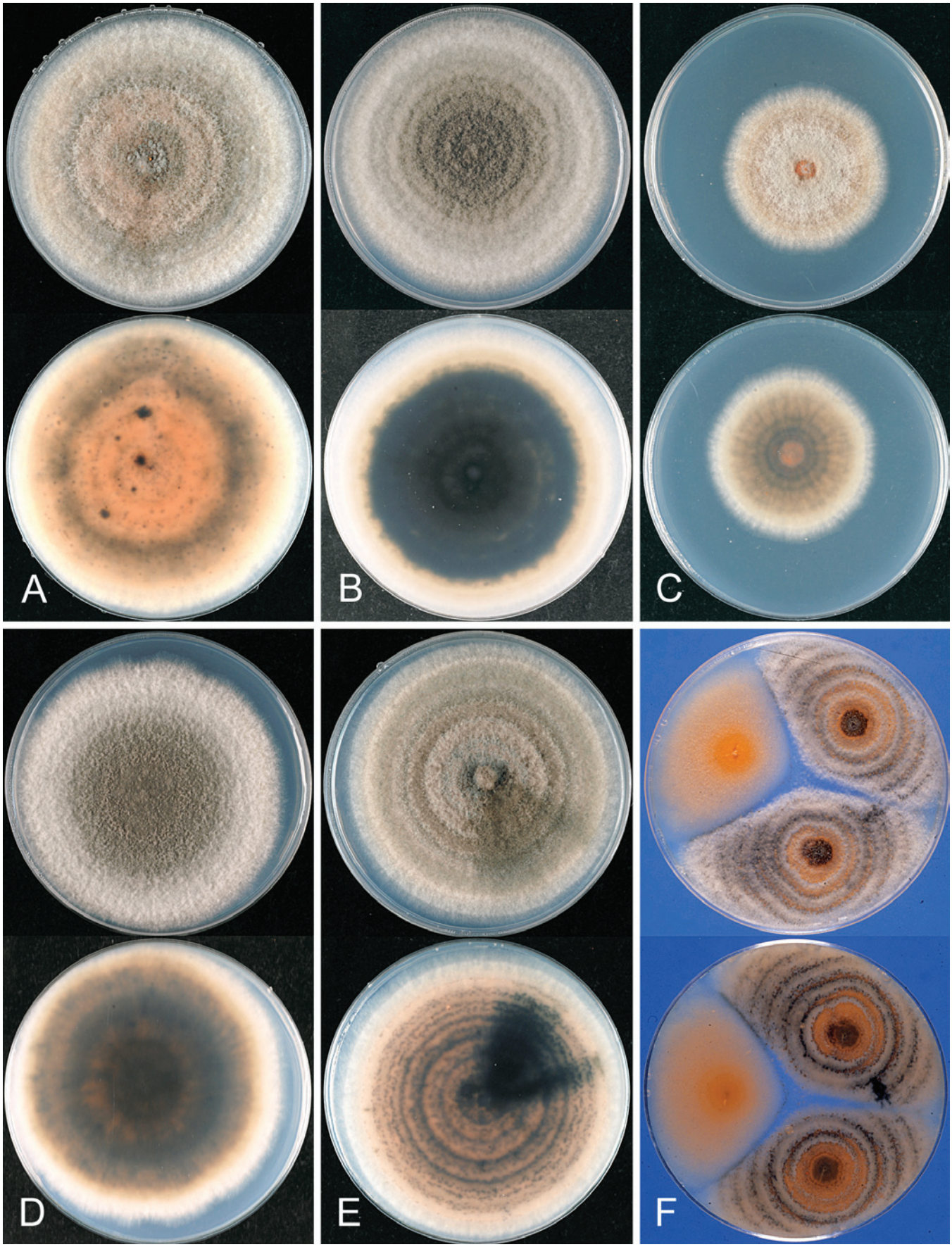


Fig. 27. *Colletotrichum kahawae* subsp. *ciggaro*. A. ICMP 12953. B. ICMP 18534. C. ICMP 17922 (ex CBS 237.49 – ex-holotype culture of *Glomerella cingulata* var. *migrans*). D. ICMP 17932 (ex CBS 112984). E. ICMP 18539 – ex-holotype culture of *C. kahawae* subsp. *ciggaro*. F. ICMP 12952 – single ascospore cultures from single conidial isolate. Cultures on PDA, 10 d growth from single conidia, from above and below.

et al. (2005), and as Undescribed Group 1 by Silva et al. (2012b).

Single ascospore isolates derived from perithecia forming in single conidial cultures of the avocado-associated isolates of *C. kahawae* subsp. *ciggaro* from New Zealand showed two highly divergent growth forms (Fig. 27F). One typical of the "wild type" (cottony, grey to dark grey aerial mycelium with dark-based acervuli

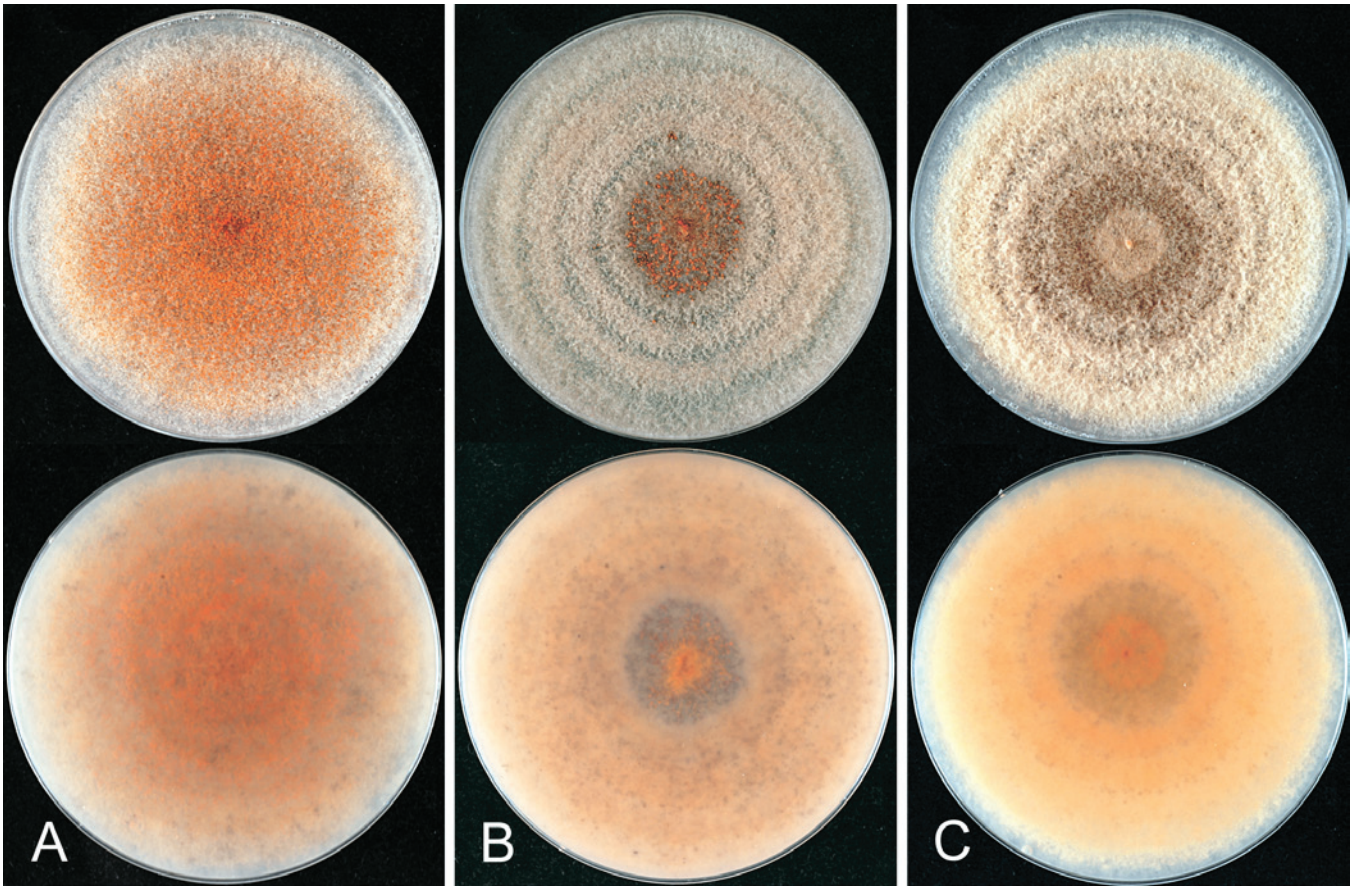


Fig. 28. *Colletotrichum musae*. A. ICMP 12930. B. ICMP 18600. C. ICMP 17817 (ex IMI 52264). Cultures on PDA, 10 d growth from single conidia, from above and below.

and orange conidial masses visible through the mycelium, in reverse with pinkish-orange pigmentation, in places this masked by irregular patches or sectors of dark grey pigmentation), the other more or less lacking aerial mycelium, the surface of the colony covered with small, pale-based acervuli with bright orange conidial ooze, in reverse bright orange from the conidial ooze. Although common from single ascospores, the bright, conidial cultural type is rarely formed by isolates from nature (unpubl. data). Similar dimorphic cultural types have been observed also from single ascospore isolates from a member of the *C. boninense* complex, *C. constrictum* (unpubl. data, P.R. Johnston).

Other specimens examined: **Brazil**, on leaves of *Miconia* sp., coll. R. Barreto RWB1054, 2009 (ICMP 18728). **Germany**, Berlin-Dahlem, on stem of *Hypericum perforatum*, Jun. 1937 (**ex-holotype culture** of *Glomerella cingulata* var. *migrans* – CBS 237.49 = ICMP 17922). **New Zealand**, Auckland, Waitakere Ranges, on leaves of *Kunzea ericoides*, coll. S. Joshee 5Kun3.10 (ICMP 18741); Auckland, Waitakere Ranges, on leaves of *K. ericoides*, coll. S. Joshee 7Kun5.2 (ICMP 18534); Auckland, Waitakere Ranges, on leaves of *Toronia toru*, coll. G. Carroll TOROTO3 (ICMP 18544); Te Puke, on *Persea americana* fruit rot, coll. W.F.T. Hartill, 19 Jan. 1989 (ICMP 18531); Te Puke, on *P. americana* fruit rot, coll. W.F.T. Hartill, 8 Feb. 1988 (ICMP 12952); Te Puke, on *P. americana* fruit rot, coll. W.F.T. Hartill, 28 Sep. 1991 (ICMP 12953). **South Africa**, Madeira, on *Dryandra* sp., coll. J.E. Taylor, 1 Apr. 2001 (CBS 112984, as *C. crassipes* = ICMP 17932). **Switzerland**, on *Dryas octopetala*, coll. P. Cannon (IMI 359911 = CBS 12988 = ICMP 17931). **USA**, on *Vaccinium macrocarpum* leaves, coll. C.L. Shear, Apr. 1922 (**authentic culture** of *G. rufomaculans* var. *vaccinii* – CBS 124.22 = ICMP 19122).

Colletotrichum manihotis Henn., Hedwigia 43: 94. 1904.

Notes: Anthracnose is an important disease of cassava (*e.g.* Chevaugeon 1956, Makambila 1994, Fokunang *et al.* 2000, Owolade *et al.* 2008), variously referred to *Colletotrichum manihotis*, *Gloeosporium manihotis* Henn., *Glomerella manihotis* (Sacc.) Petr., *Glomerella cingulata* "f. sp. *manihotis*", or *C. gloeosporioides* "f. sp. *manihotis*". The original descriptions of both *C. manihotis* and *Gloeosporium manihotis* are of species with short, broad conidia (8–15 × 4–6 µm), and Chevaugeon (1956) regarded all of these cassava-associated fungi as con-specific. However, based on Fokunang *et al.* (2000), a morphologically highly diverse set of *Colletotrichum* isolates are associated with diseased plants. There are three GenBank accessions of *Colletotrichum* from cassava, all from China, and although only ITS sequences are available for these isolates, they appear to represent a single, distinct species within the *C. gloeosporioides* complex. How these Chinese isolates relate to cassava-associated isolates from other parts of the world is not known.

**** Colletotrichum musae*** (Berk. & M.A. Curtis) Arx, Verh. Kon. Ned. Akad. Wetensch., Afd. Natuurk., Sect. 2 51(3): 107. 1957. Fig. 28.
Basionym: *Myxosporium musae* Berk. & M.A. Curtis, Grevillea 3: 13. 1874.

Su *et al.* (2011) provide a description.

Geographic distribution and host range: Found in association with fruit lesions of *Musa* spp. in many regions.

Genetic identification: ITS sequences separate *C. musae* from all other species.

Notes: *Colletotrichum musae* was originally described from North Carolina (Berkeley 1874), and the name was recently epitypified by Su *et al.* (2011) on the basis of a specimen collected in Florida

(ex-epitype culture CBS 116870). Su *et al.* (2011) cite several strains from Thailand that match their concept of *C. musae*, and isolates from anthracnose symptoms on banana fruit from several parts of the world are the same based on our study. These isolates form a well-supported clade within the *C. gloeosporioides* species complex, show low levels of genetic differentiation, and based on ITS sequences are consistent with *C. musae sensu* Sreenivasaprasad *et al.* (1996), Nirenberg *et al.* (2002) and Shenoy *et al.* (2007). The morphology in culture agrees with the description of Sutton & Waterston (1970).

We have not seen a *Glomerella* state in culture and none was mentioned by Su *et al.* (2011). However, Rodriguez & Owen (1992) reported rare production of perithecia from crosses between two of 14 isolates identified as *C. musae*. It is not known whether the isolates studied by Rodriguez & Owen (1992) match our concept of *C. musae* genetically, but it is possible that this species behaves in a similar way to some species in the *C. acutatum* complex, where the sexual morph can be generated in culture under suitable conditions (Guerber & Correll 2001). The name "*Glomerella musae*", used by Rodriguez & Owen (1992) and Krauss *et al.* (2001), has never been validly published.

More than one species of *Colletotrichum* has been found in association with rotting banana fruit. From isolates with well characterised sequence data these include a species belonging to *C. acutatum s. lat.* (Sherriff *et al.* 1994, Johnston & Jones 1997) that is described as *C. paxtonii* (Damm *et al.* 2012a, this issue), and *C. karstii* that belongs to the *C. boninense* species complex (Damm *et al.* 2012b, this issue). The latter forms a sexual stage in culture and is known from *Musa* in South America and Australia, as well as from many other hosts worldwide, often as an endophyte. Species in the *C. boninense* species complex have been previously confused with *C. gloeosporioides s. lat.* Greene (1967) referred isolates pathogenic to banana that were not associated with a teleomorph to *C. musae*, and a second non-pathogenic species that formed fertile ascospores, to *C. gloeosporioides*. Whether *Glomerella musarum* Petch, described from leaves of banana and cited as the teleomorph of *C. musae* by Sutton (1992) and Hyde *et al.* (2009), is a synonym of *C. musae* in the sense we use the name here is not known, but seems unlikely given the rare production of perithecia by this species.

Specimens examined: **Indonesia**, on *Musa* sp., coll. G. von Becze, Jan. 1931 (CBS 192.31 = ICMP 17923). **Kenya**, on *Musa sapientum*, coll. R.M. Nattrass 1850, 1 Jan. 1953 (IMI 52264 = ICMP 17817). **New Zealand**, Auckland (imported fruit), on *Musa* sp., coll. P.R. Johnston C1197.1, 24 May 1991 (ICMP 12931; PDD 59100); Auckland (fruit imported from the Phillipines), on *Musa* sp., coll. S. Bellgard, 5 May 2009 (ICMP 18600); Auckland, Mt Albert Research Centre, *Musa* sp. spots on green fruit, coll. P.R. Johnston C809.2, 12 Aug. 1987 (ICMP 12930; PDD 46160); Auckland (fruit imported from the Phillipines), on *Musa* sp., coll. B. Weir, 17 May 2009 (ICMP 18701; PDD 97438). **USA**, Florida, on *Musa* sp., coll. M. Arzanlou A-1 (**ex-epitype culture** of *C. musae* – CBS 116870 = ICMP 19119).

Glomerella musarum Petch, Ann. Roy. Bot. Gard. Peradeniya 6(3): 223. 1917.

Notes: See notes under *C. musae*.

*** *Colletotrichum nupharicola*** D.A. Johnson, Carris & J.D. Rogers, Mycol. Res. 101: 647. 1997. Fig. 29.

Johnson *et al.* (1997) provide a description.

Geographic distribution and host range: Known only from the USA, on the aquatic plants *Nuphar* and *Nymphaea* spp.

Genetic identification: One of the two ITS haplotypes of *C. nupharicola* is identical with *C. queenslandicum*. All other genes distinguish this species well from other species in the *C. gloeosporioides* complex.

Notes: Sequence data from the ex-holotype culture of *C. nupharicola* places it within the *C. gloeosporioides* complex, genetically close to *C. fructicola* and *C. alienum* in the Musae clade. This apparently host-specific species and has a distinctive, slow growth in culture and massive conidia (Johnson *et al.* 1997).

Johnson *et al.* (1997) compare *C. nupharicola* with another water plant pathogen, *C. nymphaeae*, that is epitypified and shown to belong to the *C. acutatum* species complex by Damm *et al.* (2012a, this issue).

Specimens examined: **USA**, Washington, King Co., on *Nuphar lutea* subsp. *polysepala*, coll. D.A. Johnson A-7, Oct. 1993 (CBS 469.96 = ICMP 17938); Washington, Yakima Co., on *N. lutea* subsp. *polysepala*, coll. D.A. Johnson A-2, Oct. 1993 (**ex-holotype culture** − CBS 470.96 = ICMP 17939); Rhode Island, on *Nymphaea ordorata*, coll. R.D. Goos RDG-291, 1979 (CBS 472.96 = ICMP 18187).

Gloeosporium pedemontanum Pupillo, Ann. Sperim. Agrar. n.s. 6: 57. 1952.

Notes: Placed here in synonymy with *C. gloeosporioides*. See notes under *C. gloeosporioides*.

Specimen examined: **Italy**, on *Citrus limon* juice, coll. G. Goidánich, 1951 (**ex-holotype culture** of *G. pedemontanum* – CBS 273.51 = ICMP 19121).

*** *Colletotrichum psidii*** Curzi, Atti dell'Istituto Botanico dell'Università di Pavia, ser. 3, 3: 207. 1927. Fig. 30.

Colonies grown from single conidia on Difco PDA 58–63 mm diam after 10 d, aerial mycelium dense, cottony to felted, uniform in height, white to off-white; in reverse uniformly pale creamy yellow (2A2–2A3) or in some cultures becoming dull greyish yellow (2D2–2E2) towards the centre. No *conidiogenous cells* or *conidia* seen.

Geographic distribution and host range: Known from a single isolate, from *Psidium* from Italy.

Genetic identification: Although known from only one isolate, ITS sequences separate *C. psidii* from all other taxa.

Notes: A putatively authentic isolate of this species, deposited in CBS by Curzi shortly after publication of *C. psidii*, represents a genetically distinct species within the Kahawae clade. The only available culture is stale, no longer forming conidia. Curzi (1927) describes the conidia as 12–15 × 3.5–4.5 µm, cylindric with rounded ends, straight or rarely slightly curved.

Anthracnose diseases have been noted for *Psidium* spp. (guava) from several tropical regions of the world (*e.g.* MacCaughey 1917, Venkatakrishniah 1952, Liu 1972, Misra 2004). It is likely that several *Colletotrichum* spp. are associated with guava fruit rots. Whether the fungus described by Curzi from an Italian botanical garden represents one of the species causing a guava disease in the tropics is not known. All other members of the Kahawae clade are predominantly tropical, so perhaps this fungus was introduced to Italy along with its host plant. Misra (2004) uses *C. psidii* to refer to a *Colletotrichum* species with curved conidia.

One other species has been described from this host, *Glomerella psidii* (basionym *Gloeosporium psidii*), the relationship

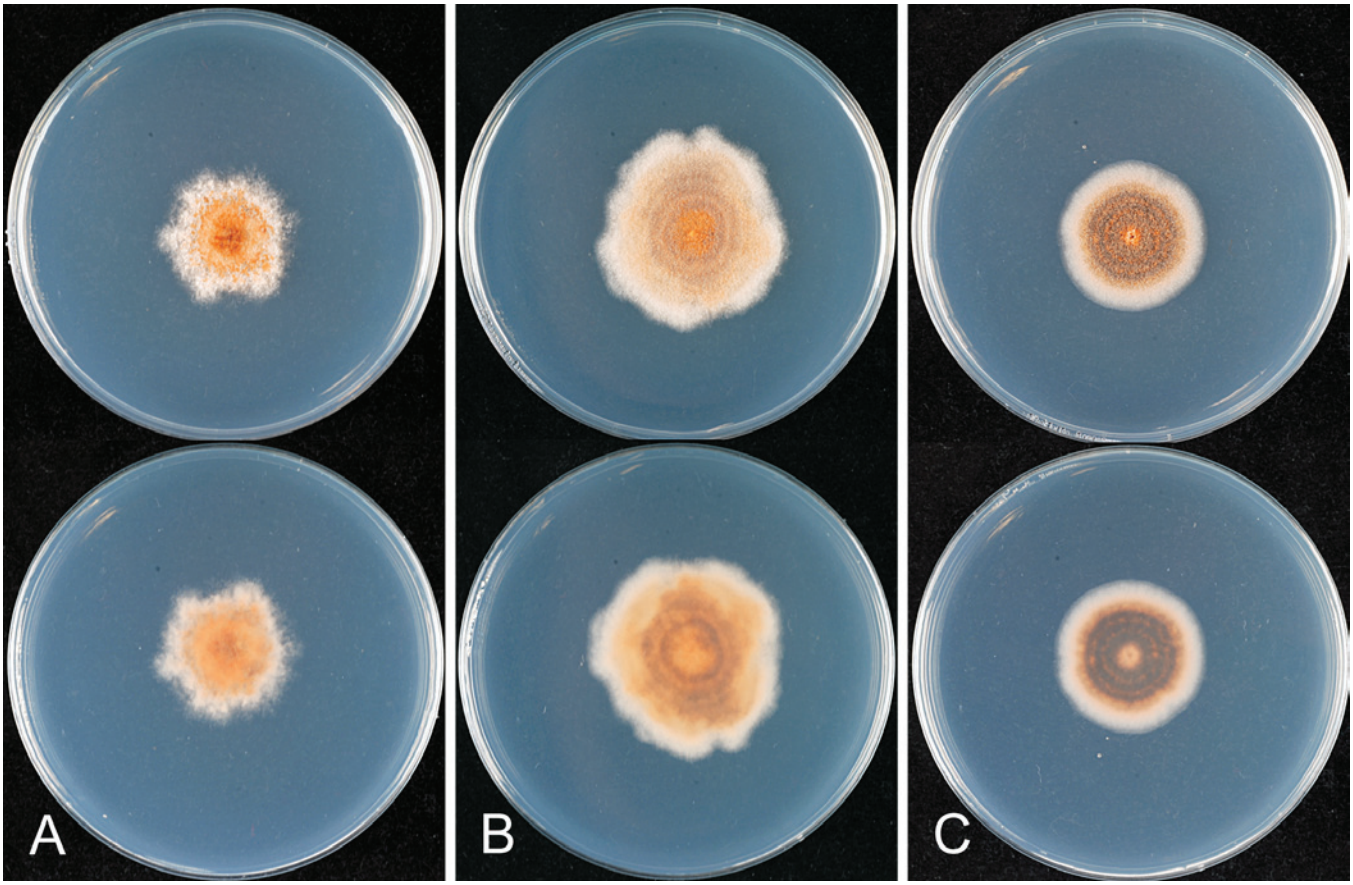


Fig. 29. *Colletotrichum nupharicola*. A. ICMP 17939 (ex CBS 470.96 – ex-holotype culture). B. ICMP 17938 (ex CBS 469.96). C. ICMP 18187 (ex CBS 472.96). Cultures on PDA, 10 d growth from single conidia, from above and below.

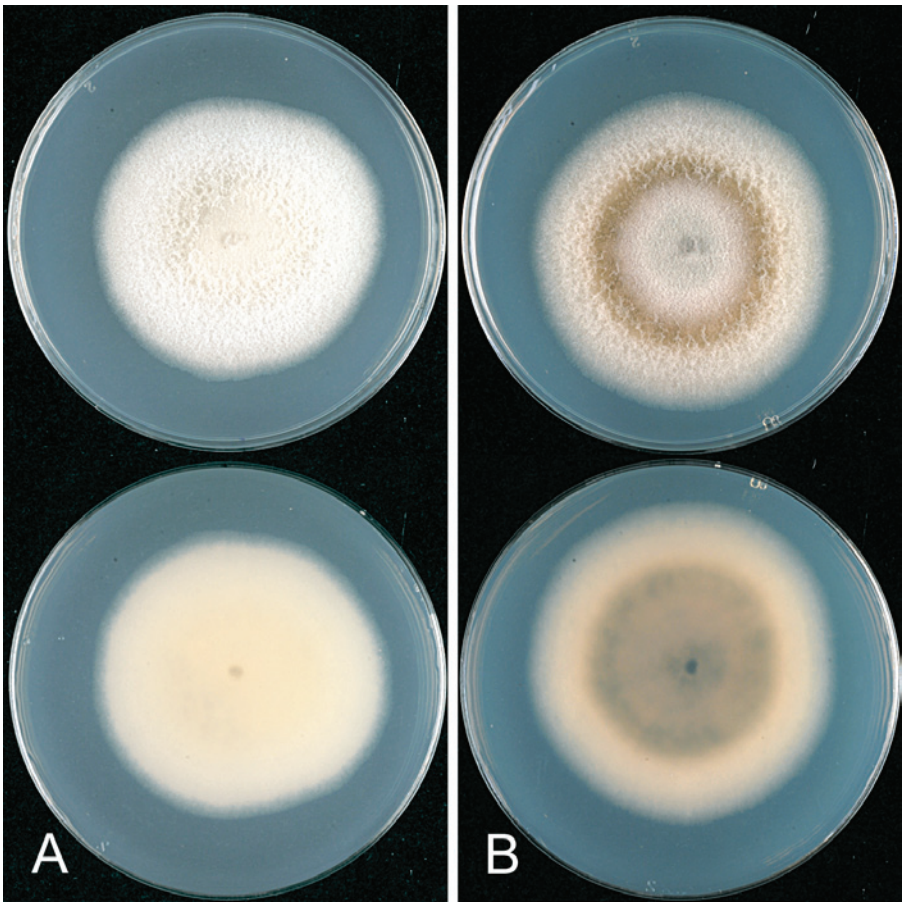


Fig. 30. *Colletotrichum psidii* (ICMP 19120, ex CBS 145.29 – authentic culture). Cultures on PDA, 10 d growth from single hyphal tips, from above and below.

of this species to *C. psidii* remains unknown. A new species on *Psidium guajava*, *C. guajavae*, belonging to the *C. acutatum* species complex, is described elsewhere in this volume (Damm *et al.* 2012a).

Specimen examined: **Italy**, Rome, on *Psidium* sp., coll. M. Curzi (**authentic culture** of *C. psidii* – CBS 145.29 = ICMP 19120).

Glomerella psidii (Delacr.) J. Sheld., Bull. West Virginia Agric. Exp. Sta. 104: 311. 1906.
Basionym: *Gloeosporium psidii* Delacr., Bull. Soc. Mycol. France. 19: 144. 1903.

Notes: Sheldon (1906) produced perithecia in culture from isolates he considered typical of *Gloeosporium psidii* and on this basis recombined the species described by Delacroix (1903) in *Glomerella*. The relationship of *G. psidii* to *Colletotrichum psidii*, also described from guava, is not known. See notes under *C. psidii*.

*** *Colletotrichum queenslandicum*** B. Weir & P.R. Johnst., **nom. nov. et stat. nov.** MycoBank MB563593. Fig. 31.
Basionym: *Colletotrichum gloeosporioides* var. *minus* Simmonds, Queensland J. Agric. Anim. Sci. 25: 178A. 1968. [as var. *minor*]

Etymology: based on the region from which the type specimen of this species was collected.

Holotype: Australia, Queensland, Ormiston, on *Carica papaya*, coll. J.H. Simmonds, Oct. 1965, IMI 117612.

Epitype: **Australia**, Queensland, Brisbane, on *Carica papaya*, coll. J.H. Simmonds 11663C, Sep. 1965, **epitype** here designated PDD 28797; ex-epitype culture ICMP 1778.

Colonies grown from single conidia on Difco PDA 62–74 mm diam after 10 d, aerial mycelium either dense, cottony, uniform, grey, or with aerial mycelium lacking, towards centre of colony with numerous, small acervuli with dark bases and orange conidial ooze; in reverse cultures with copious aerial mycelium uniformly dark grey (1F2), those with little aerial mycelium having a pinkish brown (8B4) pigment within the agar, the dark bases of the acervuli and the colour of the conidial ooze visible through the agar. *Conidia* (12–)14.5–16.5(–21.5) × (3.5–)4.5–5(–6) µm (av. 15.5 × 4.8 µm, n = 96), cylindric, straight, sometimes slightly constricted near centre, ends broadly rounded. *Appressoria* about 6–12 µm diam., globose to short-cylindric, rarely lobed. *Perithecia* not seen.

Geographic distribution and host range: Known from *Carica papaya* and *Persea americana* from Queensland, Australia, and from *Coffea* berries from Fiji. Simmonds (1965) reported from Australia what he considered to be the same fungus also from *Mangifera indica*, *Malus sylvestris*, and "many other hosts".

Genetic identification: ITS sequences do not separate *C. queenslandicum* from some *C. fructicola*, some *C. siamense*, and some *C. tropicale* isolates. It is best distinguished from these taxa using TUB2, GAPDH, or GS.

Notes: The ex-type cultures cited by Simmonds (1968) are no longer in storage at BRIP in Queensland (R. Shivas, pers. comm.) and presumably lost. However, we do have two cultures identified as *C. gloeosporioides* var. *minus* by Simmonds and isolated from the same host from the same locality as the holotype (Simmonds isolates 16633C and 1647A2), that had been sent to Joan Dingley in 1965 and subsequently stored in the ICMP culture collection. The culture selected here as epitype (Simmonds 11663C = ICMP 1778) matches the Simmonds (1965) description of this fungus as having "an abundance of aerial mycelium in culture". Our conidial measurements from ICMP 1778 and 1780 are broader than those given by Simmonds (1965), but he does note that "Confusion can occur between narrower strains of *C. gloeosporioides* and broader strains of *C. gloeosporioides* var. *minus* …". Simmonds (1965) also notes that perithecia may rarely be seen in cultures of some isolates.

The isolates accepted here as *C. queenslandicum* are genetically distinct within the Musae clade of *C. gloeosporioides s. lat*. *Colletotrichum minus* Zimm. (1901) requires that we propose a *nom. nov.* for this fungus at species rank.

Simmonds (1965) considered *C. gloeosporioides* var. *minus* to be the conidial state of *Glomerella cingulata* var. *minor* Wollenw. Wollenweber & Hochapfel (1949) used the name *Gloeosporium elasticae* Cooke & Massee for the conidial state of *G. cingulata* var. *minor*, the type specimens for both names being from *Ficus*. Simmonds (1965) noted that it was not possible to transfer *G. elasticae* to *Colletotrichum* because *Colletotrichum elasticae* had already been published for a different fungus. However, rather than proposing a nom. nov. for *Gloeosporium elasticae*, he described *C. gloeosporioides* var. *minus* as a new variety, with a different type specimen. *Glomerella cingulata* var. *minor* is genetically distinct from the specimen Simmonds chose as the type of *C. gloeosporioides* var. *minus*, see notes under *G. cingulata* var. *minor*.

Other specimens examined: **Australia**, Queensland, Brisbane, on *Carica* sp., coll. J.H. Simmonds 16347A2 (ICMP 1780, dried culture stored as PDD 28797); Queensland, Home Hill, on *Persea americana*, coll. L. Coates 22516, Feb. 1983 (ICMP 12564). **Fiji**, on *Coffea* sp. berry, coll. R. Gounder, Apr. 1988 (ICMP 18705).

Glomerella rufomaculans* var. *vaccinii Shear, Bull. Torrey Bot. Club. 34: 314. 1907.

Notes: Placed here in synonymy with *Colletotrichum kahawae* subsp. *ciggaro*. See notes under *C. kahawae* subsp. *ciggaro*. Note that Saccardo & Trotter (1913) place Shear's variety in *Glomerella fructigena* (Clint.) Sacc., a rarely used species name, placed in synonymy with *G. cingulata* by von Arx & Müller (1954).

Specimen examined: **USA**, on *Vaccinium macrocarpum* leaves, coll. C.L. Shear, Apr. 1922 (authentic isolate of *G. rufomaculans* var. *vaccinii* – CBS 124.22 = ICMP 19122).

*** *Colletotrichum salsolae*** B. Weir & P.R. Johnst., **sp. nov.** MycoBank MB563589. Fig. 32.
= *Colletotrichum gloeosporioides* "f. sp. *salsolae*" (Berner *et al.* 2009).

Etymology: Based on *C. gloeosporioides* "f. sp. *salsolae*", referring to the host from which this fungus was originally collected.

Holotype: **Hungary**, on *Salsola tragus*, coll. D. Berner [specimen from plants inoculated with strain 96-067, originally collected I. Schwarczinger & L. Vajna on *Salsola tragus* from Bugac, near Kiskunsag National Park, 1996], BPI 878740; ex-holotype culture ICMP 19051.

Colonies grown from single conidia on Difco PDA 38–42 mm diam after 10 d, aerial mycelium sparse, cottony, pale grey, surface of

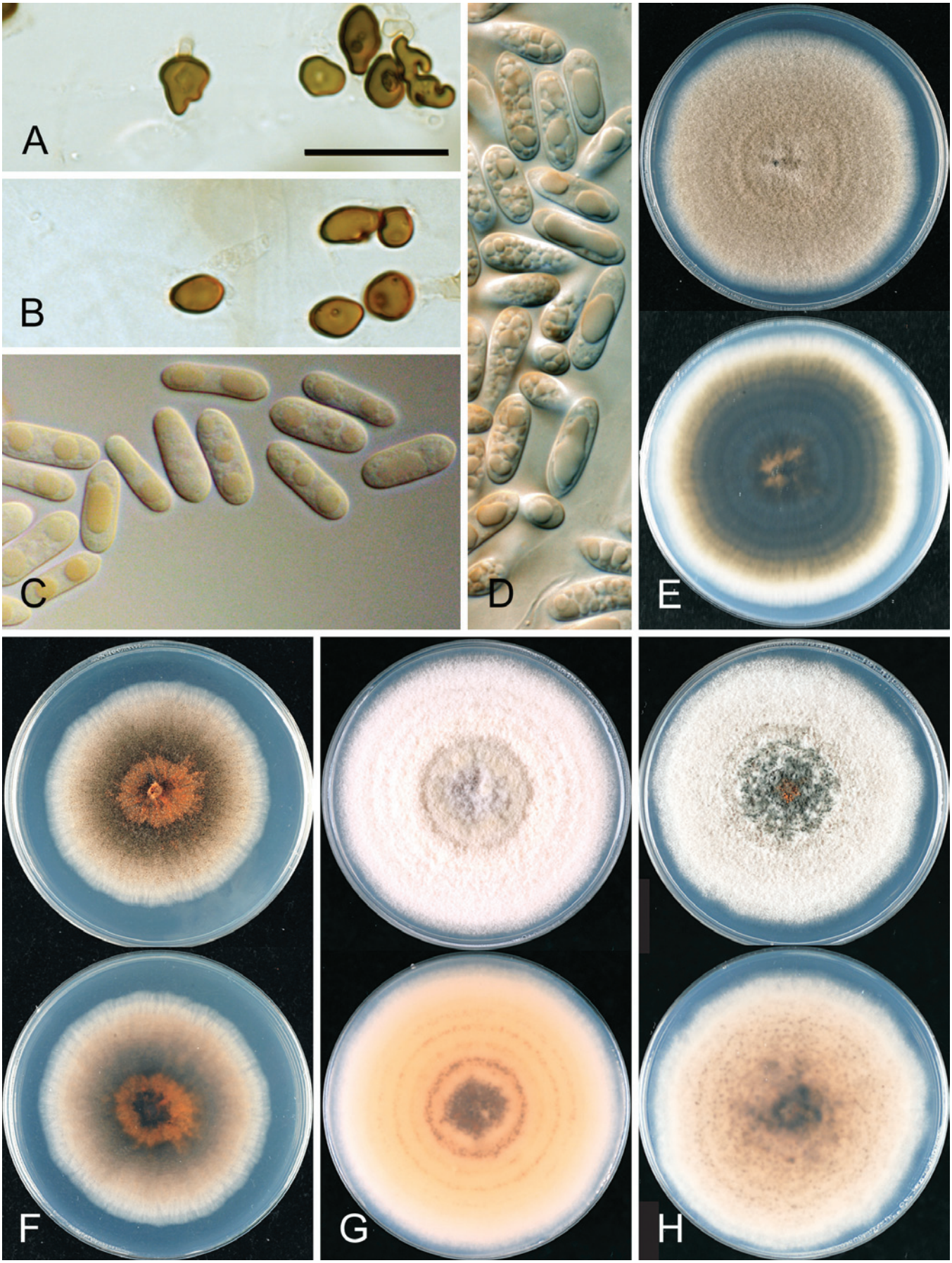


Fig. 31. *Colletotrichum queenslandicum*. A, C, E. ICMP 1778 – ex-epitype culture. B, F. ICMP 1780. D, G. ICMP 12564. H. ICMP 18705. A–B. Appressoria. C–D. Conidia. E–H. Cultures on PDA, 10 d growth from single conidia, from above and below. Scale bar A = 20 µm. Scale bar of A applies to A–D.

colony dark, a more or less continuous layer of acervulus-like structure with deep orange brown conidial masses and numerous setae; in reverse dark purplish-black near centre of colony, dark olivaceous near the margin. *Conidia* (10–)14–16.5(–20.5) × (4.5–)5.5–6(–7.5) µm (av. 15.3 × 5.8 µm, n = 24), highly variable in size and shape, subglobose to long-cylindric, apex usually broadly

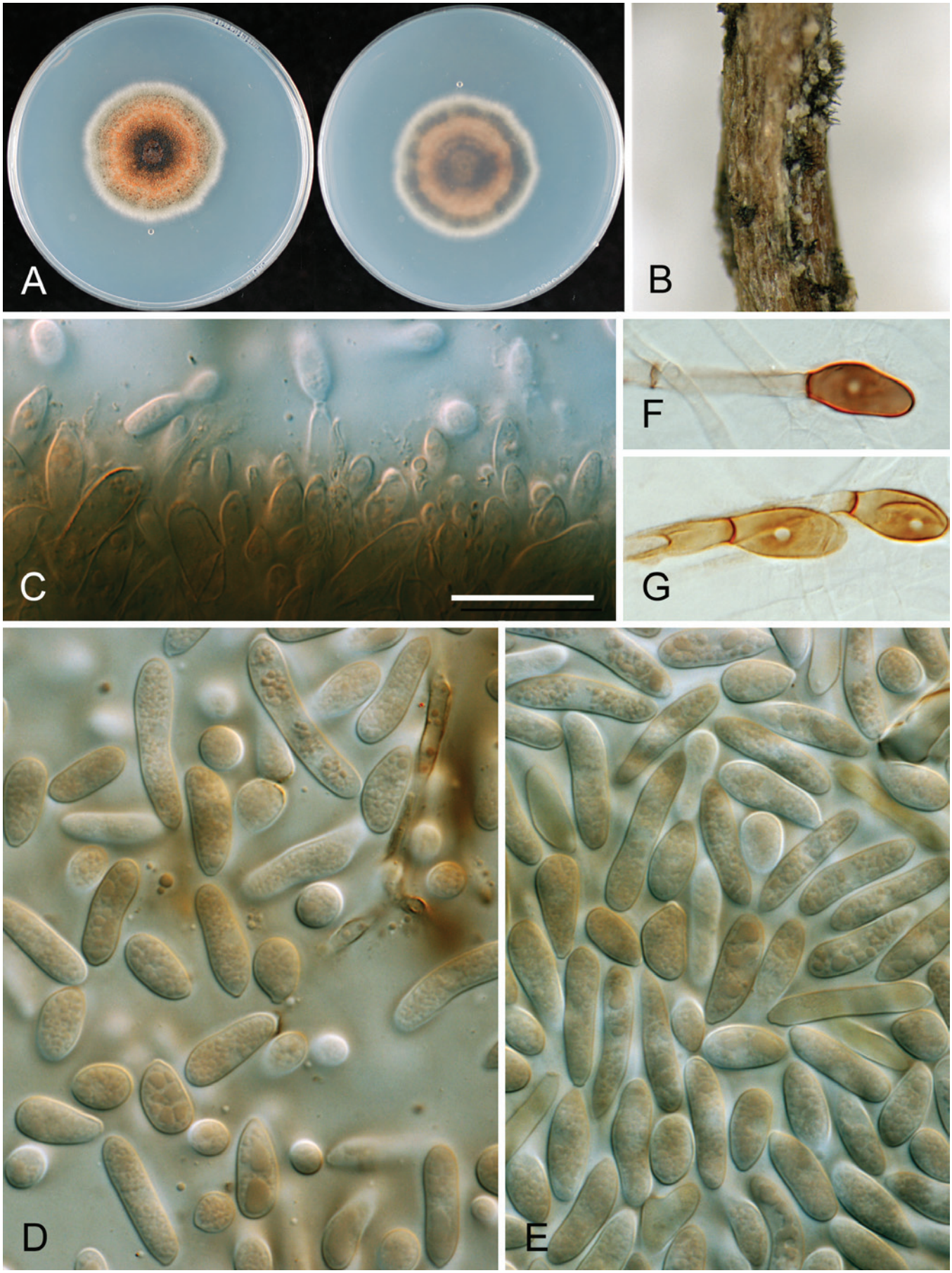


Fig. 32. *Colletotrichum salsolae*. A, C–H. ICMP 19051 – ex-holotype culture. B. BPI 878740 – holotype. A. Cultures on PDA, 10 d growth from single conidia, from above and below. B. Lesion on stem, dried type specimen. C. Conidiogenous cells. D–E. Conidia. F–G. Appressoria. Scale bars B = 1 mm, C = 20 µm. Scale bar of C applies to C–G.

rounded, small truncate scar at base. *Conidiogenous cells* 13–18 × 4–6.5 µm, cylindric to flask-shaped, tapering at apex to narrow, phialidic conidiogenous locus, wall at base often encrusted with dark brown material. *Appressoria* sparsely developed, cylindric to

elliptic, simple; many putatively partially developed appressoria, similar in shape to those with dark and thick walls and also with an appressorial pore, but the wall remains thin and only slightly pigmented. *Perithecia* not seen.

Geographic distribution and host range: Known from throughout the geographic range of *Salsola tragus* (Berner *et al.* 2009), reported in nature only from *Salsola* spp.

Genetic identification: ITS sequences of *C. salsolae* are very close to *C. alienum* and some *C. siamense* isolates. These species can be distinguished using TUB2 or GAPDH.

Notes: Isolates of *C. gloeosporioides* pathogenic to *Salsola tragus* were reported by Schwarczinger *et al.* (1998) and referred to as *C. gloeosporioides* "f. sp. *salsolae*" by Berner *et al.* (2009). Although mildly pathogenic to a wide range of hosts in glasshouse pathogenicity tests, this fungus causes severe disease only on *Salsola* spp. with the exception of *S. orientalis*, *S. soda*, and *S. vermiculata* (Berner *et al.* 2009).

Colletotrichum salsolae belongs to the Musae clade, and although genetically close to several other species, it is biologically and morphologically distinctive.

Other specimen examined: **Hungary**, additional isolate of strain selected as the holotype, recovered from inoculated *Glycine max* plants (MCA 2498 = CBS 119296 = ICMP 18693).

*** *Colletotrichum siamense*** Prihastuti, L. Cai & K.D. Hyde, Fungal Diversity 39: 98. 2009. Fig. 33.

= *Colletotrichum jasmini-sambac* Wikee, K.D. Hyde, L. Cai & McKenzie, Fungal Diversity 46: 174. 2011.

= *Colletotrichum hymenocallidis* Yan L. Yang, Zuo Y. Liu, K.D. Hyde & L. Cai, Fungal Diversity 39: 138. 2009.

Descriptions of this species are provided by Prihastuti *et al.* (2009), Wikee *et al.* (2011), and Yang *et al.* (2009).

Geographic distribution and host range: *Colletotrichum siamense* was originally described from coffee from Thailand, but our concept of this species is biologically and geographically diverse, found on many hosts across several tropical and subtropical regions.

Genetic identification: ITS sequences do not reliably separate *C. siamense* from *C. alienum*, *C. fructicola*, or *C. tropicale*. These species are best distinguished using CAL or TUB2.

Notes: Yang *et al.* (2009) and Wikee *et al.* (2011) discussed genetic and morphological differences between *C. siamense*, *C. jasmini-sambac*, and *C. hymenocallidis*. However, both studies used a limited set of isolates within the *C. gloeosporioides* complex, making interpretation of the genetic differences difficult. The morphological differences they described are commonly seen as within-species variation in other *Colletotrichum* spp. In our analysis, *C. siamense* is represented by 30 isolates from a wide range of hosts from several tropical regions, and forms a monophyletic clade that cannot be further subdivided genetically. Variation in cultural appearance is broad but in part this probably reflects the different conditions under which the isolates had been stored. Shape and size of appressoria, and the characteristically small conidia are similar in all isolates.

Based on matching translation elongation factor (TEF) and TUB2 sequences, isolates referred by Rojas *et al.* (2010) to *Colletotrichum* sp. indet. 2 also represent *C. siamense*. Note that TEF data was excluded from our phylogenetic analyses because the TEF gene tree was often incongruent with the trees from the other genes that we sequenced. For example, compare our isolate ICMP 17797 (GenBank GU174571) with isolates Rojas *et al.* (2010) cite as *Colletotrichum* sp. indet. 2, V1H1_1 (GenBank GU994297) and 7767 (GenBank GU994298).

The *C. siamense* protologue designates the holotype as MFLU 090230, but the culture derived from holotype as "BCC" with no specimen number. The ex-holotype culture is listed as BDP-I2 in Table 1 of Prihastuti *et al.* (2009) but not in the description of the species. Strain BDP-I2 was obtained from the authors (Prihastuti *et al.* 2009) for this study and deposited as ICMP 18578.

Specimens examined: **Australia**, New South Wales, Murwillumbah, on *Persea americana* fruit rot, coll. L. Coates 23695, 1 Apr. 1990 (ICMP 12567); New South Wales, Muswellbrook, on *Pistacia vera* (DAR 76934 = ICMP 18574); Queensland, Mt Tamborine, on *Persea americana* fruit rot, coll. L. Coates T10-1, 1 Sep. 1993 (ICMP 12565). **China**, Guangxi, Nanning, on *Hymenocallis americana* leaf spot, coll. Y.L. Yang CSSN2, 19 Jun. 2008 (**ex-holotype culture** of *C. hymenocallidis* − CBS 125378 = ICMP 18642); Guangxi Province, Nanning, on *H. americana* leaf, coll. Y.L. Yang CSSN3 (CBS 125379 = ICMP 18643). **Nigeria**, Ibadan, on *Dioscorea rotundata* seed, coll. M. Abang CgS2 (ICMP 18121); Ibadan, on *D. rotundata* seed, coll. M. Abang CgS6 (ICMP 18117); Ibadan, on *Commelina* sp. leaf, coll. M. Abang Cg29 (ICMP 18118). **South Africa**, on *Carica papaya* fruit, coll. L. Korsten PMS 1 (ICMP 18739). on *Persea americana*, coll. L. Korsten Cg227 (ICMP 18570); on *Persea americana*, coll. L. Korsten Cg231 (ICMP 18569). **Thailand**, Chiang Mai, Mae Lod Village, on *Coffea arabica* berries, coll. H. Prihastuti BPD-I2, 12 Dec. 2007 (**ex-holotype culture** of *C. siamense* – MFLU 090230 = ICMP 18578). Kanchanaburi, on *Capsicum annuum*, P.P. Than Ku4 (HKUCC 10884 = ICMP 18575); Nakhonpathon, on *C. annuum*, coll. P.P. Than Ku8 (HKUCC 10881 = ICMP 18618). **USA**, Florida, on *Vitis vinifera* leaf, coll. N. Peres ssgrape 10 (ICMP 18572); Florida, on *Fragaria* × *ananassa* crown, coll. N. Peres strawberry 6 (ICMP 18571); Florida, on *V. vinifera* leaf, coll. N. Peres DI-grape-6 (ICMP 18573); North Carolina, Wilkes County, on *Malus domestica* fruit, coll. T. Sutton LD Cg12 2001 (ICMP 17795); North Carolina, Johnston County, on *M. domestica* fruit, coll. T. Sutton GD 8 2002 (ICMP 17791); North Carolina, Johnston County, on *M. domestica* fruit, coll. T. Sutton GD 7 2002 (ICMP 17797); Alabama, on *M. domestica* fruit, coll. T. Sutton AL 1 2001 (ICMP 17785). **Vietnam**, Cu Chi District, Trung An Ward, on living leaves of *Jasminium sambac*, Jan. 2009, coll. Hoa Nguyen Thi LLTA–01 (**ex-holotype culture** of *C. jasmini-sambac* – CBS 130420 = ICMP 19118).

*** *Colletotrichum theobromicola*** Delacr., Bull. Soc. Mycol. France. 31: 191. 1905. Fig. 34.

= *Colletotrichum fragariae* A.N. Brooks, Phytopathology 21: 113. 1931.

= *Colletotrichum gloeosporioides* f. *stylosanthis* Munaut, Mycol. Res. 106: 591. 2002.

= *Colletotrichum gloeosporioides* f. *stylosanthis* "f. sp. *stylosanthis*" (Munaut *et al.* 2002).

= *Colletotrichum gloeosporioides* f. *stylosanthis* "f. sp. *guianensis*" (Munaut *et al.* 2002).

A modern description of this species is provided by Rojas *et al.* (2010).

Geographic distribution and host range: Broadly distributed in tropical and subtropical regions on a wide range of hosts.

Genetic identification: ITS sequences distinguish *C. theobromicola* from all other species.

Notes: The ex-epitype culture of *Colletotrichum fragariae*, the ex-neotype culture of *C. theobromicola*, and the ex-holotype culture of *C. gloeosporioides* f. *stylosanthis*, selected by Buddie *et al.* (1999), Rojas *et al.* (2010), and Munaut *et al.* (2002) respectively, belong in a clade that we accept genetically as a single species. Also in this clade are authentic isolates of C. *gloeosporioides* f. *stylosanthis* "f. sp. *stylosanthis*" and *C. gloeosporioides* f. *stylosanthis* "f. sp. *guianensis*" (but see notes under *C. gloeosporioides* f. *stylosanthis*).

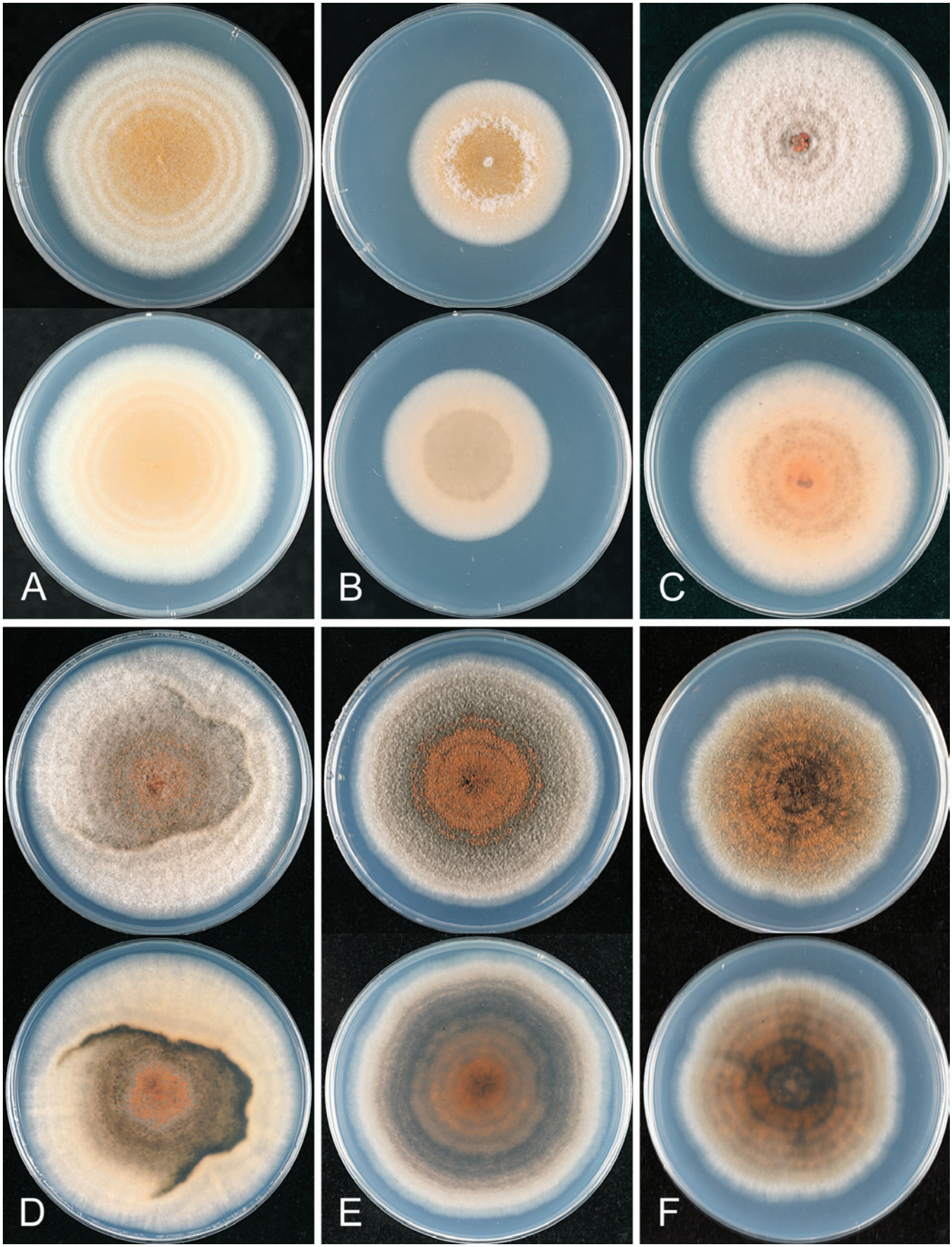


Fig. 33. *Colletotrichum siamense*. A. ICMP 18642 (ex CBS 125378 – ex-holotype culture of *C. hymenocallidis*). B. ICMP 18578 (ex MFLU 090230 – ex-holotype culture of *C. siamense*). C. ICMP 12565. D. ICMP 18574 (ex DAR 76934). E. ICMP 18618 (ex HKUCC 10881). F. ICMP 18121. Cultures on PDA, 10 d growth from single conidia, from above and below.

Colletotrichum theobromicola as accepted here contains several putatively specialised pathogens, including the pathogen of strawberry runners described by Brooks (1931) as *C. fragariae*, and the pathogens of *Stylosanthes* referred to as *C. gloeosporioides* f. *stylosanthis* (Munaut *et al.* 2002). Future studies may show that the species should be segregated based on their pathogenicity

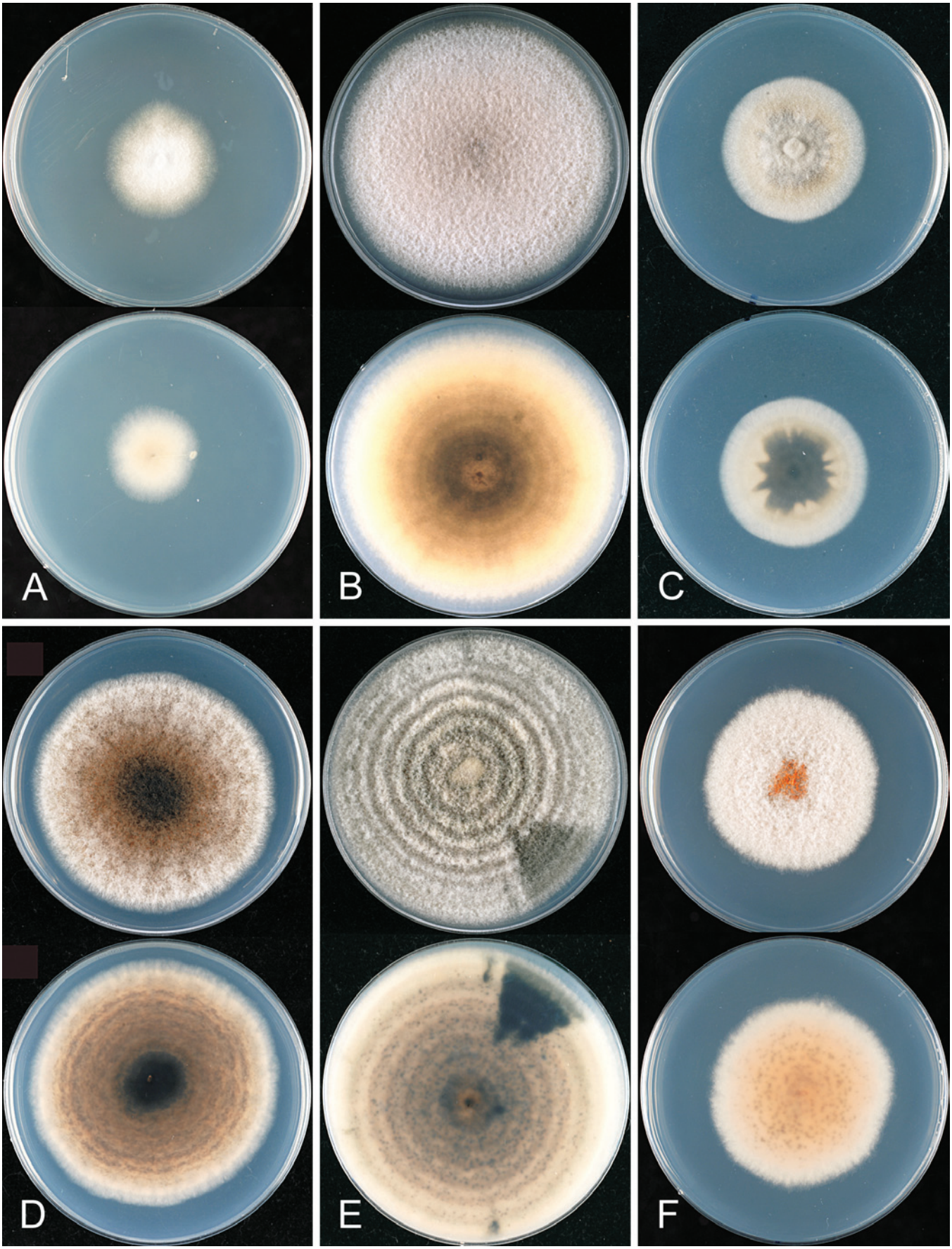


Fig. 34. *Colletotrichum theobromicola*. A. ICMP 17957 (ex MUCL 42294 – ex-holotype culture of *C. gloeosporioides* f. *stylosanthis*). B. ICMP 17927 (ex CBS 142.31 – ex-epitype culture of *C. fragariae*). C. ICMP 17958 (ex MUCL 42295). D. ICMP 17895. E. ICMP 18567. F. ICMP 18566. Cultures on PDA, 10 d growth from single conidia, from above and below.

to specific hosts. See also notes under *C. fragariae* and *C. gloeosporioides* f. *stylosanthis.*

Munaut *et al.* (2002) distinguished *C. gloeosporioides* f. *stylosanthis* from isolates they considered to represent *C.*

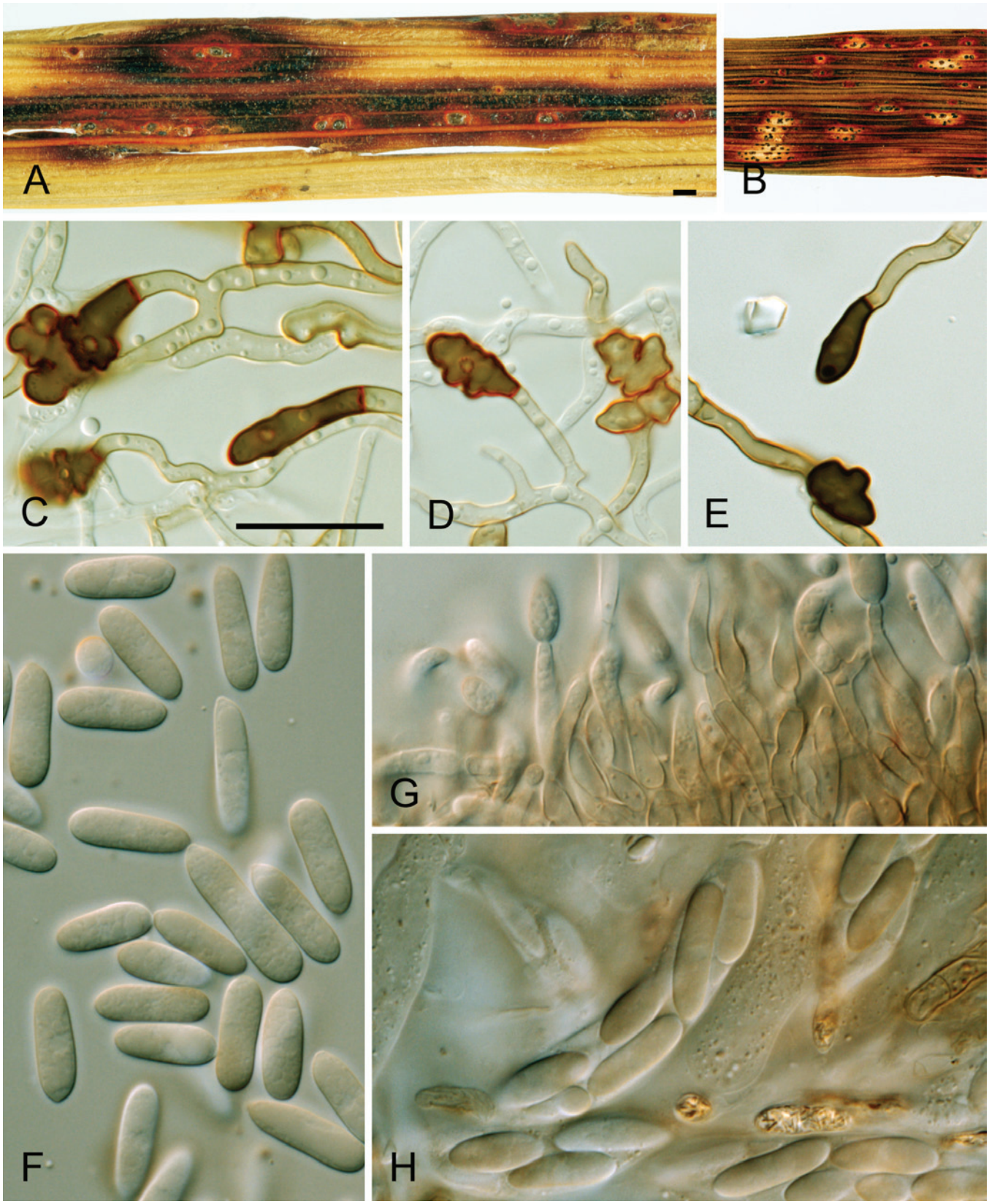


Fig. 35. *Colletotrichum ti*. A. PDD 24881 – holotype. B. PDD 30206. C, D, F, H. ICMP 4832 – ex-holotype culture. E, G. ICMP 19444. A–B. Lesions on dried herbarium specimens. C–E. Appressoria. F. Conidia. G. Conidiogenous cells. H. Ascospores. Scale bars A = 1 mm, C = 20 µm. Scale bar of A applies to A–B, scale bar of C applies to C–H.

gloeosporioides f. *gloeosporioides* because of 2 additional C's at positions 93 and 94 in the ITS1 region, giving a string of 7 C's at this position. This characteristic feature of the ITS-1 is found also in the ex-neotype isolate of *C. theobromicola*, the ex-epitype isolate of *C. fragariae* and all other isolates of *C. theobromicola*, although a few isolates have 3 additional C's rather than 2. None of the other isolates that we sampled from the *C. gloeosporioides* species complex have this characteristic string of C's.

Rojas *et al.* (2010) provide a description for their concept of *C. theobromicola*, MacKenzie *et al.* (2008) for *C. fragariae*, and Irwin & Cameron (1978) for C. *gloeosporioides* f. *stylosanthis* "f. sp. *stylosanthis*" (as *C. gloeosporioides* Type A) and *C. gloeosporioides*

f. *stylosanthis* "f. sp. *guianensis*" (as *C. gloeosporioides* Type B). In cultural appearance the isolates we accept in this species are variable, from the very dark ex-neotype isolate of *C. theobromicola* to the slow-growing, pale coloured *C. gloeosporioides* f. *stylosanthis* "f. sp. *guianensis*". None of the isolates that we examined formed perithecia in culture. All had conidia tapering slightly towards each end, this more pronounced towards the base, matching the description of *C. fragariae* by Gunnell & Gubler (1992), who regarded the conidial shape as distinctive for the species. Some of the isolates studied by Gunnell & Gubler (1992) were included in the study of MacKenzie *et al.* (2008), their genetic concept of *C. fragariae* matching ours.

See also notes under *C. fragariae* and *C. gloeosporioides* f. *stylosanthis*.

Specimens examined: **Australia**, Queensland, Townsville, on *Stylosanthes viscosa*, coll. J.A.G. Irwin 21365 (HM335), 1976 (**ex-holotype** culture of *C. gloeosporioides* f. *stylosanthis* − MUCL 42294 = ICMP 17957); Samford, on *Stylosanthes guianensis*, coll. J.A.G. Irwin 21398 (HM336), 1979 (MUCL 42295 = ICMP 17958); New South Wales, *Olea europaea* fruit, coll. V. Sergeeva UWS 128, 21 Apr. 2008 (ICMP 18566); New South Wales, *O. europaea* fruit, coll. V. Sergeeva UWS 130, 21 Apr. 2008 (ICMP 18565); New South Wales, *O. europaea* fruit, coll. V. Sergeeva UWS 98, 8 Apr. 2008 (ICMP 18567). **Israel**, on *Limonium* sp. leaf lesion, coll. S. Freeman P1 (cited in Maymon *et al.* 2006) (ICMP 18576). **Mexico**, on *Annona diversifolia*, coll. R. Villanueva-Aroe Gro-7, Jul. 2003 (ICMP 17895). **New Zealand**, Kerikeri, on *Acca sellowiana*, coll. M.A. Manning MM317, 1 Feb. 2004 (ICMP 15445). **Panama**, Chiriqui Province, San Vicente, on *Theobroma cacao* pod lesion, coll. E.J. Rojas ER08-9, Jan. 2008 (CBS 125393 = ICMP 18650); Chiriqui Province, Escobal, on *T. cacao* leaf spot, coll. E.J. Rojas GJS 08-50, Jan. 2008 (**ex-neotype culture** of *C. theobromicola* − CBS 124945 = ICMP 18649). **USA**, Florida, Dover, Plant City, on *Fragaria* × *ananassa*, coll. S. MacKenzie 326-1, 1988 (ICMP 17099); Florida, Lake Alfred, on *Quercus* sp. leaf, coll. S. MacKenzie LA-oak-13, 2002 (ICMP 17100); Louisiana, on *F. vesca*, 1985 (IMI 348152 = ICMP 17814); Florida, on *F.* × *ananassa*, coll. A.N. Brooks, 1931 (**ex-epitype culture** of *C. fragariae* − CBS 142.31 = ICMP 17927).

*** *Colletotrichum ti*** B. Weir & P.R. Johnst., **sp. nov.** MycoBank MB563594. Figs 35, 36.

Etymology: Based on the Maori name for *Cordyline australis*, tī.

Holotype: **New Zealand**, Taupo, on *Cordyline* sp., coll. J.M. Dingley 65187, Sep. 1965, PDD 24881; ex-holotype culture ICMP 4832.

Leaf spots oblong to elliptic in shape, up to about 1 × 2 mm, sometimes coalescing when close together on a leaf, pale grey and necrotic in the centre with a reddish margin; acervuli numerous, base pale to dark grey, with scattered, dark brown setae about 50–80 µm long. *Perithecia* not seen on infected leaves. Freshly isolated colonies on Difco PDA 50–55 mm diam after 10 d, margin slightly irregular and feathery, aerial mycelium lacking from ex-holotype culture, when present fine, cottony, pale grey, surface of colony dark towards the centre, pale pinkish orange (7A6) towards margin, conidia forming over all parts of culture, mostly not associated with well differentiated acervuli, setae not observed; in reverse purple (12E3) near centre, orange outside, sometimes with concentric rings of grey pigment. *Conidiogenous cells* cylindric, mostly 15–25 × 3.5–4.5 µm, towards centre of colony arranged in closely packed palisade, towards margin the conidiophores with a much looser structure, irregularly branched, conidiogenous loci at apex and often also at septa. *Conidia* (11.5–)14–17.5(–23.5) × (4–)5–5.5(–7.5) µm (av. 16 × 5.2 µm, n = 53), cylindric, ends broadly rounded, sometimes tapering towards basal end. *Appressoria* often narrow-cylindric, often tapering towards apex, sometimes irregularly lobed. *Perithecia* developing in small numbers in culture after about 4 wk, solitary, scattered across plate, dark-walled, globose with well-developed, tapering ostiolar neck. *Asci* (60–)65–75(–78) × (10–) 11(–12) µm (av. 69.6 × 11 µm, n = 5), cylindric to subfusoid, 8–spored. *Ascospores* (14.5–)15.5–16.5(–19) × (4.5–)5–5.5(–6) µm (av. 15.9 × 5.2 µm, n=18), broad-cylindric, ends broadly rounded, not tapering to the ends, in side view mostly flat on one side, often slightly curved.

Geographic distribution and host range: Known only from *Cordyline* spp. from New Zealand.

Genetic identification: ITS sequences do not distinguish *C. ti* from *C. aotearoa*. The two species can be distinguished using TUB2 or GAPDH.

Notes: A member of the Kahawae clade, this fungus causes a leaf spot of *Cordyline* spp. in New Zealand. It is genetically distinct from *C. cordylinicola*, described from *Cordyline fruticosa* from Thailand. Based on the published description of *C. cordylinicola* (Phoulivong *et al.* 2011) the two fungi are morphologically similar. Inoculation tests using culture ICMP 5285 when freshly isolated (J.M. Dingley, unpublished data), showed it to be pathogenic to *Cordyline australis*, forming spots on leaves 2 wk after inoculation, but causing no symptoms on apple, even after wounding.

Although only four of the specimens examined have been compared genetically, all of the cited specimens examined match in terms of associated symptoms and conidial size and shape. A specimen from *Cordyline banksii* (PDD 78360) has narrower conidia, forms perithecia on the infected leaves, and perhaps represents a different species. Specimens accepted here as *C. ti* were referred to *Glomerella cingulata* by Laundon (1972).

The appearance in culture varies between isolates. The J.M. Dingley cultures, first isolated in the mid-1960's, have dense, felted aerial mycelium and limited conidial production; one has a much slower growth rate than the more recent collections.

Other specimens examined: **New Zealand**, Auckland, on *Cordyline australis*, coll. J.M. Dingley 6653, Mar. 1966 (PDD 30206; ICMP 5285); Taranaki, New Plymouth, Duncan and Davies Nursery, on *C. australis* × *C. banksii* leaf spots, coll. G.F. Laundon LEV 3343, 26 May 1969 (PDD 50634); Taranaki, New Plymouth, Duncan and Davies Nursery, on *C australis* × *C. banksii* leaf spots, coll. G.F. Laundon, 26 May 1969 (PDD 26775); Waikato, Cambridge, Anton Nursery, on *C. australis* leaf spots, coll. L.A. Houghton, 23 Jul. 1992 (PDD 61219; ICMP 19444).

*** *Colletotrichum tropicale*** E.I. Rojas, S.A. Rehner & Samuels, Mycologia 102: 1331. 2010. Fig. 37.

Rojas *et al.* (2010) provide a description.

Geographic distribution and host range: Rojas *et al.* (2010) noted that *C. tropicale* has been isolated from a wide range of hosts in forests in tropical America, from rotting fruit as well as leaf endophytes. We include also an isolate from tropical Japan, from *Litchi chinensis* leaves.

Genetic identification: ITS sequences do not separate *C. tropicale* from some *C. siamense* or some *C. queenslandicum* isolates. *Colletotrichum tropicale* is best distinguished using TUB2, CHS-1, GS, or SOD2.

Notes: *Colletotrichum tropicale* is genetically close to *C. siamense* and the two species share a number of morphological features; slow growth in culture, short and broad conidia with broadly rounded ends and often slightly constricted near the centre, and simple appressoria.

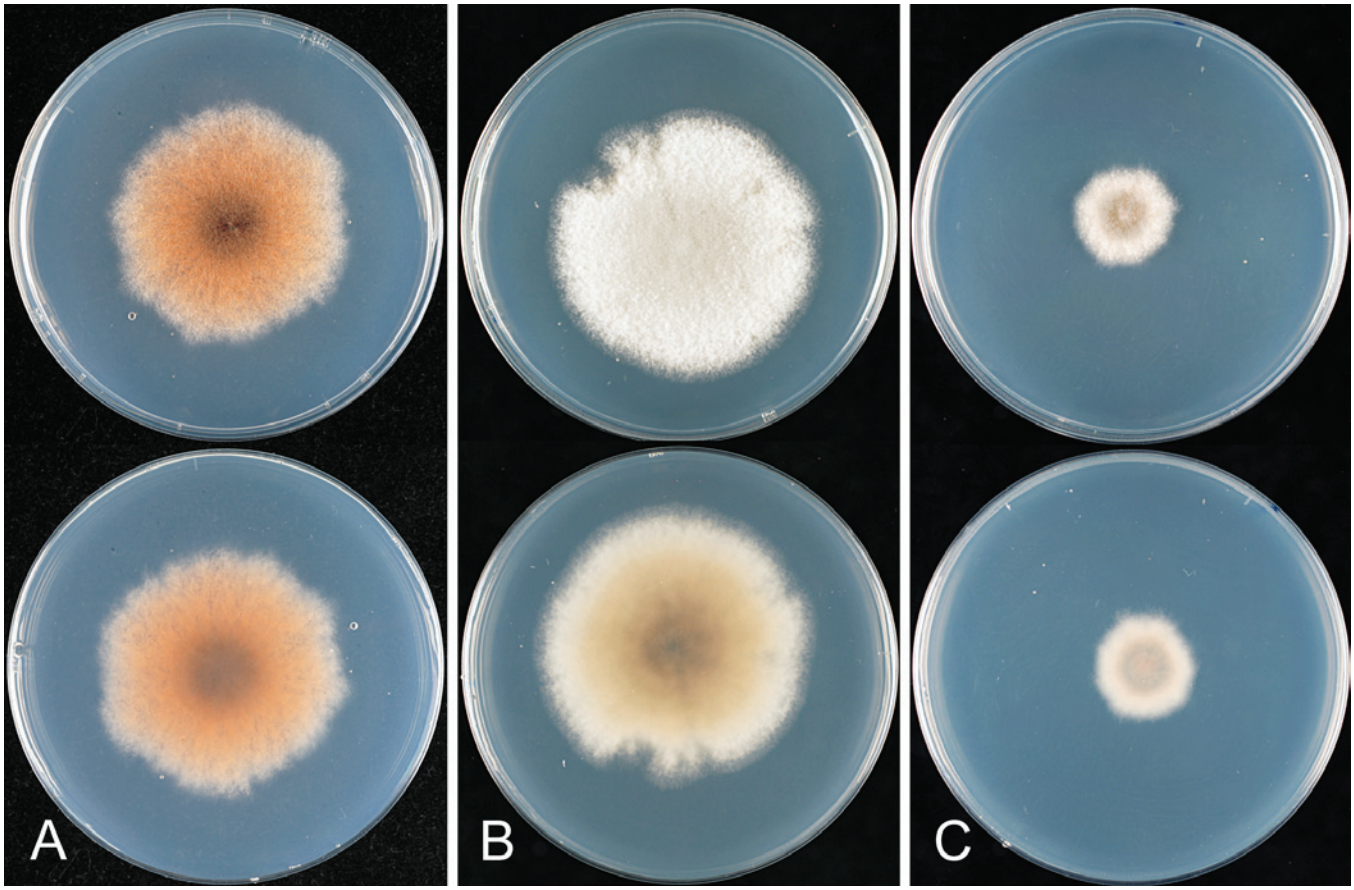


Fig. 36. *Colletotrichum ti*. A. ICMP 19444. B. ICMP 4832 – ex-holotype culture. C. ICMP 5285. Cultures on PDA, 10 d growth from single conidia, from above and below.

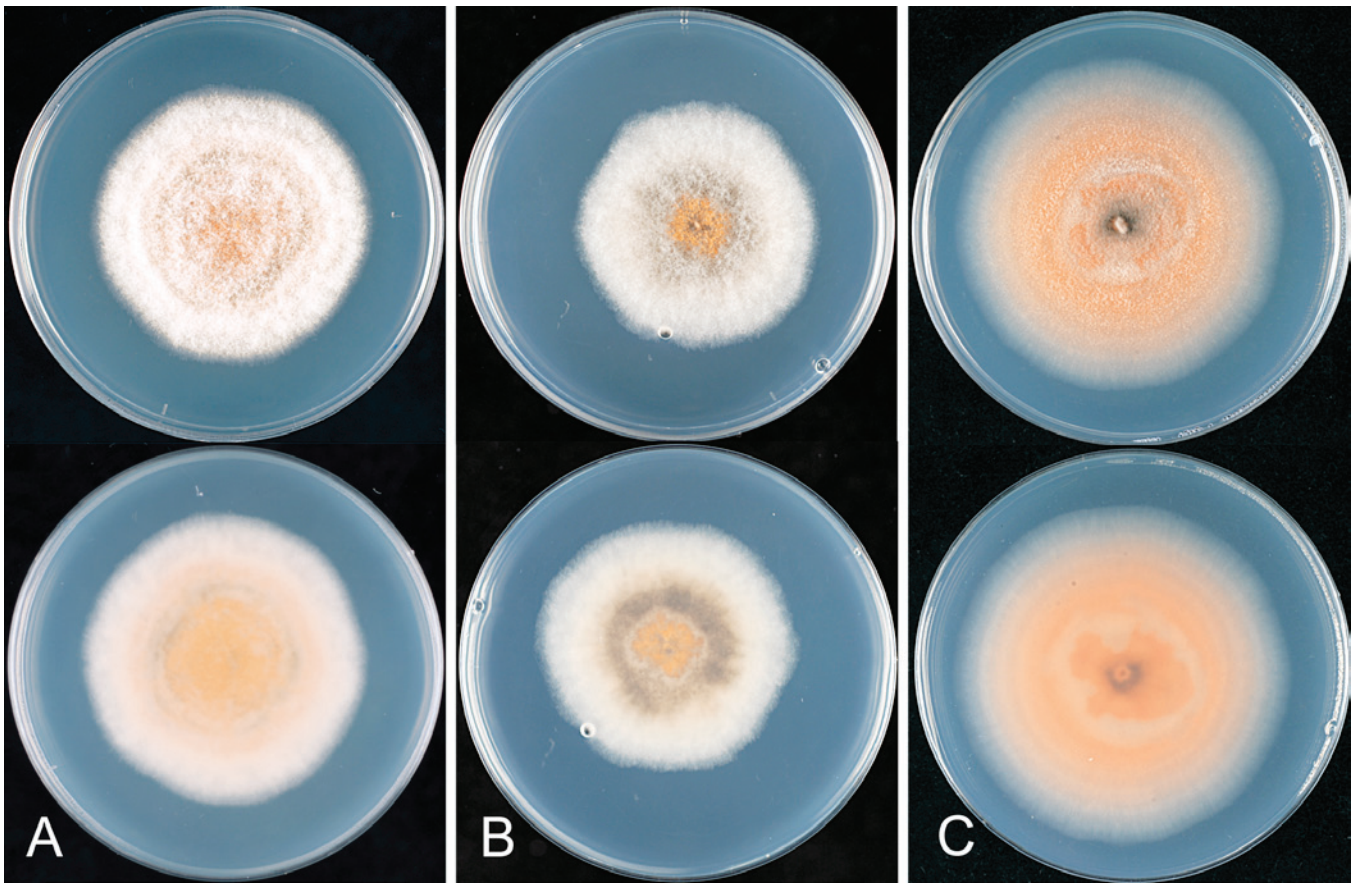


Fig. 37. *Colletotrichum tropicale*. A. ICMP 18653 (ex CBS 124949 – ex-holotype culture). B. ICMP 18651 (ex CBS 124943). C. ICMP 18672 (ex MAFF 239933). Cultures on PDA, 10 d growth from single conidia, from above and below.

Specimens examined: **Japan**, Okinawa, on *Litchi chinensis* leaf (MAFF 239933 = ICMP 18672). **Panama**, Barro Colardo Monument, on *Theobroma cacao* leaf, coll. E.I. Rojas, L.C. Mejía, Z. Maynard 5101, 2008 (**ex-holotype culture** – CBS 124949 = ICMP 18653); Escobal, Chiriqui, on *Annona muricata* fruit rot, coll. E.I. Rojas GJS 08-42 (CBS 124943 = ICMP 18651).

*** *Colletotrichum xanthorrhoeae*** R.G. Shivas, Bathgate & Podger, Mycol. Res. 102: 280. 1998. Fig. 38.

Shivas *et al.* (1998) provide a description. One of the isolates we examined (ICMP 17820) formed fertile perithecia in culture, a feature not mentioned in the original description. *Perithecia* are dark-walled, globose with a prominent, narrow neck, wall comprising several layers of pseudoparenchymatous cells 8–15 µm diam, with several layers of densely packed hyphae outside this. *Asci* 75–100 × 10–12 µm, 8-spored. *Ascospores* (17–)18.5–20(–22) × (5–)5.5–6 µm (av. 19.4 × 5.6 µm, n = 24), more or less elliptic, tapering to narrow, rounded ends, in side view flattened on one side, but generally not curved.

Genetic identification: ITS sequences distinguish *C. xanthorrhoeae* from all other species.

Notes: This pathogen of *Xanthorrhoea* has a distinctive morphology, with a very slow growth rate in culture and large conidia which taper towards the basal end. The ascospore shape is distinct to that of most taxa within the *C. gloeosporioides* group, which typically have bent or curved ascospores.

Specimens examined: **Australia**, Western Australia, Melville, on *Xanthorrhoea preissii* leaf spots, coll. F.D. Podger, Jan. 1994 (**ex-holotype culture** − BRIP 45094 = ICMP 17903 = CBS 127831); Queensland, Cunningham's Gap, Main Ranges National Park, on *Xanthorrhoea* sp. leaf spot (IMI 350817a = ICMP 17820).

DISCUSSION

The species that we accept in the *Colletotrichum gloeosporioides* species complex together form a strongly supported clade in the *Colletotrichum* ITS gene tree (fig. 1 in Cannon *et al.* 2012, this issue). All species are micro-morphologically typical of *C. gloeosporioides sensu* von Arx (1970) and Sutton (1992). However, morphology alone cannot unequivocally place an isolate in this complex, making the ITS particularly important for identification at the species complex level in *Colletotrichum*. For example, members of the *C. boninense* species complex (Damm *et al.* 2012b, this issue) and *C. cliviae* (Yang *et al.* 2009) are micro-morphologically similar to species in the *C. gloeosporioides* complex but genetically distinct (Cannon *et al.* 2012, this issue). The utility of ITS sequences is enhanced by their strong representation in GenBank, but this can also be a problem. Nilsson *et al.* (2006) summarised the frequency of inaccurately annotated data in GenBank. The diversity of taxonomic concepts around the name *C. gloeosporioides* makes this a particular problem. This is illustrated by the phylogeny presented by Hyde *et al.* (2010), based on GenBank accessions of ITS sequences identified as *C. gloeosporioides* and *Glomerella cingulata*, that shows the taxa represented belong to many species in different *Colletotrichum* species complexes. See notes under *C. boehmeriae*, *C. crassipes*, and *C. kahawae* subsp. *kahawae* for specific examples of misidentified GenBank accessions.

The species we accept are based on a phylogenetic species concept, all species forming strongly supported, monophyletic clades within our multigene phylogenies. However, not all terminal clades are recognised as named species. In most cases any well supported, within-species phylogenetic structure evident in the multi-gene phylogeny is not resolved consistently in all gene trees. This lack of congruence between gene trees is a signal that the diversity being sampled is below the species level, according to the logic of the genealogical concordance phylogenetic species recognition (GCPSR) concept (Taylor *et al*. 2000). Although the concatenation of gene sequences is a convenient way to present multigene data, it masks discordance between individual gene phylogenies. An alternative method, using a species-tree approach (Figs 3, 4B, 5B) combines multi-gene data from multiple isolates hypothesised to represent a single species, so that the evolutionary history of the species rather than that of individual isolates is estimated. Fig. 3, shows the results of such an analysis for the *C. gloeosporioides* complex, Figs 4B and 5B show relationships within the Musae and Kahawae clades respectively, at an expanded scale. Posterior probabilities for some of the speciation events are low, particularly within the Musae and Kahawae clades. This may be because although the species-trees algorithms account for incomplete lineage sorting (Heled & Drummond 2010, Chung & Ané 2011), most do not compensate for horizontal gene transfer, reassortment, or introgression. Hybridisation could also result in discordant gene phylogenies. Hybrids are known in the *C. acutatum* complex, *e.g. Glomerella acutata*, a hybrid formed by crossing *C. acutatum* and *C. fioriniae* strains in the laboratory, and a putative hybrid strain between the same two species that had been collected from terminal crook disease on *Pinus* in New Zealand, where both species occur in nature (Damm *et al*. 2012a, this issue). Hybrids also form in the *C. gloeosporioides* complex, *e.g.* the *Carya* and *Aeschynomene* populations discussed by Cisar *et al.* (1994), more or less genetically equivalent to our species within the *C. gloeosporioides* complex.

Our taxonomic conclusions are based, of necessity, on the limited set of genes sampled. Potentially more powerful genes, such as ApMAT and Apn25L (Silva *et al*. 2012a) may provide finer resolution within the species-level clades that we recognise. However, even with these potentially more informative genes, the low levels of genetic divergence across the *C. gloeosporioides* complex may always provide a technical challenge (Silva *et al*. 2012a). The low level of diversity within this species complex is reflected by the branch lengths in fig. 2, Cannon *et al*. (2012, this volume), and is especially true across the Musae clade, where average pairwise identity between all isolates treated in our 5 gene alignment is 98.6 %. Pairwise identity between isolates of *C. siamense* and *C. theobromicola*, two species showing strong within-species phylogenetic structure, are 99.4 % and 99.6% respectively. This suggests that the species recognised within the *C. gloeosporioides* complex are very recently evolved and Silva *et al*. (2012b) provide data supporting this. Their hypothesis of recent evolution of host-specialised *Colletotrichum* populations from more generalist fungi was also invoked in relation to the *C. acutatum* complex by Lardner *et al*. (1999) using the "episodic selection" framework of Brasier (1995).

Several of the species we accept contain isolates with divergent lifestyles, for example *C. aotearoa*, *C. clidemiae*, *C. kahawae*, and *C. theobromicola*. Each of these species includes isolates capable of causing specific diseases. In the case of *C. kahawae*, recent pathogenicity tests have shown that only some isolates are able to cause coffee berry disease (Silva *et al.* 2012a, Silva & Weir, unpubl. data) and that these isolates can be distinguished using GS sequences (this study), Apn25L and MAT1-2-1 (Silva *et al*. 2012b). Because of the well understood pathogenicity of isolates within

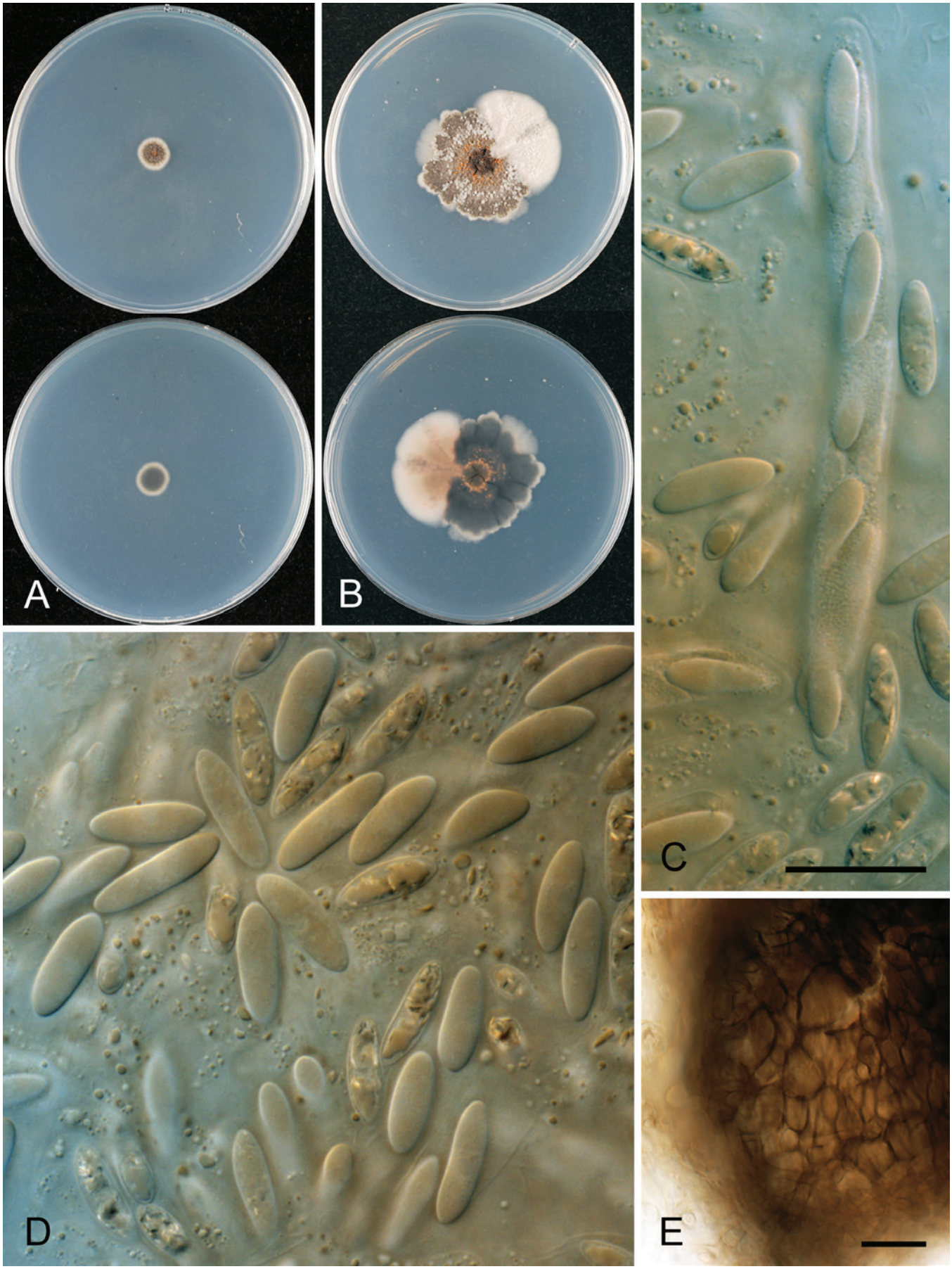


Fig. 38. *Colletotrichum xanthorrhoeae*. ICMP 17903 (ex BRIP 45094 – ex-holotype culture). A. Cultures on PDA, 10 d growth from single conidia, from above and below. B. Culture on PDA at 4 wk showing sectoring with variation in pigmentation and growth form. C–D. Asci and ascospores. E. Perithecial wall in squash mount. Scale bar C = 20 µm. Scale bar of C applies to C–E.

C. kahawae, the biosecurity importance of coffee berry disease, and the ability to distinguish the disease-causing isolates using carefully selected genetic markers, we recognise the disease-causing isolates taxonomically at the subspecific level. Future study of the comparative pathogenicity of isolates within *C. aotearoa*, *C. clidemiae*, and *C. theobromicola* may reveal genetically distinct, host-specialised pathogenic populations within these species that future workers may also choose to recognise taxonomically.

The classification we accept here is deliberately taxonomically conservative, minimising nomenclatural changes. This reflects continuing uncertainty about sensible species limits within the *C. gloeosporioides* complex that relate to low levels of genetic divergence across the complex, gene selection, isolate selection, and a lack of understanding of the mechanisms driving species and population divergence amongst these fungi. For example, the two haplotype subgroups of *C. fructicola* are not distinguished taxonomically because collectively they form a monophyletic clade, both subgroups include sets of isolates with similar geographic and host diversity, and there is no practical need to distinguish them taxonomically.

Molecular tools are increasingly being used for day-to-day identification by biosecurity officers and plant pathology researchers, providing a need for both a taxonomy that closely reflects groups that are resolved genetically, as well as simple and reliable protocols for identifying those taxa. The internal transcribed spacer region (ITS) has been proposed as the official fungal barcoding gene (Schoch *et al.* 2012). Although ITS is useful at the species complex level, it does a poor job of resolving species within the *C. gloeosporioides* complex, resolving only 10 of 22 accepted species. This reflects the low number of base changes in the ITS region across the *C. gloeosporioides* complex; species often distinguished by only one or two base changes. In some cases, chance variation in the ITS sequence within or between species means that some species cannot be distinguished (Fig. 6). Examples of taxa with identical ITS sequences include *C. clidemiae, C. tropicale*, *C. ti* and some *C. siamense* isolates; *C. fructicola* and some *C. siamense* isolates; and *C. alienum*, *C. aenigma* and some *C. siamense* isolates.

Protein-coding genes and their introns often have more variation than ITS, and the need for secondary barcodes based on these kinds of genes has been discussed in relation to some groups of fungi (Fitzpatrick *et al*. 2006, Aguileta *et al*. 2008, Weir & Johnston 2011). Ideally, one of the seven protein coding genes that were used in this study could be proposed as a secondary barcode to obtain an accurate identification of species within the *C. gloeosporioides* complex. A preliminary analysis of the genes performance as barcodes was conducted as part of Cai *et al*. (2009) with GAPDH, CAL, and ACT performing well, but CHS-1, ITS, and TEF (EF1α) poorly. However, the analysis (Cai *et al*. 2009) included only five species within the *C. gloeosporioides* complex, the Musae and Kahawae clades being treated at the level of species. With the final classification presented here, none of the genes we analysed provides an effective barcode ont its own across the entire complex. Of the single genes, TUB2, GS, and GAPDH are amongst the most effective at distinguishing species. However, *C. clidemiae* is polyphyletic in the TUB2 gene tree and GS sequences are needed to distinguish *C. fructicola* and *C. alienum*. With GS, *C. aotearoa*, *C. kahawae* subsp. *ciggaro*, and *C. siamense* are paraphyletic. GAPDH is the easiest of all the genes tested to amplify and sequence, however when using this gene GS sequences are needed to distinguish *C. fructicola* from *C. alienum* and *C. aeschynomenes* from *C. siamense*, and *C. tropicale* is paraphyletic. In the species descriptions we provide notes on which genes are the best for genetic identifications, and in Table 4 these are summarised for all species and genes. For species represented by a single or only a few isolates the species boundaries may not be accurate, we recommend two protein-coding genes in addition to ITS for sequence-based identifications. A meta-analysis of DNA barcodes across the whole genus will be required to find the combination of genes that are effective for all species of the genus that distinguish all *Colletotrichum* species.

Several studies have shown that cultural morphology can be useful for grouping isolates when they are sampled at a local or regional level (*e.g.* Johnston & Jones 1997, Prihastuti *et al.* 2009). However, our experience is that such groups often break down when the geographic sample within a clade is extended to a global scale. Many of the species we accept have few or no diagnostic morphological or cultural features that can be consistently and reliably used to identify them. Our morphological examinations were confined to cultures on Difco PDA agar plates, and we will have missed any features that develop solely in association with plant material. In addition, the cultures we used have been sourced from different labs and collections from around the world, many with no information on storage history. Storage history and method has a major impact on the appearance of *Colletotrichum* in culture. Cultures can become "stale" during storage, losing the ability to produce pigments, the aerial mycelium often becoming very dense and felted, and losing the ability to form well-differentiated acervuli, conidia, or perithecia. In some clades, even freshly isolated cultures are highly variable, forming distinct sectors with differences in the production of pigment, aerial mycelium, acervuli, and conidia. Some isolates form two very different cultural types from single conidia or ascospores derived from colonies themselves started from single ascospores. Figure 27F shows single ascospore cultures from an isolate of *C. kahawae* subsp. *ciggaro*. One has the typical appearance of cultures of this fungus isolated from the field. The other, with a uniform, dense layer of conidia across the colony surface without well differentiated acervuli and more or less no aerial mycelium, is common from single ascospore isolates in culture, but rarely found in cultures isolated directly from the field. This kind of variation, and that revealed from sectoring during colony growth, makes morphological variation difficult to interpret for accurate identification.

Many of the species recognised in this work remain poorly understood in terms of their pathogenicity and host preference. This in part reflects a lack of certainty about the biological relationship between the fungi and the plants from which they were isolated. Species that are pathogenic on one host can also be isolated from others following opportunistic colonisation of senescing tissue, such as the *C. salicis* example discussed by Johnston (2000, as *Glomerella miyabeana*). The multiple *Colletotrichum* spp. associated with a single host are likely to have a variety of life styles: primary pathogens of healthy tissue, species with the ability to invade and cause minor disease when the host plant is under stress, species that develop latent infections and fruit only following senescence of the host tissue or ripening of host fruit and endophytic species that sporulate only following host tissue death. The combination of this range of distinct life styles, the fact that several *Colletotrichum* spp. may become established on a single host, and the ability of most of these species to also establish on a range of other hosts, has been a large part of the confusion surrounding species limits within *Colletotrichum*.

In some cases, apparently clear differences in pathogenicity of isolates in the *C. gloeosporioides* complex are not reflected

Table 4. Performance of individual genes at resolving species within the *Colletotrichum gloeosporioides* species complex. Y – species distinguished from all others. N – species not distinguished from all others. N* – distinguishes at the subspecies level.

Species	ITS	GAPDH	CAL	TUB2	ACT	CHS-1	GS	SOD
C. fructicola	N	N	Y	N	N	Y	Y	Y
C. nupharicola	N	Y	Y	Y	Y	Y	Y	Y
C. alienum	N	N	Y	N	N	Y	Y	Y
C. musae	Y	Y	Y	Y	Y	Y	Y	Y
C. aenigma	N	Y	Y	Y	N	Y	Y	Y
C. siamense	N	N	Y	Y	N	N	N	N
C. aeschynomenes	N	N	N	Y	N	Y	Y	Y
C. tropicale	N	N	N	Y	Y	N	Y	Y
C. queenslandicum	N	Y	Y	Y	N	N	Y	N
C. salsolae	N	Y	Y	Y	Y	Y	N	Y
C. asianum	Y	Y	Y	Y	Y	Y	Y	Y
C. gloeosporioides	Y	Y	Y	Y	Y	Y	Y	Y
C. alatae	Y	Y	Y	Y	Y	Y	Y	Y
C. theobromicola	Y	Y	Y	Y	Y	Y	Y	Y
C. xanthorrhoeae	Y	Y	Y	Y	Y	Y	Y	Y
C. horii	Y	Y	Y	Y	Y	Y	Y	Y
C. aotearoa	N	N	Y	Y	N	Y	Y	N
C. ti	N	Y	Y	Y	N	Y	Y	Y
C. kahawae	N	Y	N	Y	Y	N	N*	N
G. cingulata "f. sp. *camelliae*"	Y	N	Y	Y	Y	N	Y	Y
C. clidemiae	N	N	N	N	Y	Y	Y	N
C. psidii	Y	Y	Y	Y	N	Y	Y	Y
C. cordylinicola	Y	Y	Y	Y	N	Y	Y	Y

genetically. For example, the fungi referred to as *C. gloeosporioides* f. *stylosanthis* "f. sp. *guianensis*" and *C. gloeosporioides* f. *stylosanthis* "f. sp. *stylosanthis*", are reportedly associated with two distinct diseases of *Stylosanthes* (Irwin & Cameron 1978; Munaut *et al.* 2002), but both taxa genetically match *C. theobromicola* and are here placed in synonymy with *C. theobromicola*. It is possible that screening additional genes across a set of isolates from *Stylosanthes* with known pathogenicity will reveal one or more genes that generate a phylogeny that correlates with pathogenicity. This is the case with another specialised pathogen, *C. kahawae*. Originally described as a pathogen of green coffee berries, almost genetically identical isolates have subsequently been found on a wide range of hosts (see notes under *C. kahawae*). The isolates from other hosts are not pathogenic to coffee berries (Silva *et al.* 2012b). The difference in pathogenicity correlates with a genetic difference in the GS gene, and we taxonomically recognise this biologically specialised population at the subspecies level. A similar approach could potentially be taken for other biologically distinct populations within a genetically strongly supported species.

Despite the epitypification of *C. gloeosporioides* in 2008, web search hits on the name *C. gloeosporioides* from papers published over the past 12 mo show that many authors will continue to use the name in the sense of the *C. gloeosporioides* species complex, presumably regarding this level of identification as sufficient for their research. All of the isolates that we accept in the *C. gloeosporioides* complex share the string 5'–GGGCGGGT–3' about 139–142 bases after the ITS1F primer binding site. Based on a comparison with GenBank data, this string appears to be specific to isolates that we would accept as members of the *C. gloeosporioides* complex.

Several authors have developed PCR-based, rapid identification tools for distinguishing members of the *C. gloeosporioides* complex from members of the *C. acutatum* species complex. This has been prompted because some members of the *C. acutatum* complex have conidia without the acute ends characteristic of this species as described by Simmonds (1965), and have at times been confused with *C. gloeosporioides* (Damm *et al.* 2012, this issue). Primers reportedly specific to *C. gloeosporioides* include the CgInt primer for ITS (Mills *et al.* 1992). In our data set this primer sequence is found in *C. gloeosporioides s. str.*, *C. fructicola*, and *C. siamense* but all of the other taxa that we recognise within the *C. gloeosporioides* complex have one or more bases not matching the CgInt primer. The practical impact of these differences will depend in part on the position of the mismatch and stringency of the PCR reaction. Talhinas *et al.* (2005) discussed the TBCG primer for β-tubulin, and this is found within all of our taxa within the *C. gloeosporioides* group except *C. musae* and *C. asianum*. Liu *et al.* (2011) describe characteristic RFLP bands from glutamine synthetase using the restriction enzyme Pst1. Based on our sequences, this method will generate the characteristic *C. gloeosporioides* bands reported by Liu *et al.* (2011) for *C. aenigma*, *C. alienum*, *C. aotearoa*, *C. asianum*, *C. clidemiae*, *C. cordylinicola*, *C. fructicola*, *C. gloeosporioides s. str.*, *C. horii*, *C. queenslandicum*, *C. salsolae*, *C. siamense*, *C. ti*, and *C. tropicale*. Different banding patterns will be produced by *C. aeschynomenes* (band sizes 253, 316, 388), the two *C. kahawae* subspp. (band sizes 112, 388, 457), *G. cingulata* "f. sp. *camelliae*" (band sizes 51, 112, 337, 457), and *C. musae* (band sizes 388, 552), but none match the bands reported for *C. acutatum* by these authors.

Comparison of our data with gene sequences reported as *C. gloeosporioides* in recent papers allows most to be placed with confidence in one of the species that we accept. There are exceptions, such as the pecan-associated isolates from Liu *et al.* (2011), and the pistachio-associated isolates reported by Yang *et al.* (2011), both of which appear to represent undescribed species within the *C. gloeosporioides* complex. Clearly, more species remain to be described within the *C. gloeosporioides* complex. In addition, taxonomic issues still to be resolved amongst the species discussed in this paper include the relationship between *G. cingulata* "f. sp. *camelliae*" and *C. camelliae*, the identity of the cotton pathogens referred to *C. gossypii*, the identity of the cassava pathogens referred to *C. manihotis*, the relationship between *C. aeschynomenes* and *C. gloeosporioides* "f. sp. *jussiaeae*", whether the various yam diseases discussed in the literature are all caused by *C. alatae*, and whether the isolates of *C. aotearoa* from *Meryta* leaf spots form a biologically distinct population. A more general question relates to better understanding the frequency of hybrids within the *C. gloeosporioides* complex and the impact of this on the interpretation of the phylogenies within the complex. The impact of hybridisation on the evolution of disease specialised populations has barely been explored.

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REFERENCES

Aa HA van der (1978). A leaf spot of *Nymphaea alba* in the Netherlands. *Netherlands Journal of Plant Pathology* **84**: 109–115.

Abang MM, Winter S, Green KR, Hoffmann P, Mignouna HD, Wolf GA (2002). Molecular identification of *Colletotrichum gloeosporioides* causing anthracnose of yam in Nigeria. *Plant Pathology* **51**: 63–71.

Abang MM, Winter S, Mignouna HD, Green KR, Asiedu R (2003). Molecular taxonomic, epidemiological and population genetic approaches to understanding yam anthracnose disease. *African Journal of Biotechnology* **2**: 486–496.

Afanador-Kafuri L, Minz D, Maymon M, Freeman S (2003). Characterisation of *Colletotrichum* isolates from tamarillo, passiflora, and mango in Colombia and identification of a unique species from the genus. *Phytopathology* **93**: 579–587.

Aguileta G, Marthey S, Chiapello H, Lebrun MH, Rodolphe F, *et al.* (2008). Assessing the Performance of Single-Copy Genes for Recovering Robust Phylogenies *Systematic Biology* **57**: 613–627.

Alahakoon PW, Brown AE, Sreenivasaprasad S (1994). Genetic characterisation of *Colletotrichum gloeosporioides* isolates obtained from mango. *International Journal of Pest Management* **40**: 225–229.

Alfieri Jr SA, Langdon KR, Wehlburg C, Kimbrough JW (1984). Index of Plant Diseases in Florida (Revised). *Florida Department of Agriculture and Consumer Services, Division of Plant Industries Bulletin* **11**: 1–389.

Archibald JK, Mort ME, Crawford DJ (2003). Bayesian inference of phylogeny: a non-technical primer. *Taxon* **52**: 187–191

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

Arx JA von (1970). A revision of the fungi classified as *Gloeosporium*. *Bibliotheca Mycologica* **24**: 1–203.

Arx JA von, Müller E (1954). Die Gattung der amerosporen Pyrenomyceten. *Beiträge zur Kryptogamenflora der Schweiz* **11(1)**: 1–434.

Bailey JA, Nash C, Morgan LW, O'Connell RJ, TeBeest DO (1996). Molecular taxonomy of *Colletotrichum* species causing anthracnose on the *Malvaceae*. *Phytopathology* **86**: 1076–1083.

Beever RE (1984). Observations on puka (*Meryta sinclairii*) on the Chickens Islands, with an assessment of the hypothesis that it was transferred there by the Maori. *Tane* **30**: 77–92.

Berkeley MJ (1874). Notices of North American fungi. *Grevillea* **3**: 1–17.

Berner DK, Bruckart WL, Cavin CA, Michael JL, Carter ML, Luster DG (2009). Best linear unbiased prediction of host-range of the facultative parasite *Colletotrichum gloeosporioides* f. sp. *salsolae*, a potential biological control agent of Russian thistle. *Biological Control* **51**: 158–168.

Bogo A, Casa RT, Rufato L, Gonçalves MJ (2012). The effect of hail protection nets on *Glomerella* leaf spot in 'royal Gala' apple. *Crop Protection* **31**: 40–44

Boyette CD, Templeton GE, Smith JR (1979). Control of waterprimrose (*Jussiaea decurrens*) and northern jointvetch (*Aeschynomene virginica*) with fungal pathogens. *Weed Science* **27**: 497–501.

Brasier CM (1995). Episodic selection as a force in fungal microevolution, with special reference to clonal speciation and hybrid introgression. *Canadian Journal of Botany* **73** (Supplement 1): S1213–S1221.

Brooks AN (1931). Anthracnose of strawberry caused by *Colletotrichum fragariae* n. sp. *Phytopathology* **21**: 739–744.

Buddie AG, Martínez-Culebras P, Bridge PD, García MD, Querol A, *et al.* (1999). Molecular characterisation of *Colletotrichum* strains derived from strawberry. *Mycological Research* **103**: 385–394.

Cai L, Hyde KD, Taylor PWJ, Weir BS, Waller J, *et al.* (2009). A polyphasic approach for studying *Colletotrichum*. *Fungal Diversity* 39: 183–204.

Cannon PF, Buddie AG, Bridge PD (2008). The typification of *Colletotrichum gloeosporioides*. *Mycotaxon* **104**: 189–204.

Cannon PF, Damm U, Johnston PR, Weir BS (2012). *Colletotrichum* – current status and future directions. *Studies in Mycology* **73**: 181–213.

Carbone I, Kohn LM (1999). A method for designing primer sets for speciation studies in filamentous ascomycetes. *Mycologia* **91**: 553–556.

Carpenter JB, Stevenson JA (1954). A secondary leaf spot of the *Hevea* rubber tree caused by *Glomerella cingulata*. *Plant Disease Reporter* **38**: 494–499.

Castro RA, Mendes-Costa MC, Souza EA (2006). Dimorfismo de ascósporos em *Glomerella cingulata* f. sp. *phaseoli*. *Fitopatologia Brasileira* **31**: 598–600.

Chevaugeon J (1956). Les maladies cryptogamiques du manioc en Afrique Occidentale. *Encyclopédie Mycologique* **28**: 1–205.

Chung WS, Ishii H, Nishimura K, Fukaya M, Yano K, Kajitani Y (2006). Fungicide sensitivity and phylogenetic relationship of anthracnose fungi isolated from various fruit crops in Japan. *Plant Disease* **90**: 506–512.

Chung Y, Ané C (2011). Comparing Two Bayesian Methods for Gene Tree/Species Tree Reconstruction: Simulations with Incomplete Lineage Sorting and Horizontal Gene Transfer. *Systematic Biology* **60**: 261–275

Cisar CR, Spiegel FW, TeBeest DO, Trout C (1994). Evidence for mating between isolates of Colleto*trichum gloeosporioides* with different host specificities. *Current Genetics* **25**: 330–335.

Correll JC, Rhoads DD, Guerber JC (1993). Examination of mitochondrial DNA restriction fragment length polymophisms, DNA fingerprints, and randomly amplified polymorphic DNA of *Colletotrichum orbiculare*. *Phytopathology* **83**: 1199–1204.

Crouch JA, Clarke BB, Hillman BI (2006). Unravelling evolutionary relationships amongst divergent lineages of *Colletotrichum* causing anthracnose disease in turfgrass and corn. *Phytopathology* **96**: 46–60.

Crous PW, Gams W, Stalpers JA, Robert V, Stegehuis G (2004). MycoBank: an online initiative to launch mycology into the 21st century. *Studies in Mycology* **50**: 19–22.

Curzi M (1927). De novis Eumycetibus. *Atti dell'Istituto Botanico della Università e Laboratorio Crittogamico di Pavia* **3 (3)**: 203–208.

Damm U, Cannon PF, Woudenberg JHC, Crous PW (2012a). The *Colletotrichum acutatum* species complex. *Studies in Mycology* **73**: 37–113.

Damm U, Cannon PF, Woudenberg JHC, Johnston PR, Weir BS, *et al*. (2012b). The *Colletotrichum boninense* species complex. *Studies in Mycology* **73**: 1–36.

Daniel JT, Templeton GE, Smith RJ, Fox WT (1973). Biological control of northern jointvetch in rice with an endemic fungal disease. *Weed Science* **21**: 303–307.

Delacroix G (1903). De la tavelure goyaves produite par le *Gloeosporium psidii* nov. sp. G. Del. *Bulletin de la Société Mycologique de France* **19**: 143–145.

Deng Y, Zhang M, Luo H (2012). Identification and antimicrobial activity of two alkaloids from traditional Chinese medicinal plant *Tinospora capillipes*. *Industrial Crops and Products* **37**: 298–302.

Dickens JSW, Cook RTA (1989). *Glomerella cingulata* on *Camellia*. *Plant Pathology* **38**: 75–85.

Ditmore M, Moore JW, TeBeest DO (2008). Interactions of two selected field isolates of *Colletotrichum gloeosporioides* f. sp. *aeschynomene* on *Aeschynomene virginica*. *Biological Control* **47**: 298–308.

Drummond AJ, Ashton B, Buxton S, Cheung M, Cooper A, *et al.* (2011). Geneious v5.4, Available from http://www.geneious.com/

Drummond AJ, Suchard MA, Xie D, Rambaut A (2012). Bayesian phylogenetics with BEAUti and the BEAST 1.7. *Molecular Biology and Evolution* **29**: 1969–1973.

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

Edgerton CW (1909). The perfect stage of the cotton anthracnose. *Mycologia* **1**: 115–120.

Farr DF, Aime MC, Rossman AY, Palm ME (2006). Species of *Colletotrichum* on Agavaceae. *Mycological Research* **110**: 1395–1408.

Fitzpatrick DA, Logue ME, Stajich JE, Butler G (2006). A fungal phylogeny based on 42 complete genomes derived from supertree and combined gene analysis. *BMC Evolutionary Biology* **6**: 99.

Fokunang CN, Dixon AGO, Akem CN, Ikotun T (2000). Cutural, morphological and pathogenic variability in *Colletotrichum gloeosporioides* f. sp. *manihotis* isolates from cassava (*Manihot esculenta*) in Nigeria. *Pakistan Journal of Biological Sciences* **3**: 542–546.

Gardes M, Bruns TD (1993). ITS primers with enhanced specificity for basidiomycetes – application to the identification of mycorrhizae and rusts. *Molecular Ecology* **2**: 113–118.

Glass NL, Donaldson GC (1995). Development of primer sets designed for use with the PCR to amplify conserved genes from filamentous ascomycetes. *Applied and Environmental Microbiology.* **61**: 1323–1330.

Gielink AJ, Vermeulen H (1983). The ability of American and African *Colletotrichum* isolates to cause coffee berry disease symptoms and the association of some isolates with *Glomerella cingulata*. *Netherlands Journal of Plant Pathology* **89**: 188–190.

Gorter GJMA (1956). Anthracnose fungi of olives. *Nature* **178**: 1129–1130.

Green KR, Simons SA (1994). 'Dead skin' on yams (*Dioscorea alata*) caused by *Colletotrichum gloeosporioides*. *Plant Pathology* **43**: 1062–1065.

Greene GL (1967). Effect of 2-dehydroxy-D-glocose on the respiration of tropical anthracnose fungi. *Physiologia Plantarum* **20**: 580–586.

Guerber JC, Correll JC (2001). Characterisation of *Glomerella acutata*, the teleomorph of *Colletotrichum acutatum*. *Mycologia* **93**: 216–229.

Guerber JC, Liu B, Correll, JC, Johnston PR (2003). Characterization of diversity in *Colletotrichum acutatum sensu lato* by sequence analysis of two gene introns, mtDNA and intron RFLPs, and mating compatibility. *Mycologia* **95**: 872–895.

Gunnell PS, Gubler WD (1992). Taxonomy and morphology of *Colletotrichum* species pathogenic to strawberry. *Mycologia* **84**: 157–165.

Harris P (1993). Effects, constraints and the future of weed biocontrol. *Agriculture, Ecosystems and Environment* **46**: 289–303.

Heled J, Drummond AJ (2010). Bayesian Inference of Species Trees from Multilocus Data. *Molecular Biology and Evolution* **27:** 570–580.

Higgins BB (1926). Anthracnose of pepper (*Capsicum anuum* L.). *Phytopathology* **16**: 333–345.

Hildebrand PD, Jensen KIN (1991). Potential for the biological control of St Johns's-wort (*Hypericum perforatum*) with an endemic strain of *Colletotrichum gloeosporioides*. *Canadian Journal of Plant Pathology* **13**: 60–70.

Hindorf H (1973). *Colletotrichum*-Population auf *Coffea arabica* L. in Kenia II. Qualitative und quantitative Unterschiede in der *Colletotrichum*-Population. *Phytopathologische Zeitschrift* **77***:* 216–234

Hosdson A, Mills PR, Brown AE (1993). Ribosomal and mitochondrial DNA polymorphisms in *Colletotrichum gloeosporioides* isolated from tropical fruits. *Mycological Research* **97**: 329–335.

Hsiang T, Goodwin PH (2001). Ribosomal DNA sequence comparisons of *Colletotrichum graminicola* from turfgrasses and other hosts. *European Journal of Plant Pathology* **107**: 593–599.

Hyde KD, Cai L, Cannon PF, Crouch JA, Crous PW, *et al*. (2009). *Colletotrichum* – names in current use. *Fungal Diversity* **39**: 147–182.

Hyde KD, Chomnunti P, Crous PW, Groenewald JZ, Damm U, *et al.* (2010). A case for re-inventory of Australia's plant pathogens. *Persoonia* **25**: 50–60.

Irwin JAG, Cameron DF (1978). Two diseases in *Stylosanthes* caused by *Colletotrichum gloeosporioides* in Australia, and pathogenic specialisation within one of the causal organisms. *Australian Journal of Agricultural Research* **29**: 3015–317.

Johnson DA, Carris LM, Rogers JD (1997). Morphological and molecular characterization of *Colletotrichum nymphaeae* and *C. nupharicola* sp. nov. on water-lilies (*Nymphaea* and *Nuphar*). *Mycological Research* **101**: 641–649.

Johnston PR (2000). The importance of phylogeny in understanding host relationships within *Colletotrichum*. In: *Colletotrichum: host specificity, pathogenicity, and host-pathogen interactions* (Prusky D, Dickman MB, Freeman S eds). APS Press, St Paul, Minnesota: 21–28.

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

Johnston PR, Pennycook SR, Manning MA (2005). Taxonomy of fruit-rotting fungal pathogens: what's really out there? *New Zealand Plant Protection* **58**: 42–46.

Kaan F (1973). A study on inheritance of eggplant (*Solanum melongena* L.) resistance to fruit anthracnose (*Colletotrichum gloeosporioides* f. sp. *melongenae* Penzig Fournet). *Annales De l'Amelioration des Plantes* **23**:127–151.

Kenny MK, Galea VJ, Price TV (2012). Germination and growth of *Colletotrichum acutatum* and *Colletotrichum gloeosporioides* isolates from coffee in Papua New Guinea and their pathogenicity. *Australasian Plant Pathology* (online, doi:10.1007/s13313-012-0117-7).

Killgore EM, Sugiyama LS, Barreto RW, Gardner DE (1999). Evaluation of *Colletotrichum gloeosporioides* for Biological Control of *Miconia calvescens* in Hawaii. *Plant Disease* **83**: 964.

Kornerup A, Wanscher JH (1963). *Methuen handbook of colour*. Methuen and Co. London.

Krauss U, Matthews P, Bidwell R, Hocart M, Anthony F (2001). Strain discrimination by fungal antagonists of *Colletotrichum musae*: implications for biocontrol of crown rot of banana. *Mycological Research* **105**: 67–76.

Lardner R, Johnston PR, Plummer KM, Pearson MN (1999). Morphological and molecular analysis of *Colletotrichum acutatum sensu lato*. *Mycological Research* **103**: 275–285.

Larkin MA, Blackshields G, Brown NP, Chenna R, McGettigan PA, *et al*. (2007). Clustal W and Clustal X v. 2.0. *Bioinformatics* **23**: 2947–2948.

Laundon GF (1972) [1971]. Records of fungal plant diseases in New Zealand – 2. *New Zealand Journal of Botany* **9**: 610–624.

Li R, Ma H (1993). Studies in the occurrence and control of ramie anthracnose. Acta *Phytophylacica Sinica* **20**: 83–89. [in Chinese]

Liu LJ (1972). Identification and occurrence of perfect stage and cultural and morpholoical variants of *Colletotrichum gloeosporioides* from guava in Puerto Rico. *Journal of Agriculture of the University of Puerto Rico* **56**: 171–180.

Liu B, Louws FJ, Sutton TB, Correll JC (2011). A rapid qualitative molecular method for the identification of *Colletotrichum acutatum* and *C. gloeosporioides*. *European Journal of Plant Pathology* **132**: 593–607.

Lubbe CM, Denman S, Cannon PF, Groenewald JZ, Lamprecht SC, Crous PW (2004). Characterisation of *Colletotrichum* species associated with *Proteaceae*. *Mycologia* **96**: 1268–1279.

MacCaughey V (1917). The guavas of the Hawaiian Islands. *Bulletin of the Torrey Botanical Club* **44**: 513–524.

Mackenzie SJ, Seijo TE, Legard DE, Timmer LW, Peres NA (2007). Selection for pathogenicity to strawberry in populations of *Colletotrichum gloeosporioides* from native plants. *Phytopathology* **97**: 1130–1140.

Mackenzie SJ, Mertely JC, Seijo TE, Peres NA (2008). *Colletotrichum fragariae* is a pathogen on hosts other than strawberry. *Plant Disease* **92**: 1432–1438.

McNeill J, Barrie FR, Burdet HM, Demoulin V, Hawksworth DL, *et al.* (2006). *International Code of Botanical Nomenclature (Vienna Code). Adopted by the Seventeenth International Botanical Congress, Vienna, Austria, July 2005*. Regnum Vegetabile 146. 568 p.

Makambila C (1994). The fungal diseases of cassava in the Republic of Congo, Central Africa. *African Crop Science Journal* **2**: 511–517.

Makowski RMD, Mortensen K (1989). *Colletotrichum gloeosporioides* f. sp. *malvae* as a bioherbicide for round-leafed mallow (*Malva pusilla*): conditions for successful control in the field. In: *Proceedings of the 7th International Symposium for the Biological Control of Weeds*. (Delfosse ES ed.). *Istituto Sperimentale per la Patalogia Vegetale, Rome*: 513–522.

Marcelino J, Giordano R, Gouli S, Gouli V, Parker BL, *et al.* (2008). *Colletotrichum acutatum* var. *fioriniae* (teleomorph: *Glomerella acutata* var. *fioriniae* var. nov.) infection of a scale insect. *Mycologia* **100**: 353–374.

Martínez-Culebras PV, Barrio E, García MD, Querol A (2000). Identification of *Colletotrichum* species responsible for anthracnose of strawberry based on the internal transcribed spacers of the ribosomal region. *FEMS Microbiology Letters* **189**: 97–101.

Martinez-Culebras PV, Querol A, Suarez-Fernandez MB, Garcia-Lopez MD, Barrio E (2003). Phylogenetic relationships among *Colletotrichum* pathogens of strawberry and design of PCR primers for their identification. *Journal of Phytopathology* **151**: 135–143.

Maymon M, Zveibil A, Pivonia S, Minz D, Freeman S (2006). Identification and characterisation of benomyl-resistant and sensitive- populations of *Colletotrichum gloeosporioides* from statice (*Limonium* spp.). *Phytopathology* **96**: 542–548.

Menten JOM, Kimati H, Costa CP (1980). Reação de populações de pepino (*Cucumis sativus* L.) a *Colletotrichum gloeosporioides* f. sp. *cucurbitae* (Berk. et Mont.) N. Comb. *Summa Phytopathologica* **5**: 127–133.

Mills PR, Sreenivasaprasad S, Brown AE (1992). Detection and differentiation of *Colletotrichum gl* Maymon *oeosporioides* isolates using PCR. *FEMS Microbiological Letters* **98**: 137–144.

Misra AK (2004). Guava diseases – their symptoms, causes and management. In: *Diseases of fruits and vegetables. Diagnosis and management Volume 2*. (Naqvi SAMH. ed.). Kluwer Academic Publishers, Dordrecht: 81–119.

Mordue JEM (1971). *Glomerella cingulata*. CMI Desriptions of Plant Pathogenic Fungi No. 315. Commonwealth Mycological Institute, Kew.

Moriwaki J, Sato T, Tsukiboshi T (2003). Morphological and molecular characterisation of *Colletotrichum boninense* sp. nov. from Japan. *Mycoscience* **44**: 47–53.

Moriwaki J, Sato T (2009). A new combination for the causal agent of tea anthracnose: *Discula theae-sinensis* (I. Miyake) Moriwaki & Toy. Sato, comb. nov. *Journal of General Plant Pathology* **75**: 359–361.

Moriwaki J, Tsukiboshi T (2009). *Colletotrichum echinochloae*, a new species on Japanese barnyard millet (*Echinochloa utilis*). *Mycoscience* **50**: 273–280.

Munaut F, Hamaide N, Maraite H (2002). Genomic and pathogenic diversity in *Colletotrichum gloeosporioides* from wild native Mexican *Stylosanthes* spp., and taxonomic implications. *Mycological Research* **106**: 579–593.

Munaut F, Hamaide N, Vander Stappen J, Maraite H (1998). Genetic relationships among isolates of *Colletotrichum gloeosporioides* from *Stylosanthes* spp. in Africa and Australia using RAPD and ribosomal DNA markers. *Plant Pathology* **47**: 641–648.

Muraleedharan N, Baby UI (2007). Tea disease: ecology and control. In: *Encyclopedia of Pest Management Vol. 2* (Pimentel D, ed.) [electronic resource]. CRC Press, Boca Raton: 668–671.

Nilsson RH, Ryberg M, Kristiansson E, Abarenkov K, Larsson KH, Kõljalg U (2006). Taxonomic reliability of DNA sequences in public sequence databases: a fungal perspective. *PLoS ONE* **1(1)**: e59.

Nirenberg HI, Feiler U, Hagedorn G (2002). Description of *Colletotrichum lupini* comb. nov. in modern terms. *Mycologia* **94**: 307–320.

Noak F (1901). Die Krankheiten des Kaffeebaumes in Brasilien. *Zeitschrift für Pflanzenkrankheiten* **11**: 196–203.

Ocfemia, GO, Agati JA (1925). The cause of anthracnose of avocado, mango and upo in the Philippine Islands. *Philippine Agriculturalist* **14**: 199–216.

O'Donnell K, Cigelnik E (1997). Two divergent intragenomic rDNA ITS2 types within a monophyletic lineage of the fungus *Fusarium* are nonorthologous. *Molecular Phylogenetics and Evolution* **7**:103–116.

O'Donnell K, Nirenberg HI, Aoki T, Cigelnik E (2000). A Multigene phylogeny of the *Gibberella fujikuroi* species complex: Detection of additional phylogenetically distinct species. *Mycoscience* **41**: 61–78.

Owolade OF, Dixon AGO, Alabi BS, Akande SR, Olakojo SA (2008). A combining ability analysis of cassava *Manihot esculenta* Crantz genotypes to anthracnose disease. *Electronic Journal of Environmental, Agricultural and Food Chemistry* **7**: 2959–2968.

Parvin S, Lee OR, Sathiyaraj G, Khorolragchaa A, Kim YJ, *et al.* (2012). Interrelationship between calmodulin (CaM) and H2O2 in abscisic acid-induced antioxidant defense in the seedlings of *Panax ginseng*. *Molecular Biology Reports* **39**: 7327–7338.

Penzig AGO (1882). Fungi agrumicoli. Contribuzione allo studio dei funghi parassiti degli agrumi. *Michelia* **2**: 385–508.

Phoulivong S, Cai L, Parinn N, Chen H, Abd-Elsalam K, *et al.* (2011). A new species of *Colletotrichum* from *Cordyline fruticosa* and *Eugenia javanica* causing anthracnose disease. *Mycotaxon* **114**: 247–257.

Polashock JJ, Caruso FL, Oudemans PV, McManus PS, Crouch JA (2009). The North American cranberry fruit rot fungal community: a systematic overview using morphological and phylogenetic affinities. *Plant Pathology* **58**: 1116–1127.

Pollacci G (1899). Contribuzione alla micologia ligustica. *Atti dell' Istituto Botanico dell' Università di Pavia, Serie 2* **5**: 29–46.

Posada D. (2008). jModelTest: Phylogenetic Model Averaging. *Molecular Biology and Evolution* **25**: 1253–1256

Prasad N, Singh RD (1960). Anthracnose disease of *Dioscorea alata* L. (Yam, Eng., Ratalu, Hind.). *Current Science* **29**: 66–67.

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

R Development Core Team (2011). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna, Austria.

Rambaut A, Drummond AJ (2007). Tracer v. 1.4, Available from http://beast.bio.ed.ac.uk/Tracer

Rodrigues CJ, Varzea VMP, Hindorf H, Medeiros EF (1991). Strains of *Colletotrichum coffeanum* Noack causing coffee berry disease in Angola and Malawi with characteristics different to the Kenya strain. *Journal of Phytopathology* **131**: 205–209.

Rodriguez RJ, Owen JL (1992). Isolation of *Glomerella musae* [teleomorph of *Colletotrichum musae* (Berk. & Curt.) Arx] and segregation analysis of ascospore progeny. *Experimental Mycology* **16**: 291–301.

Rodríguez-Guerra R, Ramírez-Rueda M, Cabral-Enciso M, García-Serrano M, Lira-Maldonado Z, *et al.* (2005). Heterothallic mating observed between Mexican isolates of *Glomerella lindemuthiana*. *Mycologia* **97**: 793–803.

Rojas EI, Rehner SA, Samuels GJ, Van Bael SA, Herre EA, *et al.* (2010). *Colletotrichum gloeosporioides* s.l. associated with *Theobroma cacao* and other plants in Panamá: multilocus phylogenies distinguish host-associated pathogens from asymptomatic endophytes. *Mycologia* **102**: 1318–1338.

Ronquist F, Teslenko M, van der Mark P, Ayres D, Darling A, *et al.* (2012). MrBayes v. 3.2: Efficient Bayesian phylogenetic inference and model choice across a large model space. *Systematic Biology* **61**: 539–542.

Saccardo PA, Trotter A (1913). Supplementum Universale Pars. IX. Ascomycetae-Deuteromycetae. *Sylloge Fungorum* **22**: 1–1612.

Sanders GM, Korsten L (2003). Comparison of cross inoculation potential of South African avocado and mango isolates of *Colletotrichum gloeosporioides*. *Microbiological Research* **158**: 143–150.

Sawada T (1922). New Japanese fungi notes and translations – XI. *Mycologia* **14**: 81–89.

Schoch CL, Seifert KA, Huhndorf S, Robert V, Spouge JL, *et al.* (2012). Nuclear ribosomal internal transcribed spacer (ITS) region as a universal DNA barcode marker for Fungi. *Proceedings of the National Academy of Sciences* **109**: 6241–6246.

Schwarczinger I, Vajna L, Bruckart WL (1998). First report of *Colletotrichum gloeosporioides* on Russian thistle. *Plant Disease* **82**: 1405.

Seifert KA (2009). Progress towards DNA barcoding of fungi. *Molecular Ecology Resources* **9** (Suppl. 1): 83–89.

Shear CL (1907). New species of fungi. *Bulletin of the Torrey Botanical Club* **34**: 305–317.

Shear CL, Wood AK (1907). Ascogenous forms of *Gloeosporium* and *Colletotrichum*. *Botanical Gazette* **43**: 259–266.

Shear CL, Wood AK (1913). Studies of fungus parasites belonging to the genus *Glomerella*. *USDA Bureau of Plant Industry Bulletin* **252**: 1–110.

Sheldon JL (1906). The ripe rot or mummy disease of guavas. *Bulletin of the West Virginia University Experimental Station* **104**: 299–315.

Shenoy BD, Jeewon R, Lam WH, Bhat DJ, Than PP, *et al.* (2007). Morpho-molecular characterisation and epitypification of *Colletotrichum capsici* (*Glomerellaceae, Sordariomycetes*), the causative agent of anthracnose on chilli. *Fungal Diversity* **27**: 197–211.

Sherf AF, MacNab AA (1986). *Vegetable diseases and their control*. John Wiley and Sons. USA.

Sherriff C, Whelan MJ, Arnold GM, Lafay JF, Brygoo Y, Bailey JA (1994). Ribosomal DNA sequence analysis reveals new species groupings in the genus *Colletotrichum*. *Experimental Mycology* **18**: 121–138.

Shivas RG, Bathgate J, Podger FD (1998). *Colletotrichum xanthorrhoeae* sp. nov. on *Xanthorrhoea* in Western Australia. *Mycological Research* **102**: 280–282.

Silva DN, Talhinas P, Várzea V, Cai L, Paulo OS, Batista D (2012a). Application of the Apn2/MAT locus to improve the systematics of the *Colletotrichum gloeosporioides* complex: an example from coffee (*Coffea* spp.) hosts. *Mycologia* **104**: 396–409.

Silva DN, Talhinhas P, Cai L, Manuel L, Gichuru EK, *et al.* (2012b). Host-jump drives rapid and recent ecological speciation of the emergent fungal pathogen *Colletotrichum kahawae*. *Molecular Ecology* **21**: 2655–2670.

Silva VN da, Guzzo SD, Mantovanello-Lucon CM, Harakava R (2011). Promoção de crescimento e inducção de resistência à antracnose por *Trichoderma* spp. em pepineiro. *Pesquisa Agropecuária Brasileira* **46**: 1609–1618.

Silva-Mann R, Carvalho Vieira MGG, Machado JC, Bernandino Filho JR, Salgado KCC, Stevens MR (2005). AFLP markers differentiate isolates of *Colletotrichum gossypii* from *C. gossypii* var. *cephalosporioides*. *Fitopatologia Brasileira* **30**: 169–172.

Simmonds JH (1965). A study of the species of *Colletotrichum* causing ripe fruit rots in Queensland. *Queensland Journal of Agricultural and Animal Sciences* **22**: 437–459.

Simmonds JH (1968). Type specimens of *Colletotrichum gloeosporioides* var. *minor* and *Colletotrichum acutatum*. *Queensland Journal of Agricultural and Animal Sciences* **25**: 178A.

Singh UP (1974). A new forma specialis of *Colletotrichum gloeosporioides* Penz. from India. *Beihefte zur Nova Hedwigia* **47**: 451–452.

Singh UP (1975). *Colletotrichum gloeosporioides* Penzig - A mycoparasite on *Ravenelia sessilis* Berkeley. *Current Science* **44**: 623–624.

Singh RD, Prasad N, Mathur RL (1966). On the taxonomy of the fungus causing anthracnose of *Dioscorea alata* L. *Indian Phytopathology* **19**: 65–71.

Small W (1926). On the occurrences of a species of *Colletotrichum*. *Transactions of the British Mycological Society* **11**: 112–137.

Snowdon AL 1991. *A colour atlas of post-harvest diseases and disorders of fruit and vegetables. Volume 2. Vegetables*. Wolfe Scientific.

Sosa de Castro NT, Cabrera de Alvarez MG, Alvarez RE (2001). Primera información de *Colletotrichum camelliae* como patógeno de *Camellia japonica*, en Corrientes. Retrieved 6 Oct 2010 from www1.unne.edu.ar/cyt/2001/5-Agrarias/A-056.pdf.

Southworth EA (1891). Antracnose of cotton. *Journal of Mycology* **6**: 100–105.

Spaulding P (1958). *Diseases of foreign trees growing in the United States, an annotated list*. USDA Agriculture Handbook 139.

Spegazzini CL (1878). Ampelomiceti Italici, ossia enumerazione, diagnosi e storia dei principali parassiti della vite. *Rivista Viticoltura ed Enologia* **2**: 405–411.

Sreenivasaprasad S, Mills PR, Meehan B M, Brown AE (1996). Phylogeny and systematics of 18 *Colletotrichum* species based on ribosomal DNA spacer sequences. *Genome* **39**: 499–512.

Stephenson SA, Green JR, Manners JM, Maclean DJ (1997). Cloning and characterisation of glutamine synthetase from *Colletotrichum gloeosporioides* and demonstration of elevated expression during pathogenesis on *Stylosanthes guianensis*. *Current Genetics* **31**: 447–454.

Stevens FL, Hall JG (1909). Eine neue Feigen-Anthraknose (Colletotrichose). *Zeitschrift für Pflanzenkrankheiten* **19**: 65–68.

Stoneman B (1898). A comparative study of the development of some anthracnoses. *Botanical Gazette* **26**: 69–120.

Su YY, Noireung P, Liu F, Hyde KD, Moslem MA, *et al.* (2011). Epitypification of *Colletotrichum musae*, the causative agent of banana anthracnose. *Mycoscience* **52**: 376–382.

Sutton BC, Waterston JM (1970). *Colletotrichum musae*. *CMI Descriptions of Plant Pathogenic Fungi and Bacteria* No. 222.

Sutton BC (1980). *The Coelomycetes*. Commonwealth Mycological Institite. Kew.

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

Talhinas P, Sreenivasaprasad S, Neves-Martins J, Oliviera H (2005). Molecular and phenotypic analyses reveal association of diverse *Colletotrichum acutatum* groups and a low level of *C. gloeosporioides* with olive anthracnose. *Applied and Environmental Microbiology* **71**: 2987–2998.

Taylor JW, Jacobson DJ, Kroken S, Kasuga T, Geiser DM, *et al.* (2000). Phylogenetic species recognition and species concepts in fungi. *Fungal Genetics and Biology* **31**: 21–32.

Taylor JW, Berbee ML (2006). Dating divergences in the Fungal Tree of Life: review and new analyses. *Mycologia* **98**: 838–849.

TeBeest DO (1988). Additions to host range of *Colletotrichum gloeosporioides* f. sp. *aeschynomene*. *Plant Disease* **72**: 16–18.

Templeton MD, Rikkerink EHA, Solon SL, Crowhurst RN. (1992). Cloning and molecular characterization of the glyceraldehyde-3-phosphate dehydrogenase-encoding gene and cDNA from the plant pathogenic fungus *Glomerella cingulata*. *Gene* **122**: 225–230.

Than PP, Jeewon R, Hyde KD, Pongsupasamit S, Mongkolporn O, Taylor PWJ (2008). Characterisation and pathogenicity of *Colletotrichum* species asscoaited with anthracnose on chilli (*Capsicum* spp.) in Thailand. *Plant Pathology* **57**: 562–572.

Thang MM (2008). Biodiversity survey of coelomycetes in Burma. *Australasian Mycologist* **27**: 74–110.

Trujillo EE, Latterell FM, Rossi AE (1986). *Colletotrichum gloeosporioides*, a possible biological control agent for *Clidemia hirta* in Hawaiian forests. *Plant Disease* **70**: 974–976.

Tsurushima T, Ueno T, Fukami H, Irie H, Inoue M (1995). Germination of self-inhibitors from *Colletotrichum gloeosporioides* f. sp. *jussiaea*. *Molecular Plant-Microbe Interactions* **8**: 652–657.

Vajna L, Bagyinka T (2002). Occurrence of privet anthracnose in Hungary caused by Glomerella cingulata. *Plant Disease* **51**: 403.

Varzea VMP, Rodrigues Junior CJ, Lewis BG (2002). Distinguishing characteristics and vegetative compatibility of *Colletotrichum kahawae* in comparison with other related species from coffee. *Plant Pathology* **51**: 202–207.

Venkatakrishniah NS (1952). *Glomerella psidii* (Del.) Sheld. and *Pestalotia psidii* Pat. associated with a cankerous disease of guava. *Proceedings of the Indian Academy of Plant Sciences* **36**: 129–134.

Vermeulen H, De Ferrante B, Gielink AJ (1984). Genetic and morphological diversity of mono-spore isolates of *Glomerella cingulata* associated with coffee berry disease. *Netherlands Journal of Plant Pathology* **90**: 213–223.

Vinijsanun T, Irwin JAG, Cameron DF (1987). Host range of three strains of *Colletotrichum gloeosporioides* from tropical pasture legumes, and comparative histological studies of interactions between Type B disease-producing strains and *Stylosanthes scabra* (non-host) and *S. guianensis* (host). *Australian Journal of Botany* **35**: 665–677.

Waller JM, Bridge PD, Black R, Hakiza G (1993). Characterisation of the coffee berry disease pathogen, *Colletotrichum kahawae* sp. nov. *Mycological Research* **97**: 989–994.

Wang XX, Wang B, Liu JL, Chen J, Cui XP, *et al.* (2010). First reports of anthracnose caused by *Colletotrichum gloesporioides* on ramie in China. *Plant Disease* **94**: 1508.

Weir BS, Johnston PR (2009). Defining and delimiting genetic species in *Colletotrichum*. Asian Mycologyical Congress 2009. Taichung Taiwan November 15–19. pg O-128.

Weir BS, Johnston PR (2010). Characterisation and neotypification of *Gloeosporium kaki* Hori as *Colletotrichum horii* nom. nov. *Mycotaxon* **111**: 209–219.

Weir BS, Johnston PR (2011). Towards a secondary fungal barcode for Colletotrichum [Sordariomycetes, Ascomycota]. Forth international barcode of life conference, Adelaide Australia, 28 November – 3 December 2011.

White TJ, Bruns T, Lee S, Taylor JW. (1990). Amplification and direct sequencing of fungal ribosomal RNA genes for phylogenetics. In: *PCR Protocols: A Guide to Methods and Applications*. (Innis MA, Gelfand DH, Sninsky JJ, White TJ eds). Academic Press: New York: 315–322.

Wickham H (2009). *ggplot2: elegant graphics for data analysis*. Springer New York.

Wikee S, Cai L, Pairin N, McKenzie EHC, Su YY, *et al.* (2011). *Colletotrichum* species from Jasmine (*Jasminum sambac*). *Fungal Diversity* **46**: 171–182.

Willis JC (1899). DCLII - Tea and coffee diseases. *Bulletin of Miscellaneous Information Royal Botanical Gardens Kew* **1899**: 89–94.

Winch JE, Newhook FJ, Jackson GVH, Cole JS (1984). Studies of *Colletotrichum gloeosporioides* disease on yam, *Dioscorea alata*, in Solomon Islands. *Plant Pathology* **33**: 467–477.

Wollenweber HW, Hochapfel H (1949). Beiträge zur Kenntnis parasitärer und saprophytischer Pilze. VI. *Vermicularia*, *Colletotrichum*, *Gloeosporium*, *Glomerella* und ihre Beziehung zur Fruchtfäule. *Zeitschrift für Parasitenkunde* **14**: 181–268.

Xie L, Zhang JZ, Cai L, Hyde KD (2010a). Biology of *Colletotrichum horii*, the causal agent of persimmon anthracnose. *Mycology* **1**: 242–253.

Xie L, Zhang JZ, Wan Y, Hu DW (2010b). Identification of *Colletotrichum* spp. isolated from strawberry in Zhejiang Province and Shanghai City, China. Journa*l of Zhejiang University Science B (Biomedicine & Biotechnology)* **11**: 61–70.

Yamamoto W (1960). A revision of the genus and species names of anthracnose fungi in Japan. *Plant Protection* **14**: 49–52. [in Japanese]

Yan J, Wu PS, Du HZ, Zhang QE (2011). First report of black spot caused by *Colletotrichum gloeosporioides* on paper mulberry in China. *Plant Disease* **95**: 880.

Yang SY, Su SC, Liu T, Fan G, Wang J (2011). First report of anthracnose caused by *Colletotrichum gloeosporioides* on pistachio (*Pistacia vera*) in China. *Plant Disease* **95**: 1314.

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

Zhang TY (1985). A forma specialis of *Colletotrichum gloeosporioides* on *Cuscuta* sp. *Acta Mycologica Sinica* **4**: 223–239. [In Chinese]

Zhang X, Yang G, Yang J, Shu Q (2012). Physiological mechanism of resistance to anthracnose of different *Camellia* varieties. *African Journal of Biotechnology* **11**: 2026–2031.