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. cortynicola, C. fructicola, C. gloeosporioides, C. horii, C. kahawae subsp. kahawae, C. musae, C. nupharicola, C. pisi, C. siamense, C. theobromicola, C. tropical, and C. xanthorhoeae, along with the taxa described here as new, C. aenigma, C. aeschynomenes, C. alatae, C. ailenum, C. acetaneae, C. clidemiae, C. kahawae subsp. ciggaro, C. salsoleae, 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 some 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 concern. 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 fomaeae species 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. ailenum B. Weir & P.R. Johnst., C. acetaneae B. Weir & P.R. Johnst., C. clidemiae B. Weir & P.R. Johnst., C. salsoleae 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 appressorium, growth rate in culture, culture of colours, 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-differentiated taxa will not always infect their preferred host. 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 appressorium, growth rate in culture, culture of colours, 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-differentiated taxa will not always infect their preferred host.

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 authors 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 specialae* 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 specialae* 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 micropipette 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], chinin synthase (CHS-1) [229 bp], glycolaldehyde-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 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 3130xl Avant Genetic analyzer using BigDye v. 3.1 chemistry, electropherograms were analysed and assembled in Sequencer 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 10^6 generations, and twice for 2 x 10^6 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. hippocastri 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.
| 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 | JX100111 | JX009739 | JX009470 | JX009846 | JX010136 | JX010371 | JX010449 |
| C. alienum       | IMI 313842, ICMP 18691 | Persea americana | Australia | JX010217 | JX10018 | JX009684 | JX009580 | JX009754 | JX010074 | JX010307 | JX010385 |
|                  | ICMP 18703 | Persea americana | New Zealand | JX010252 | JX100030 | JX009656 | JX009528 | JX009885 |     |      |      |
|                  | ICMP 12071* | Malus domestica | New Zealand | JX010251 | JX10028 | JX009654 | JX009572 | JX009882 | JX010101 | JX010333 | JX010411 |
|                  | ICMP 17972 | Diospyros kaki | New Zealand | JX010247 | JX00944 | JX009655 | JX009497 | JX009750 |     |      |      |
|                  | ICMP 18704 | Persea americana | New Zealand | JX010253 | JX10045 | JX009658 | JX009456 | JX009886 |     |      |      |
|                  | ICMP 18621 | Persea americana | New Zealand | JX010246 | JX009959 | JX009657 | JX009532 | JX009755 | JX010075 | JX010308 | JX010368 |
|                  | ICMP 12068 | Malus domestica | New Zealand | JX010255 | JX10025 | JX009690 | JX009492 | JX009889 |     |      |      |
|                  | ICMP 18725 | Malus domestica | New Zealand | JX010254 | JX10043 | JX009659 | JX009530 | JX009887 |     |      |      |
| C. aoteaqua      | ICMP 18532 | Vitex lucens | New Zealand | JX010220 | JX009906 | JX009614 | JX009544 | JX009746 | JX010108 | JX010338 | JX010421 |
|                  | ICMP 18734 | Agathis australis | New Zealand | JX010211 | JX10004 | 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 | Pseudopanax fergiuea | New Zealand | JX010197 | JX10026 | JX009624 | JX009522 | JX009769 | JX010110 | JX010340 | JX010416 |
|                  | ICMP 18535 | Dacrycarpus dacrydioides | New Zealand | JX010201 | JX009868 | JX009617 | JX009545 | JX009756 | 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 | JX009893 |     |      |      |
|                  | ICMP 18537* | Coprosma sp. | New Zealand | JX010205 | JX10005 | 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 | JX009433 | JX009858 |     |      |      |
|                  | ICMP 17326 | Podocarpus totara | New Zealand | JX010202 | JX10049 | JX009616 | JX009578 | JX009768 | JX010106 | JX010341 | JX010422 |
|                  | ICMP 18540 | Genistostoma lugustrifolium | New Zealand | JX010207 | JX10043 | JX009622 | JX009514 | JX009855 |     |      |      |
|                  | ICMP 18541 | Coprosma sp. | New Zealand | JX010208 | JX009900 | JX009607 | JX009513 | JX009856 |     |      |      |
|                  | ICMP 18742 | Meryta sinclairii | New Zealand | JX010210 | JX10025 | JX009626 | JX009477 | JX009862 |     |      |      |
|                  | ICMP 18740 | Dysoxylum spectabile | New Zealand | JX010218 | JX009988 | JX009625 | JX009517 | JX009763 | JX010135 | JX010368 | JX010446 |
|                  | ICMP 18530 | Vitex lucens | New Zealand | JX010268 | JX00911 | JX009623 | JX009521 | JX009884 | JX010112 | JX010339 | JX010419 |
|                  | ICMP 18735 | Hedychium gardnerianum | New Zealand | JX010221 | JX10023 | JX009620 | JX009500 | JX009880 | JX010115 | JX010343 | JX010424 |
| Species | Culture* | Host | Country | GenBank accession number |
|---------|----------|------|---------|--------------------------|
|         |          |      |         |                          |
|         | ICMP 18736 | Lonicera japonica | New Zealand | JX010200 JX009912 JX009608 JX009454 JX009894 |
|         | ICMP 18548 | Coprosma sp. | New Zealand | JX010206 JX009961 JX009609 JX009584 JX009445 JX010114 JX010342 JX010425 |
|         | ICMP 18543 | Melicoccus ramiflorus | New Zealand | JX010156 JX009833 JX009621 JX009524 JX009859 |
| C. asianum | IMI 315833, ICMP 18696 | Mangifera indica | Australia | JX010192 JX009915 JX009723 JX009576 JX009753 JX010073 JX010306 JX010384 |
|         | MAFF 306627, ICMP 18603 | Mangifera indica | Philippines | JX010195 JX009838 JX009725 JX009579 JX009825 |
|         | HKUCC 10862, ICMP 18605 | Mangifera indica | Thailand | JX010194 JX010021 JX009726 JX009465 JX009787 |
|         | ICMP 18580*, CBS 130418 | Coffea arabica | Thailand | FJ972812 JX010053 FJ917506 JX009584 JX009867 JX010096 JX010328 JX010406 |
|         | CBS 124460, ICMP 18648 | Mangifera indica | Panama | JX010193 JX010017 JX009724 JX009546 JX009871 |
| C. boninense | MAFF 305972*, ICMP 17904, CBS 123755 | Crinum asiaticum var. sincum | Japan | JX010232 JX009905 JX009583 JX009827 |
|         | ICMP 18706 | Vitis sp. | USA | JX010274 JX009909 JX009639 JX009476 JX009777 JX010128 JX010353 JX010439 |
|         | ICMP 18658* | Clidemia hirta | USA, Hawaii | JX010265 JX009899 JX009645 JX009537 JX009787 JX010129 JX010356 JX010438 |
| C. cordylinicola | MFLUCC 090551*, ICMP 18579 | Cordyline fruticosa | Thailand | JX010226 JX00975 JX009447 JX009583 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 18719 | Fragaria × ananassa | Canada | JX010180 JX009907 JX009688 JX009499 JX009820 |
|         | ICMP 18613 | Limonium sinuatum | Israel | JX010167 JX009998 JX009675 JX009491 JX009772 JX010077 JX010310 JX010388 |
|         | ICMP 18698 | Limonium sp. | Israel | JX010168 JX010052 JX009777 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 JX009929 JX009666 JX009543 JX00973 JX010098 JX010330 JX010408 |
|         | ICMP 18581*, CBS 130416 | Coffea arabica | Thailand | JX010165 JX010033 FJ917508 FJ90726 FJ917508 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 JX10009 JX00969 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 |
| 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 17921, CBS 112999 | Citrus sinensis | Australia | JX010152 | JX010066 | JX009731 | JX009531 | JX009818 | JX010085 | JX010365 | JX010445 |
|         | ICMP 12939 | Citrus sp. | New Zealand | JX010149 | JX009931 | JX009728 | JX009462 | JX009747 |
|         | ICMP 12166 | Ficus sp. | New Zealand | JX010158 | JX009955 | JX009734 | JX009550 | JX009888 |
|         | ICMP 12938 | Citrus sinensis | New Zealand | JX010147 | JX009935 | JX009732 | JX009560 | JX009746 |
|         | ICMP 18694 | Mangifera indica | South Africa | JX010155 | JX009980 | JX009729 | JX009481 | JX009796 |
|         | CBS 119304, 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 |
|         | CBS 273.51* | Citrus limon | Italy | JX010148 | JX010054 | JX009745 | JX009558 | JX009903 |
| C. gloeosporioides (syn. Gloeosporium pedemontanum) | CBS 241.78, ICMP 17920 | Hippeastum sp. | Netherlands | JX010293 | JX009932 | JX009740 | JX009485 | JX009838 |
| C. horii | ICMP 12942 | Diospyros kaki | New Zealand | GQ329867 | GQ329868 | JX009603 | JX009533 | JX009748 | JX010072 | JX010296 | JX010375 |
|         | ICMP 12951 | Diospyros kaki | New Zealand | GQ329869 | GQ329870 | JX009602 | JX009466 | JX009751 |
|         | NBRC 4748*, ICMP 10492 | Diospyros kaki | Japan | JX010212 | GQ329871 | JX009604 | JX009438 | JX009752 | JX010137 | JX010370 | JX010450 |
|         | ICMP 17968 | Diospyros kaki | China | JX010213 | GQ329872 | JX009605 | JX009547 | JX009811 | JX010068 | JX010300 | JX010378 |
|         | MAFF 306542, ICMP 17970 | Diospyros kaki | Japan | JX010214 | GQ329873 | 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 | JX010240 | JX009209 | JX009632 | JX009430 | JX009860 |
|         | ICMP 18534 | Kunzea ericoides | New Zealand | JX010241 | JX009904 | JX009634 | JX009473 | JX009765 | JX010116 | JX010351 | JX010427 |
|         | ICMP 18544 | Torenia toru | New Zealand | JX010242 | JX009920 | JX009632 | JX009430 | JX009860 |
|         | ICMP 18531 | Persia americana | New Zealand | JX009463 | JX009999 | JX009647 | JX009463 | JX009749 |
|         | ICMP 12952 | Persia americana | New Zealand | JX010243 | JX009971 | JX009648 | JX009431 | JX009757 | JX010126 | JX010348 | JX010426 |
|         | ICMP 12953 | Persia americana | New Zealand | JX010245 | JX009928 | JX009646 | JX009499 | JX009758 |
|         | CBS 112984, ICMP 17932 | Dryandra sp. | South Africa | JX010237 | JX009973 | JX009633 | JX009434 | JX009833 |
|         | IMI 359911, ICMP 17931, CBS 12088 | Dryas octopetala | Switzerland | JX010238 | JX009965 | JX009637 | JX009475 | JX009832 | JX010121 | JX010354 | JX010428 |
| C. kahawae subsp. ciggaro (syn. Glomerella cingulata var. migrans) | CBS 237.49* | Hypericum perforatum | Germany | JX010239 | JX010042 | JX009636 | JX009450 | JX009840 | JX010120 | JX010355 | JX010432 |
| Species | Host | Country |
|---------|------|---------|
| C. abbreviatum subsp. digitatum (syn. Glomerella cingulata var. vaccinii) | USA | California, Oregon |
| C. abbreviatum subsp. lechuanum | USA | California, Oregon |
| C. cibaria | Philippines | Philippines |
| C. cichoraceae | Hungary | Hungary |
| C. coffeicola | USA | Georgia |
| C. coffeicola | Cameroon | Cameroon |
| C. coffeicola | Kenya | Kenya |
| C. coffeicola | Malawi | Malawi |
| C. coffeicola | India | India |
| C. coffeicola | China | China |
| C. coffeicola | Nigeria | Nigeria |
| C. coffeicola | Tanzania | Tanzania |
| C. coffeicola | South Africa | South Africa |
| C. coffeicola | Kenya | Kenya |
| C. coffeicola | Tanzania | Tanzania |
| C. coffeicola | South Africa | South Africa |
| C. coffeicola | Kenya | Kenya |
| C. coffeicola | Tanzania | Tanzania |
| C. coffeicola | South Africa | South Africa |
| C. coffeicola | Kenya | Kenya |
| C. coffeicola | Tanzania | Tanzania |
| C. coffeicola | South Africa | South Africa |
| C. coffeicola | Kenya | Kenya |
| C. coffeicola | Tanzania | Tanzania |
| C. coffeicola | South Africa | South Africa |
| C. coffeicola | Kenya | Kenya |
| C. coffeicola | Tanzania | Tanzania |
| C. coffeicola | South Africa | South Africa |
| C. coffeicola | Kenya | Kenya |
| C. coffeicola | Tanzania | Tanzania |
| C. coffeicola | South Africa | South Africa |
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| C. coffeicola | Tanzania | Tanzania |
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| C. coffeicola | Kenya | Kenya |
| C. coffeicola | Tanzania | Tanzania |
| C. coffeicola | South Africa | South Africa |
| C. coffeicola | Kenya | Kenya |
| C. coffeicola | Tanzania | Tanzania |
| C. coffeicola | South Africa | South Africa |
| C. coffeicola | Kenya | Kenya |
| C. coffeicola | Tanzania | Tanzania |
| C. coffeicola | South Africa | South Africa |
| C. coffeicola | Kenya | Kenya |
| C. coffeicola | Tanzania | Tanzania |
| C. coffeicola | South Africa | South Africa |
| C. coffeicola | Kenya | Kenya |
| Species | Culture* | Host | Country | GenBank accession number |
|---------|----------|------|---------|-------------------------|
| C. siamense (syn. C. hymenocallicida) | CBS 125378(*), ICMP 18642 | Hymenocallis americana | China | JX010278 JX010019 JX009709 GQ856775 GQ856730 |
| C. siamense (syn. C. jasmini-sambac) | CBS 130420(*), ICMP 19118 | Jasminium sambac | Vietnam | HM131511 HM131567 HM131507 |
| C. theobromicina | MUCL 42295, ICMP 17958, CBS 124250 | Stylosanthes guianensis | Australia | JX010291 JX009948 JX009598 JX009498 JX009822 JX010067 JX010303 JX010381 |
| 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 18689 | Persea americana | South Africa | JX010262 JX009963 JX009711 JX009459 JX009795 |
| ICMP 18578*, CBS 130417 | Coffea arabica | Thailand | JX010171 JX009924 FJ917505 FJ907423 |
| HKUCC 10884, ICMP 18575 | Capsicum annuum | Thailand | JX010256 JX009738 JX009545 JX009785 |
| HKUCC 10881, ICMP 18618 | Capsicum annuum | Thailand | JX010257 JX009945 JX009718 JX009512 JX009786 |
| ICMP 18572 | Vitis vinifera | USA | JX010160 JX009961 JX009705 JX009487 JX009783 |
| ICMP 18571 | Fragaria × ananassa | USA | JX010159 JX009922 JX009710 JX009482 JX009782 |
| ICMP 18573 | Vitis vinifera | USA | JX010271 JX009966 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. hymenocallicida) | CBS 125378(*), ICMP 18642 | Hymenocallis americana | China | JX010278 JX010019 JX009709 GQ856775 GQ856730 |
| C. siamense (syn. C. jasmini-sambac) | CBS 130420(*), ICMP 19118 | Jasminum sambac | Vietnam | HM131511 HM131567 HM131507 |
| C. theobromicina | 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 JX009966 JX009599 JX009457 JX009803 JX010069 JX010299 JX010377 |
| ICMP 18576 | Limonium sp. | Israel | JX010279 JX010022 JX009595 JX009532 JX009771 |
| ICMP 17895 | Anmona diversifolia | Mexico | JX010284 JX010057 JX009600 JX009568 JX009828 JX010066 JX010304 JX010382 |
| ICMP 15445 | Acca sellowiana | New Zealand | JX010260 JX010027 JX009601 JX009509 JX009893 |
| CBS 125393, ICMP 18650 | Theobroma cacao | Panama | JX010260 JX009982 JX009590 JX009503 JX009872 |
| CBS 124945*, ICMP 18649 | Theobroma cacao | Panama | JX010294 JX010006 JX009991 JX009444 JX009869 JX010139 JX010372 JX010447 |
| ICMP 17099 | Fragaria × ananassa | USA | JX010285 JX009957 JX009598 JX009493 JX009778 |
| ICMP 17100 | Quercus sp. | USA | JX010281 JX009947 JX009866 JX009507 JX009781 |
| IMI 348152, ICMP 17814 | Fraxinella vesca | USA | JX010286 JX010033 JX009699 JX009448 JX009819 JX010062 JX010301 JX010379 |
| C. theobromicina (syn. C. fragariae) | CBS 142.31(*), ICMP 17927 | Fragaria × ananassa | USA | JX010286 JX010024 JX009992 JX009516 JX009830 JX010064 JX010295 JX010373 |
| C. theobromicina (syn. C. gloeosporioides f. stylosanthis) | MUCL 42294(*), ICMP 17957, CBS 124251 | Stylosanthes viscosa | Australia | JX010280 JX009962 JX009597 JX009575 JX009821 JX010063 JX010302 JX010380 |
### Table 1. (Continued)

| Species                     | Culture*                       | Country              | GenBank accession number | ITS*                  | GAPDH*               | CAL*                  | ACT*                  | CHS-1*               | GS*                  | SOD2*                | TUB2*               |
|-----------------------------|--------------------------------|----------------------|--------------------------|-----------------------|----------------------|----------------------|----------------------|----------------------|----------------------|----------------------|----------------------|
| C. ti                        | Cordyline australis             | New Zealand          | JX010267                 | JX009877              | JX010124             | JX010363             | JX009897             | JX009650             | JX009553             | JX009897             | JX010124             |
| C. tropicale                 | Litchi chinensis               | Japan                | JX010275                 | JX009480              | JX009826             | JX009520             | JX009870             | JX009649             | JX009520             | JX009870             | JX010131             |
| C. xanthorrhoeae             | Australia                       | Australia            | JX010261                 | JX009893              | JX009833             | JX009833             | JX009833             | JX009833             | JX009833             | JX009833             | JX010318             |
| Glomerella cingulata "f.sp. camelliae" | ICMP 10646 | UK                    | JX010262                 | JX009894              | JX009826             | JX009817             | JX009870             | JX009820             | JX009817             | JX009820             | JX010124             |

* = 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.

**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).
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.
- 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.

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

| Gene | Product name | Primer | Direction | Sequence (5′–3′) | Reference |
|------|--------------|--------|-----------|----------------|-----------|
| ACT  | Actin        | ACT-512F | Forward   | 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     | Forward   | 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    | Forward   | GAA TTC AAG GAG GCC TTC TC | This study |
|      |              | CL2C    | Reverse   | CTT CGT CAT CAT GAG CTG GAC | This study |
| CHS-1| Chitin synthase | CHS-79F | Forward   | TGG GCC AGG AG TGC TGG AGG AAG | Carbone & Kohn 1999 |
|      |              | CHS-345R | Reverse   | TGG AAG AAC CAT CTG TGA TTG TTG | Carbone & Kohn 1999 |
| GAPDH| Glyceraldehyde-3-phosphate dehydrogenase | GDF | Forward | GCC GTG AAC GAC CCC TTC ATT GA | Templeton et al. 1992 |
|      |              | GDR     | Reverse   | GGG TGG AGT CCT ACT TGA GCA TGT | Templeton et al. 1992 |
| GS   | Glutamine synthetase | GSF1 | Forward | ATG GCC GAG TAC TGC TGG | Stephenson et al. 1997 |
|      |              | GSF3    | Forward   | GCC GGT GGA GGA ACC GTC G | This study |
|      |              | GSR1    | Reverse   | GAA CGG TCG AAG TCT CAG | Stephenson et al. 1997 |
|      |              | GSR2    | Reverse   | GAA CGG TCG AAG TCT CAC | This study |
| ITS  | Internal transcribed spacer | ITS-1F | Forward | 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 |
| SOO2 | Manganese-superoxide dismutase | SOO2glo2-F | Forward | CAG ATC ATG GAG CTG CAC CA | Moriwaki & Tsukiboshi 2009 |
|      |              | SOO2glo2-R | Reverse | TAG TAC GCG TGC TGC GAC AT | Moriwaki & Tsukiboshi 2009 |
| TUB2 | β-Tubulin 2  | T1      | Forward   | AAC ATG CGT GAG ATT GTA AGT | O’Donnell & Cigelnik 1997 |
|      |              | T2      | Reverse   | TAG TGA CCC TTG GCC CAGT TG | O’Donnell & Cigelnik 1997 |
|      |              | Bi2b    | Reverse   | ACC CTC AGT GAT GTG ACC CTT GCC | 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    | TPM1u+H+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     |               |
| SOO2 | HKY+G    | GTR+H+G    |               |
| TUB2 | TrN+G    | HKY+G      |               |
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: 2312–3238, 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: 2312–3238, ITS: 3239–3823, SOD2: 3824–4199. The additional genes sequenced provided additional support for our initial species delimitations with better resolution. 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: 2312–3238, ITS: 3239–3823, SOD2: 3824–4199.

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 interspecific genetic distance between the recognised species. 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 UPGMA-based ITS gene tree (Fig. 6), shows that C. theobromicola, C. horii, C. gloeosporioides, G. cingulata “f. sp. camelliae”, C. asiyanum, 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. fruticola, 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 conidigenous 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. fruticola 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. fruticola, C. kahawae subsp. ciggaro, C. siamense, and C. theobromicola. Colletotrichum gloeosporioides s. str. is commonly isolated from Citrus in many
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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, GPDH, and ITS genes each with a separate model of DNA evolution. Bayesian posterior probability values ≥ 0.8 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. The scale bar indicates the number of expected changes per site.
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 built 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
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. aescynomenes, 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. asiaticum, 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).
The Colletotrichum gloeosporioides species complex

Ascospore length variation

- C. xanthorrhoeae
- C. ti
- C. kahawae ssp. ciggar
- C. fructicola
- C. clidemiae
- C. alienum
- C. aenigma

Ascospore width variation

- C. xanthorrhoeae
- C. ti
- C. kahawae ssp. ciggar
- C. fructicola
- C. clidemiae
- C. alienum
- C. aenigma

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, conidial mass 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 (12–14–15–18.5) × (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 *Persea 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. It has also been reported from *Pyrus pyrifolia* in Japan, the other from *Persea americana* in Arkansas.

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

= *C. gloeosporioides* “f. *sp. aechynomenes*” (Daniel et al. 1973, as *aechynomenes*).

**Etymology:** Based on *C. gloeosporioides* “f. *sp. aechynomenes*”, 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. 17.8 × 4.1 µm, n = 30), cylindrical, 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 *Aeschynomene*.

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

**Notes:** *Colletotrichum gloeosporioides* “f. *sp. aechynomenes*” 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. aechynomenes*” (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. *aechynomenes* in CBS (CBS 796.72) by G.E. Templeton, one of the early *C. gloeosporioides* f. sp. *aechynomenes* 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. *aechynomenes* 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. aechynomenes*” 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. aechynomenes*” 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.
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...
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, Barbados, 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 bomplandioid 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 more or less concentric bands of dark grey pigment, variable in intensity, in some isolates this colour partially hidden by 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 (12.5–17.5 × (3–)5–5.5(–6) µm (av. 16.5 × 5.0 µm, n = 70), cylindrical with broadly rounded ends. Appressoria mostly simple, globose to short-cylindric, a few with broad, irregular lobes; ICMP 18691 has mostly lobed appressoria. Penicillium forming in most cultures after about 10 d, dark-walled, globose with short, narrow ostiolar neck. Ascospores (14.5–19.5 × (2)–4–5(–6) µm (av. 18.1 × 4.6 µm, n = 55), cylindrical, 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, Munaiullumbah, 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. Harlitt, 2 Feb. 1988 (ICMP 18704); Bay of Plenty, Te Puna, on Persea americana ripe fruit rot, coll. W.F.T. Harlitt, 25 Jan. 1988 (ICMP 18703); Bay of Plenty, on Persea americana ripe fruit rot, coll. W.F.T. Harlitt, Feb. 1991 (ICMP 18621); Waikato, Hamilton, on Malus domestica fruit rot, coll. G.J. Robertson, May 1988 (ICMP 12065).

* 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.

**Coloniess** grown from single conidia on Difco PDA 85 mm diam after 10 d, several isolates with restricted growth, 50–55 mm diam with an irregularly scalloped margin. Aerial mycelium cotonny 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 (12.5–17.5 × (3–)5–5.5(–6) µm (av. 16.5 × 5.0 µm, n = 70), cylindrical with broadly rounded ends. Appressoria mostly simple, globose to short-cylindric, a few with broad, irregular lobes; ICMP 18691 has mostly lobed appressoria. Penicillium forming in most cultures after about 10 d, dark-walled, globose with short, narrow ostiolar neck. Ascospores (14.5–19.5 × (2)–4–5(–6) µm (av. 18.1 × 4.6 µm, n = 55), cylindrical, curved, tapering slightly to each end.

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**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 cotonny to felted mycelium, 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 (12.5–17.5 × (3–)5–5.5(–6.5) µm (av. 16.5 × 5.2 µm, n = 216), cylindrical, 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.
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 18552; 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 18258); 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 8Mf5.1, Jan. 2004 (ICMP 18533); Auckland, Waitakere Ranges, on *Dacrycarpus dacrydioides* leaf endophyte, coll. S. Joshee SK5.9, Jan. 2004 (ICMP 18535); Auckland, St. Johns, Auckland University campus, on *Coprosma* sp. incubated berries, coll. B. Weir C1282.3, 30 Apr. 2009 (ICMP 18577); Auckland, Mt Albert, on *Acmena smithii* lesions fruit, coll. P.R. Johnston C347, 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. S. Joshee & D. Than M136.3 (ICMP 18748); Auckland, Waitakere Ranges, on *Podocarpus totara* leaf endophyte, coll. S. Joshee 3Ts5.6, Jan. 2004 (ICMP 18526); Auckland, Waitakere Ranges, on *Genista* sp. leaf endophyte, coll. S. Bellgard M129, 8 Jul. 2010 (ICMP 18540); Auckland, Waitakere Ranges, on *Coprosma* sp. rotten berry, coll. S. Bellgard M130-2, 8 Jul. 2010 (ICMP 18541); Auckland, Waieke 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.
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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 JS (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.
Three earlier species, originally described from leaves rather than fruit of *Mangifera*, may provide earlier names for *C. asiamum* 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. 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.
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
Colletotrichum boehmeriae

Colletotrichum camelliae

Notes: Colletotrichum camelliae was described by Masssee (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 (AB216993), 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 as C. 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) Bertl. & 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 (Spaullding 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 Masssee (in Willis 1899) and Sutton (1980) respectively.

Glomerella cingulata

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 (Sutton and 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. [Ite 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. Affieri 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.
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,
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; **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 & Hochpfel (1949) used the name Gloeosporium elastaeg 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 239.49 = 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. phaseoll” (Kimiati & Galli 1970).

Notes: Both G. cingulata “f. sp. phaseoll” (e.g. Castro et al. 2006) and Glomerella lindemuthiana (e.g. Rodriguez-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. sorrhicola 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(−25.5) × (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. aotearae. 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 coffeaeon F. Noak, Z. Pflanzenkrankh. 11: 202. 1901.

Notes: Waller et al. (1993) discussed the use of the names Colletotrichum coffeaeon and Gloeosporium coffeaeon Delacr. and the geographic and biological differences between these
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.
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Agavaceae (Cordyline) and from Cordyline accession HM470236) supports placing the isolates from with the sequences provided by Phoulivong calmodulin gene tree generated from our sequence data together sister relationship amongst the taxa included in their analysis. The two hosts are genetically somewhat distinct, although forming a vice versa, and they also showed that the specimens from the isolate from Cordyline was not pathogenic to Eugenia and C. cordylinicola et al. (2011) report from Notes from all other species.

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. cordylina 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 cordylina 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 remains unresolved. There is confusion regarding its morphology. Von Arx (1970) uses the name C. cordylines 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 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, FN557338, 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, HM585412), C. fructicola (strain 080912009 Jining, unpubl. data, FJ150076), 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.

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
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 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 clade. 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-116 in Table 1 of Prihastuti et al. (2009) but this number is not mentioned in the description. Culture BDP-116 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, Brisbane, 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).
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, Panghegot 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. 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.
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 sinuatulum, 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, Baaden, 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 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. Phitsanulok BPD-146, 12 Dec. 2007 (ex-holotype culture of C. fusiforma, 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 CROTT.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 illinoiensis (DAR 76936; ICMP 18738). Italy, Calabria, on Citrus sinensis, (ex-holotype culture of *C. gloeosporioides* – IMI 356878 = CBS 112999 = ICMP 17821); on Citrus limon juice, coll. G. Godinich, 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 12933); Auckland, Sandringham, on Ficus sp. fruit, coll. P.R. Johnston C945.2, 9 May 1983 (ICMP 12066); Auckland, on Citrus sp. fruit, coll. G. Carroll, Feb 2010 (ICMP 18730); Northland, Kerikeri, Kapiro Rd, on Citrus sinensis fruit, coll. P.R. Johnston C1009.2, 10 Aug. 1988 (ICMP 12338). South Africa, on Mangifera indica, coll. L. Korsten Cg68 (ICMP 18694). USA, Georgia, on *Pueraria lobata* (AR2799 = BPI 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. aescynomenes” (Daniel et al. 1973, as *aescynomenes*).

Notes: See *Colletotrichum aescynomenes*.

*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. montba* 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” (Menton 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. floriniae*, 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. *gomphrena* 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, Rendicont., 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 x 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 exoholotype culture of *G. cingulata* var. *migrants*, 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 *Jussiaeae 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 *Jussiaeae* 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.-Saccà 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 melongena* Ellis & Halst. 1891 and *C. 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. nectrioida** 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 ‘stable’ 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 21366 (HM336), 1976 (*ex-holotype culture of C. gloeosporioides* f. *stylosanthis* – MUCL 42294 = ICMP 17967 = CBS 124231); *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 *Ravenelias 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, *Mycoologia* 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 ramulosus, 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.
Colletotrichum 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 125376 = 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** Wikke, 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 Wikke et al. (2011).

Wikke 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 LTAT–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. coffeaeum (see notes under C. coffeaeum). Colletotrichum kahawae is an apparently clonal population (Varzera 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
The Colletotrichum gloeosporioides species complex

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 Ferragens do Caffeiro). 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 result, *C. kahawae* subsp. *kahawae* was not known to form ascospores. Waller et al. 1993 grew cultures from 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 growing even more slowly, had little or no pigmentation within the agar, and the colony 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, (11.9–16.9)–29 (4.5–5) × (5–9) µm (av. 17.8 × 5.1 µm, n = 214), cylindrical, straight, apex rounded, often tapering slightly towards the base. *Appressoria* typically cylindrical 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 ascospore isolates 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* are broad. *Glomerella cingulata var. migrans* from *C. kahawae* subsp. *ciggaro* 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*
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 et al. (1998).
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
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 8Kun3.10 (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 12952); 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 112964, as C. crassipes = ICMP 17932). Switzerland, on Dryas octopetala, coll. P. Cannon (IMI 359911 = CBS 12968 = 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 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 Sreenivasapradas 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 1650, 1 Jan. 1953 (IMI 52264 = ICMP 17817). New Zealand, Auckland (imported fruit), on Musa sp., coll. P.R. Johnston C1197.1, 24 May 1981 (ICMP 12931; PDD 59100); Auckland (fruit imported from the Philippines), on Musa sp., coll. S. Bellard, 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 Philippines), 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 11919).

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 epiptyped 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 odorata, coll. R.D. Goos R-291, 1979 (CBS 472.96 = ICMP 16187).

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. Godnàich, 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, cylindrical 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. MacCaughy 1917, Venkatarkrishna 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
The Colletotrichum gloeosporioides species complex

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 perithecium 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:** *Gloeosporium queenslandicum* 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), cylindric, straight, sometimes slightly constricted near centre, (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. *Appressorium* 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 116663C = 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 *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 *Gloeosporium 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 16347A (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 frugigena* (Clin.) 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*" (Bemer *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
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...
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. *Penthetia* 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 Schwarzinger 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 *C. gloeosporioides* to as *(1998)* and referred *(2011)*, and *Yang *(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 115296 = ICMP 186593).

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

= Colletotrichum jasmini-sambac *Wieke,* 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), *Wieke* 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 *Wieke* et al. (2011) discussed genetic and morphological differences between *C. siamense,* *C. jasminisambac,* 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 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-12 in Table 1 of *Prihastuti* et al. (2009) but not in the description of the species. Strain BDP-12 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 americanae* leaf spot, coll. Y.L. Yang CSSN2, 19 Jun. 2008 (ex-holotype culture of *C. hymenocallidis* = CBS 125578 = ICMP 18642); Guangxi Province, Nanning, on *H. americana* leaf, coll. Y.L. Yang CSSN3 (CBS 125573 = ICMP 18643). *Nigeria,* Ibadan, on *Dioscorea rotundata* seed, coll. M. Abang CG52 (ICMP 18121); Ibadan, on *D. rotundata* seed, coll. M. Abang CG56 (ICMP 18117); Ibadan, on *Commelina sp.* leaf, coll. M. Abang CG29 (ICMP 18118). *South Africa,* on *Canica 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 Loe Village, on Coffea arabica berries, coll. H. Prihastuti BPD-12, 12 Dec. 2007 (ex-holotype culture of *C. siamense* – MFLU 090230 = ICMP 18578). Kanchanaburi, on *Capaicum annuum,* P.P. Than Ku4 (HKUCC 10848 = ICMP 18575); Nakornpathom, on *C. annuum,* coll. P.P. Than Ku4 (HKUCC 10881 = ICMP 18616). *USA,* Florida, on *Vitis vinifera* leaf, coll. N. Peres sspgrape 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 Th LITA–51 (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 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. 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.
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. 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.
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 21396 (HM336), 1979 (MUCL 42295 = ICMP 17958); New South Wales, Olea europea 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 Anonna diversifolia, coll. R. Villanueva-Aroe Gro-7, Jul. 2003 (ICMP 17895). New Zealand, Kerikeri, on Acca sellowiana, coll. M.A. Manning MM157, 1 Feb. 2004 (ICMP 15445). Panama, Chiriqui Province, San Vicente, on Theobroma cacao pod lesion, coll. E.J. Rojas ER08-9, Jan. 2008 (CBS 125933 = ICMP 18560); Chiriqui Province, Escazul, on T. cacao leaf spot, coll. E.J. Rojas QJS 08-50, Jan. 2008 (ex-neotype culture of C. theobromicola – CBS 124945 = ICMP 18569). USA, Florida, Dover, Plant City, on Fragaria x ananassa, coll. S. MacKenzie 326-1, 1988 (ICMP 17099); Florida, Lake Alfred, on Quercus sp. leaf, coll. S. MacKenzie LA-0ak-13, 2002 (ICMP 17100); Louisiana, on F. vesca, 1985 (IMI 341512 = ICMP 17814); Florida, on F. x ananassa, coll. A.N. Brooks, 1931 (ex-epiphyte 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, ti.

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 cylindrical, 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–(7–7.5) 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.
Fig. 36. Colletotrichum tl. 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. Mejia, 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. crassicps*, and *C. kahawae* subsps. *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. floriniae* 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. acutata*, *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. aoeaao, C. clidemiae, and C. theobromica 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, Aguilera 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. aoeaao, 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. aescynomenes 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. salcis 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
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GenBank data, this string appears to be specific to isolates that after the ITS1F primer binding site. Based on a comparison with complex share the string 5’–GGGCGGGT–3’ about 139–142 bases C. gloeosporioides research. All of the isolates that we accept in the presumably regarding this level of identification as sufficient for their C. gloeosporioides the name in the sense of the over the past 12 mo show that many authors will continue to use C. gloeosporioides populations within a genetically strongly supported species. A biologically specialised population at the subspecies level. A similar from other hosts are not pathogenic to coffee berries (Silva et al. 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 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. Talhanas 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. asiunam. 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. xanthorrhoeae, C. fructicola, and C. siamense. These bands will be produced by C. xanthorrhoeae (band sizes 253, 316, 388), the two C. kahawae subsp. (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.

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. nuphanicola   | 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    | N    | Y    | Y     | Y    | Y    |
| C. siamense      | N    | N     | Y    | N    | N    | N     | N    | N    |
| C. aescynomenes  | N    | N     | N    | Y    | N    | Y     | Y    | Y    |
| C. tropicale     | N    | N     | N    | Y    | N    | Y     | Y    | Y    |
| C. queenslandicum| N    | Y     | Y    | Y    | N    | N     | Y    | N    |
| C. salsoiae      | 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    | N    | N*    | N    | N    |
| G. cingulata “f. sp. camelliae” | Y | N | Y | Y | Y | Y | N | Y |
| C. clidemiae     | N    | N     | N    | N    | Y    | Y     | Y    | N    |
| C. paidii        | Y    | Y     | Y    | N    | Y    | Y     | Y    | Y    |
| C. cordylincola  | Y    | Y     | Y    | Y    | N    | Y     | Y    | Y    |

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. 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 beans, 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.
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 C. g. 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. aegyptiacomones and C. gloeosporioides f. sp. jussiaeiæ, 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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