Colletotrichum – current status and future directions

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Abstract: A review is provided of the current state of understanding of Colletotrichum systematics, focusing on species-level data and the major clades. The taxonomic placement of the genus is discussed, and the evolution of our approach to species concepts and anamorph-teleomorph relationships is described. The application of multilocus technologies to phylogenetic analysis of Colletotrichum is reviewed, and selection of potential genes/loci for barcoding purposes is discussed. Host specificity and its relation to speciation and taxonomy is briefly addressed. A short review is presented of the current status of classification of the species clusters that are currently without comprehensive multilocus analyses, emphasising the orbiculare and destructivum aggregates. The future for Colletotrichum biology will be reliant on consensus classification and robust identification tools. In support of these goals, a Subcommission on Colletotrichum has been formed under the auspices of the International Commission on Taxonomy of Fungi, which will administer a carefully curated barcode database for sequence-based identification of species within the BiobMICS web environment.

Key words: anamorph-teleomorph linkages, barcoding, Colletotrichum, database, Glomerella, host specialisation, phylogeny, systematics, species concepts.

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INTRODUCTION

The genus Colletotrichum includes a number of plant pathogens of major importance, causing diseases of a wide variety of woody and herbaceous plants. It has a primarily tropical and subtropical distribution, although there are some high-profile species affecting temperate crops. Fruit production is especially affected, both high-value crops in temperate markets such as strawberry, mango, citrus and avocado, and staple crops such as banana. Colletotrichum species cause devastating disease of coffee berries in Africa, and seriously affect cereals including maize, sugar cane and sorghum. The genus was recently voted the eighth most important group of plant pathogenic fungi in the world, based on perceived scientific and economic importance (Dean et al. 2012).

As plant pathogens, Colletotrichum species are primarily described as causing anthracnose diseases, although other maladies are also reported such as red rot of sugar cane, coffee berry disease, crown rot of strawberry and banana, and brown blotch of cowpea (Lenné 2002). Anthracnose disease symptoms include limited, often sunken necrotic lesions on leaves, stems, flowers and fruit, as well as crown and stem rots, seedling blight etc. (Waller et al. 2002, Agris 2005). A range of disease symptoms is illustrated in Fig. 1. Many species may be seed-borne and can survive well in soil by growing saprobically on dead plant fragments, and may be spread via water-splash dispersal of conidia and air transmission of ascospores from the sexual morph (Nicholson & Moraes 1980). Infection occurs via an appressorium that develops from the germinating spore on the plant surface, followed by turgor-driven penetration of the cuticle (Deising et al. 2000) and in some cases also of epidermal cells by infective hyphae (Bailey et al. 1992). Establishment within plant tissues is aided via production by the fungus of host-induced virulence effectors (Kleeman et al. 2012, O’Connell et al. 2012). Nascent colonies in most cases then enter a biotrophic phase with infected tissues remaining externally symptomless and which may be short (1–3 d; O’Connell et al. 2000) or extended and presumably involving dormancy (Prusky & Plumbley 1992). Then, the fungus enters a necrotrophic phase that results in significant death of plant cells and the emergence of pathogenic lesions. This delayed onset of disease symptoms may lead to significant post-harvest losses, with apparently healthy crops degenerating in storage (Prusky & Plumbley 1992). The biotrophic life strategies adopted by Colletotrichum species may also contribute to their prominence as symptomless endophytes of living plant tissues (Lu et al. 2004, Joshee et al. 2009, Rojas et al. 2010, Yuan et al. 2011). There are no comprehensive modern reviews of the biology, pathology and host/parasite interactions of Colletotrichum species, but useful information can be found in Bailey & Jeger (1992) and Prusky et al. (2000).

Colletotrichum species are also extensively studied as model organisms for research into genetics. This work has a long history; the first investigation into mating types in Glomerella was published a century ago (Edgerton 1912, 1914), and genetic mechanisms in G. cingulata were extensively studied in the 1940’s and 50’s (e.g. Andes 1941, Lucas et al. 1944, Wheeler 1950, 1954, Olive 1951).

Research into host/parasite systems has had almost as long a history, originating with work on the C. lindemuthianum/Phaseolus vulgaris interaction by Barrus (1918). Mechanisms of infection and disease development in the same model system were extensively studied in the 1980’s (e.g. Bell et al. 1984, O’Connell et al. 1985, 1986).

Maize anthracnose caused by Colletotrichum graminicola is an economically important disease on a global level, stimulating...
a further body of research into Colletotrichum genetics, pathology and host-parasite interactions. It has been reviewed by Nicholson (1992), Bergström & Nicholson (1999), Vaillancourt et al. (2000) and Crouch & Beirn (2009).

The relationship between Colletotrichum higginsianum and its Brassica hosts has also been the subject of much recent research (Perfect et al. 1999, O’Connell et al. 2004). Huser et al. (2009) discovered pathogenicity genes in C. higginsianum by random insertional mutagenesis. Jaulneau et al. (2010) compared the defence reactions of resistant or susceptible lines of Medicago trunculata to the alfalfa pathogen C. trifoli with reactions of the nonadapted pathogens C. lindemuthianum and C. higginsianum. O’Connell et al. (2012) studied the genomes and transcriptomes of two species, C. higginsianum and C. graminicola with different infection strategies.

Work on the genetics of pathogenicity in the C. orbiculare species aggregate (e.g. Pain et al. 1994, Rodríguez & Redman 2000) led to transformation of pathogenic strains to endophytic forms. These were shown to exhibit mutualistic activity by protection against virulent strains of the same species, and also to Fusarium pathogens. Gene manipulation techniques such as Agrobacterium tumefaciens-mediated transformation or protoplast transformation are established (Tsui et al. 2003) and for host parasite interaction studies with C. orbiculare, a model plant Nicotiana benthamiana is being used. Several genes involved in signal transduction pathways essential for the formation of infection structures were identified (Takano et al. 1997, Tanaka et al. 2009) and two peroxisome biogenesis genes, PEX6 and PEX13 that are essential for pathogenesis were functionally analysed (Kimura et al. 2001, Fujihara et al. 2010). Asakura et al. (2009) discovered the importance of the pexophagy factor ATG26 for appressorium function.

Whole-genome sequences of C. graminicola and C. higginsianum have been completed (O’Connell et al. 2012) – the latter genome from a pathogen of the model plant organism Arabidopsis thaliana – and projects to sequence several other species are in progress or preparation (Damm et al. 2010). The research to date is already demonstrating step changes in our understanding of host-parasite interactions in Colletotrichum. Colletotrichum is traditionally recognised as an asexual genus of fungi, with a number of species linked to sexual morphs assigned to the genus Glomerella (Glomerellaceae, Glomerellales; Zhang et al. 2006, Rébllová et al. 2011). In the light of recent moves towards a unified nomenclatural system for the Fungi, we will for the most part refer to species using asexual names, which not only have date priority in all cases we have identified, but are much better known in the applied sciences.

HOST RELATIONS AND SPECIFICITY

For many years, Colletotrichum species were assumed to be specific to the plants they infected, leading to large numbers of taxa described with little in the way of distinctive features apart from the identity of their plant partners.

Our current understanding of the extent that Colletotrichum species exhibit host specificity is imperfect. This is due to a number of factors, including incomplete sampling, restriction of data largely to populations affecting crop or ornamental plants, and poor knowledge of pathogenic effects. Information on most strains in culture collections indicates an association with a particular plant species, but rarely provides details of the interaction. Many studies on Colletotrichum are restricted to strains affecting single crop species (e.g. Buddie et al. 1999, González et al. 2006, Gazis et al. 2011), significantly reducing the extent of the gene pool being sampled. Mackenzie et al. (2007) demonstrated gene flow between populations of C. acutatum from native plants and those from adjacent strawberry crops, demonstrating the limitations of host-restricted studies.

The ability of many Colletotrichum species to exist as endophytes adds extra complications to our understanding of host specificity (Lu et al. 2004, Liu et al. 2007, Rojas et al. 2010). Isolation from living plant tissue does not necessarily imply that the species is a latent pathogen with a hemibiotic phase (Lattunde-Dada 2001, Peres et al. 2005, Münch et al. 2008), and distinguishing between the two life strategies is problematic. Freeman & Rodríguez (1993) and Redman et al. (1999) demonstrated that a single disruption event of a pathogenicity gene transformed a pathogenic strain of Glomerella magna from Citrullus lanatus into an endophyte that conferred protection for the host plant against wild type strains and other pathogens. Similar single gene effects on pathogenicity are documented from the interaction between C. graminicola and maize (Thon et al. 2000, 2002). Research into the molecular basis of host-parasite interactions in Colletotrichum is currently highly active (see O’Connell et al. 2012), and such approaches will dominate research in the future into the extent of host specificity exhibited by Colletotrichum species.

We are not aware of any major group of angiosperms that does not harbour endophytic Colletotrichum colonies. There are also well-documented cases of Colletotrichum living as endophytes and disease agents of conifers (Dingley & Gilmour 1972, Wang et al. 2008, Joshee et al. 2009, Damm et al. 2012a) and ferns (Leathy et al. 1995, MacKenzie et al. 2009). Species are associated with both herbaceous and woody plants, though the latter appear mainly to contain colonies in fruits, leaves and other non-lignified tissues.

There are isolated accounts of Colletotrichum species causing infections of insects, including C. floriniae on hemlock scale insects in New England and a claimed member of the C. gloeosporioides aggregate on citrus scale insects in Brazil (Marcelino et al. 2008). Infection mechanisms are not fully understood; under experimental conditions the insects became infected after being sprayed with a conidial suspension (Marcelino et al. 2009). In the field it seems possible that endophytic colonies of the fungus are ingested via the insect mouth-parts, the reverse of a process that has been shown in members of the Clavicipitaceae to infect plants via the stylets of sap-sucking insects (Torres et al. 2007, Tadych et al. 2009).
In rare instances, *Colletotrichum* species have been implicated in human disease, causing keratitis and subcutaneous infections (e.g. Ritterband et al. 1997, Guarro et al. 1998, Shiraishi et al. 2011, Shivaprakash et al. 2011). A single occurrence of disseminated mycotic infection of a sea turtle has also been recorded (Manire et al. 2002). Cano et al. (2004) reviewed the identification procedures for *Colletotrichum* species of clinical interest.

Some *Colletotrichum* clades appear to contain species that show at least a degree of host specificity, though these data may be linked to incomplete sampling and/or species concepts that assume specificity. The orbiculare clade is a case in point; here species seem to be restricted to individual host genera (Liu et al. 2007). That clade is a basal group (see Fig. 2), which might suggest that the extraordinary flexibility in host preference demonstrated by most other clades evolved subsequent to appearance of the genus itself. The graminicola group contains several species that are limited to host genera within the Poaceae (Crouch et al. 2009a). *Colletotrichum cereale*, a grass-inhabiting taxon which occupies a separate clade from the graminicola aggregate, does not appear to show genus-level specificity, though all strains to date derive from the same family (Crouch et al. 2009c). Here, population-level specificity is found in some cases, though the basal lineage is plurivorous, suggesting that host specialisation is in the process of development.

At a finer scale, several *Colletotrichum* species have been shown to exhibit substantial pathogenic variation at race level, although in most cases the precise phylogenetic position and diversity of the strains studied has not been established. In a large-scale project on strains identified as *C. lindemuthianum* from South, Central and North America, Balardin et al. (1997) characterised 41 races from a total of 138 isolates, based on virulence to 12 cultivars of *Phaseolus vulgaris*. No coevolutionary pattern within a small area. Heterothallic mating and teleomorph formation was recently re-established as an independent species (Damm 2009), and will not be repeated here. Any move to establish *Vermicularia* as a replacement name for *Colletotrichum* would have disastrous consequences for scientific communication, and would certainly trigger a conservation proposal. *Vermicularia* was adopted quite widely for curved-spored species in the early years of *Colletotrichum* systematics, even though the type species of *Colletotrichum* also has curved conidia. The genus *Gloeosporium* (Montagne 1849) was also frequently confused with *Colletotrichum* in the late 19th and early 20th centuries. It was used for taxa of *Colletotrichum* without conidiomatal setae (their development in many species is variable) but also included quite unrelated fungi. The type of *Gloeosporium*, *G. castagnæi* is not congeneric with *Colletotrichum* and is currently included in *Marssonina*, technically providing an earlier name for that genus (von Arx 1957a, 1970). A further 10 generic synonyms for *Colletotrichum* were listed by Sutton (1980); none has been in recent use.

Two further species (both currently of uncertain application) were added to *Colletotrichum* by Corda in the years following the original publication of the genus name (Corda 1837, 1840), but the group only came to prominence in the late 19th century with publication of Saccardo's *Sylloge Fungorum* compilations. Fifty new taxa at species level or below were described between 1880 and 1900, and this trend of new species recognition accelerated well into the 20th century. At the time of the first formal monographic treatment of *Colletotrichum*, by von Arx (1957b), around 750 names were in existence. This explosion of what might now be regarded as largely futile taxonomic activity seems to have been driven largely by uncritical assumptions that *Colletotrichum* species are strongly host-specific. The result was that in many instances a new taxon was erected each time an infection caused by a *Colletotrichum* species was discovered on a plant genus for which no disease had previously been reported, even in the absence of unique morphological diagnostic characters.

The impact of von Arx's monograph (von Arx 1957b) was considerable, and it set the stage for a new era in *Colletotrichum* taxonomy. His approach was based on morphological characteristics with little or no emphasis on placed on pathological features, which led to a reduction in accepted species from around 750 to 11 (within a total of 23 accepted specific and infraspecific taxa). Many taxa were evaluated based on descriptions from the literature rather than evaluation of type specimens. Such a drastic reduction in numbers of taxa provided a new foundation on which to develop subsequent systematic treatments, but it is clear that even von Arx himself regarded the 11 accepted species as broadly circumscribed aggregates rather than individual taxa. In particular, the account of *C. gloeosporioides* (itself with around 600 synonyms) incorporated

**HISTORY OF CLASSIFICATION**

The generic name *Colletotrichum* was introduced by Corda (1831) for *C. lineola*, a species found associated with a member of the Apiaceae in the Czech Republic. *Colletotrichum lineola* was long considered a synonym of the older taxon *C. dematium*, but was recently re-established as an independent species (Damm et al. 2009). That work included the acquisition and culture of a recent collection of *C. lineola* from a similar host and locality, and designation of an epitype for the name.

The genus *Vermicularia* (Tode 1790) could be regarded as an earlier name for *Colletotrichum* according to some interpretations of the Code of Nomenclature for Algae, Fungi and Plants. The nomenclatural details have been outlined successively in the light of the then current rules by Duke (1929), Sutton (1992) and Damm et al. (2009), and will not be repeated here. Any move to establish *Vermicularia* as a replacement name for *Colletotrichum* would have disastrous consequences for scientific communication, and would certainly trigger a conservation proposal. *Vermicularia* was adopted quite widely for curved-spored species in the early years of *Colletotrichum* systematics, even though the type species of *Colletotrichum* also has curved conidia. The genus *Gloeosporium* (Montagne 1849) was also frequently confused with *Colletotrichum* in the late 19th and early 20th centuries. It was used for taxa of *Colletotrichum* without conidiomatal setae (their development in many species is variable) but also included quite unrelated fungi. The type of *Gloeosporium*, *G. castagnæi* is not congeneric with *Colletotrichum* and is currently included in *Marssonina*, technically providing an earlier name for that genus (von Arx 1957a, 1970). A further 10 generic synonyms for *Colletotrichum* were listed by Sutton (1980); none has been in recent use.

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a series of nine “abweichende Formen” [variant forms], including five taxa combined into *Colletotrichum* by von Arx in this work or the companion volume on *Gloeosporium* (von Arx 1957a). These variant forms were considered to be host-specific variants that could not reliably be distinguished on a morphological basis from the main bulk of *C. gloeosporioides*. Included were species now treated within the *C. orbiculare*, *C. acutatum* and *C. gloeosporioides* aggregates, as well as other taxa that are currently of uncertain affiliation. Von Arx’s approach to *Colletotrichum* classification now appears crude even in purely morphological terms, and as Sutton (1992) and Cannon et al. (2000) both noted, more attention to matters of typification would have been valuable. Nonetheless, this seminal work of von Arx laid the foundation for all subsequent morphological taxonomic work on the genus *Colletotrichum*.

Subsequent taxonomic treatments primarily focused on species groups, or taxa associated with particular crop plants. Important contributions were made in the 1960s by Simmonds (1965; recognition of *Colletotrichum acutatum*), and by Sutton (1966, 1968; taxonomy of the *C. graminicola* complex and the value of apressorial morphology in classification). The next comprehensive treatment of *Colletotrichum* was by Sutton (1980), who accepted 22 species, and a study of 11 South African species was contributed by Baxter et al. (1983). Both of these accounts focused primarily on morphological and cultural characteristics, and most of the taxa were considered to be plurivorous. Similar approaches were adopted by Smith & Black (1990) for species on strawberry, and Walker et al. (1991) for those associated with *Xanthium*, but with increased emphasis on integration of taxonomic and pathological data.

The first International Workshop on *Colletotrichum* was held in late 1990 at the University of Bath, UK (Bailey & Jeger 1992), bringing together experts on taxonomy, molecular biology, host/parasite interactions and pathology. This marked the advent of the wide-scale application of molecular methods in *Colletotrichum* studies, which has revolutionised research in that genus as with many other fungal groups. Initially, work focused on infraspecific variation; DNA polymorphisms were detected in *C. gloeosporioides* by Dale et al. (1988), Braithwaite & Manners (1989) and Braithwaite et al. (1990a, b), and strains of that species (as then circumscribed) were found to have variable numbers of chromosomes (Masel et al. 1990).

The first applications of DNA sequence data to distinguish between *Colletotrichum* species were published by Mills et al. (1992) and Sreenivasaprasad et al. (1992), who identified sequence variation in the ITS1 region of rDNA between six species of *Colletotrichum*, as well as detecting polymorphisms in the same region between strains of *C. gloeosporioides* from different hosts. More comprehensive studies followed rapidly; Sherriff et al. (1994) presented the first bootstrapped NJ trees for *Colletotrichum*, using ITS2 and LSU sequences of 27 strains indicated as belonging to 13 species. This study recognised the *C. orbiculare* aggregate as a distinct taxonomic unit, and detected genetic congruence between the four curved-spored species studied. In a portent of things to come, Sherriff et al. showed that not all of the strains examined were correctly identified using morphological characteristics, with one strain each of *C. gloeosporioides* and *C. lindemuthianum* clustering separately from the others. A second phylogenetic study of the genus was published by Sreenivasaprasad et al. (1996) using parsimony analysis of ITS 1 and 2 sequences from 18 species of *Colletotrichum*, and the authors were able to identify six infrageneric groups. Sreenivasaprasad et al. also used infra- and interspecific nucleotide identity in the ITS region as indicators of the taxonomic rank at which strains should be differentiated, as an early forerunner of the DNA barcoding initiatives.

The number of papers using molecular methods to elucidate relationships in *Colletotrichum* increased rapidly after the early 1990s. Most of these studies focused on small groups within the genus, usually associated with a particular crop (see Table 1). More wide-ranging studies were presented by Johnston & Jones (1997), who used LSU rDNA sequences to analyse strains from diseased fruit crops in New Zealand, and Moriwaki et al. (2002) who studied ITS-2/LSU rDNA of *Colletotrichum* species from Japan. The first multilocus phylogenetic analyses of *Colletotrichum* species were published by Talhinhas et al. (2002), a study of the *C. acutatum* aggregate associated with lupins using ITS, TUB2 and HIS4 sequences, and Vinnere et al. (2002) using ITS, TUB2 and mISSU in a study on the same species cluster associated with *Rhododendron* in Sweden and Latvia. Talhinhas et al. (2002) found that the three loci they studied displayed broadly similar levels of phylogenetic resolution. Guerber et al. (2003) used glyceraldehyde-3-phosphate dehydrogenase (GAPDH) and glutamine synthetase (GS) nucleotide sequences in a further study of the *C. acutatum* group, and the HMG-box section of the mating-type genes MAT-1 was found to be a valuable evolutionary marker by Du et al. (2005). From around this time, multilocus analyses became the norm as sequencing costs reduced, with sequence data generated from loci such as actin (ACT), calmodulin (CAL), chitin synthase I (CHS-1), DNA lyase (APN2), manganese superoxide dismutase (SOD2), the large subunit of RNA polymerase II (RPB1) and the translation elongation factor 1-α (EF1α) (see Table 1 for references).

A further milestone in *Colletotrichum* systematics was reached with publication of a special issue of the journal *Fungal Diversity* in late 2009, containing a group of papers presenting taxonomic revisions and review articles relevant to the genus. This includes an introductory paper focusing on the need for correct identification (Hyde et al. 2009b), a review of the cereal-inhabiting species (Crouch & Beirn 2009), a revision of the species with curved conidia from herbaceous hosts (Damm et al. 2009), a study of the species affecting coffee berries in Thailand (Prihashuti et al. 2009), a partial revision of the *C. acutatum* group (Shivas & Tan 2009) and research on the species associated with *Amaryllidaceae* (Yang et al. 2009). The issue concludes with a review of the status of *Colletotrichum* names in current use (Hyde et al. 2009a) and recommendations for polyphasic methods (Cai et al. 2009).

The list of *Colletotrichum* names in current use (Hyde et al. 2009a) accepted a total of 66 species, with an additional 20 recently used names considered as doubtful. This assessment represented a substantial increase in the number of recognised species compared with the 23 taxa recognised by von Arx (1957) and the 39 species accepted by Sutton (1992), and reflected the increasing reliance on molecular methods for species definition. With publication of the current volume of *Studies in Mycology*, a further 41 species are introduced, bringing the current number of accepted *Colletotrichum* species to over 100. It is likely that further *Colletotrichum* taxa remain to be recognised in the major clades that have not yet been the subject of comprehensive multilocus studies.

*Colletotrichum* species from non-cultivated plants in natural and semi-natural habitats are much less commonly studied than those associated with cultivated plant hosts, with most studies being of endophytic strains. A study on leaf endophytes of native forest trees by Lu et al. (2004) examined diversity within the *C. gloeosporioides* and *C. boninense* species clusters, and Xiao et al. (2004) and Mackenzie et al. (2007) compared strains of the *C. gloeosporioides*
Table 1. Summary of principal phylogenetic research papers on *Colletotrichum* species based on DNA sequence data.

| Publication                        | Clade                   | Host taxa                  | Geographical limits | Loci used          |
|-----------------------------------|-------------------------|----------------------------|---------------------|--------------------|
| Mills et al. (1992)               | genus-wide              | Tropical fruits            |                     | ITS                |
| Sreenivasaprad et al. (1992)      | acutatum, gloeosporioides | Strawberry                |                     | ITS                |
| Sreenivasaprad et al. (1993)      | gloeosporioides         | Coffee                     |                     | ITS                |
| Sherriff et al. (1994)            | genus-wide              |                            |                     | ITS-2, LSU         |
| Sherriff et al. (1995)            | graminicola             | Poaceae                    |                     | LSU                |
| Bailey et al. (1996)              | orbiculare              | Malvaceae                  |                     | ITS, LSU           |
| Sreenivasaprad et al. (1996)      | genus-wide              |                            |                     | ITS                |
| Johnston & Jones (1997)           | genus-wide              | Fruit crops                | New Zealand         | LSU                |
| Munaut et al. (1998)              | gloeosporioides         | Stylosanthes               | Africa, Australia   | ITS                |
| Balardin et al. (1999)            | orbiculare              | Phaseolus                  |                     | ITS                |
| Martin & García-Figuerees (1999)  | acutatum, gloeosporioides | Olive                     | Spain               | ITS                |
| Freeman et al. (2000)             | acutatum, gloeosporioides | Almond, avocado, strawberry | Israel, USA         | ITS, LSU           |
| Freeman et al. (2001)             | acutatum                | Mostly fruit crops         |                     | ITS                |
| Hsiang & Goodwin (2001)           | graminicola             | Poaceae                    |                     | ITS                |
| Abang et al. (2002)               | gloeosporioides         | Yam                        | Nigeria             | ITS                |
| Chen et al. (2002)                | graminicola             | Agrostis                   | Canada              | MAT2               |
| Moriwaki et al. (2002)            | genus-wide              | Japan                      |                     | ITS-2, LSU         |
| Munaut et al. (2002)              | gloeosporioides         | Stylosanthes               | Mexico              | ITS                |
| Nirenberg et al. (2002)           | acutatum                | Lupin                      |                     | ITS                |
| Talhinhas et al. (2002)           | acutatum                | Lupin                      |                     | ITS, TUB2, HIS4    |
| Vinnere et al. (2002)             | acutatum                | *Rhododendron*             | Sweden, Latvia      | ITS, TUB2, mtSSU   |
| Afanador-Kafuri et al. (2003)     | acutatum, gloeosporioides | Mango, passion-fruit, tamarillo | Colombia            | ITS                |
| Deroyes-Rothan et al. (2003)      | acutatum, gloeosporioides | Strawberry                |                     | ITS                |
| Guerber et al. (2003)             | acutatum                |                            | USA, New Zealand    | GAPDH, GS         |
| Martinez-Culebras et al. (2003)   | acutatum, gloeosporioides | Strawberry                |                     | ITS                |
| Moriwaki et al. (2003)            | boninense               | Japan                      |                     | ITS                |
| Sanders & Korsten (2003)          | gloeosporioides         | Avocado, mango             | South Africa        | ITS                |
| Ford et al. (2004)                | destructivum            | Legumes                    |                     | ITS                |
| Lu et al. (2004)                  | boninense, gloeosporioides | Endophytes of tropical trees | Guyana              | ITS                |
| Lubbe et al. (2004)               | Genus-wide              | Proteaceae                 | primarily Africa    | ITS, TUB2          |
| O’Connell et al. (2004)           | destructivum            |                            |                     | ITS                |
| Du et al. (2005)                  | acutatum, graminicola, gloeosporioides |                     |                     | ITS, MAT1-2 (HMG marker) |
| Lee et al. (2005)                 | boninense               | *Euonymus japonicus*       | Korea               | ITS                |
| Lotter & Berger (2005)            | acutatum                | Lupin                      | South Africa        | ITS, TUB1, TUB2    |
| Photita et al. (2005)             | genus-wide              |                            | Thailand            | ITS                |
| Talhinhas et al. (2005)           | acutatum, gloeosporioides | Olive                     | Portugal            | ITS, TUB2          |
| Chung et al. (2006)               | acutatum, gloeosporioides | Fruit crops               | Japan               | ITS                |
| Crouch et al. (2006)              | graminicola             | Poaceae                    | USA                 | ITS, MAT1-2 (HMG marker), SOD2 |
| Farr et al. (2006)                | genus-wide              | Agavaceae                  |                     | ITS, LSU           |
| González et al. (2006)            | acutatum, gloeosporioides | Apple                     | USA, Brazil         | GAPDH              |
| Ramos et al. (2006)               | acutatum, gloeosporioides | Citrus                    | Portugal            | ITS, TUB2          |
| Latunde-Dada & Lucas (2007)       | destructivum, truncatum, graminicola |                     |                     | ITS, LSU           |
| Lee et al. (2007)                 | acutatum, gloeosporioides | Apple                     | Korea               | ITS, TUB2          |
| Liu et al. (2007a)                | orbiculare              |                            |                     | GAPDH, GS         |
| Liu et al. (2007b)                | dracaenophilum          | Buxus                      | China               | ITS                |
| Shenoy et al. (2007)              | truncatum               | Solanaceae                 |                     | ITS, TUB2          |
| Whitelaw-Weckert et al. (2007)    | acutatum                | Grape                      | Australia           | ITS, TUB2          |
| Cannon et al. (2008)              | gloeosporioides         |                            |                     | ITS                |
Table 1. (Continued).

| Publication                          | Clade         | Host taxa          | Geographical limits   | Loci used                                      |
|-------------------------------------|---------------|--------------------|-----------------------|-----------------------------------------------|
| Crouch et al. (2008)                | graminicola   | Poaceae            |                       | Ccret2                                        |
| LoBuglio & Pfister (2008)           | acetatum      | Acer platanoides   | USA                   | ITS, LSU, TUB2, GAPDH, GS, MAT1-2             |
| Marcelino et al. (2008)             | acetatum      | Insects            | USA                   | ITS, LSU, TUB2, GAPDH, GS, MAT1-2             |
| Peres et al. (2008)                 | acetatum      | Citrus             | N and S America       | ITS, GAPDH                                    |
| Than et al. (2008a)                 | acetatum, truncatum, gloeosporioides |             |                       | ITS, TUB2                                     |
| Than et al. (2008b)                 | acetatum      |                    |                       | ITS, TUB2                                     |
| Crouch et al. (2009c)               | graminicola   | Poaceae            |                       | ITS, APN2/IGS/MAT1-2, SOD2                    |
| Crouch et al. (2009d)               | graminicola   | Poaceae            |                       | ITS, APN2/IGS/MAT1-2, SOD2                    |
| Damm et al. (2009)                  | dematium, spaethianum, truncatum |             |                       | ITS, ACT, GAPDH, CHS-1, TUB2, HIS3           |
| Garrido et al. (2009)               | acetatum      | Strawberry         | Spain                 | ITS                                           |
| MacKenzie et al. (2009)             | acetatum      |                    | USA, Costa Rica       | ITS, GAPDH, GS                               |
| McKay et al. (2009)                 | acetatum, boninense, gloeosporioides | Almond  | Australia             | ITS                                           |
| Moriwaki & Tsukiboshi (2009)        | graminicola   | Echinochloa        | Japan                 | ITS, MAT1-2 (HMG marker), SOD2                |
| Pileggi et al. (2009)               | boninense, gloeosporioides | Maytenus ilicifolia | Brazil                | ITS                                           |
| Polashock et al. (2009)             | acetatum, gloeosporioides | Cranberry | N America             | ITS, LSU                                      |
| Prihastuti et al. (2009)            | gloeosporioides | Coffee             | Thailand              | ITS, ACT, TUB2, CAL, GS, GAPDH                |
| Shivas & Tan (2009)                 | acetatum      |                    |                       | ITS, TUB2                                     |
| Sun & Zhang (2009)                  | destructivum  |                    |                       | ITS                                           |
| Talhinhas et al. (2009)             | acetatum, gloeosporioides | Olive          | Portugal              | ITS, TUB2                                     |
| Yang et al. (2009)                  | genus-wide    | Amaryllidaceae     | China, Thailand       | ITS, ACT, TUB2, CAL, CHS-1, GAPDH             |
| Giaretta et al. (2010)              | acetatum, gloeosporioides | Apple           | Brazil, Thailand      | ITS                                           |
| Hemelrijk et al. (2010)             | acetatum      | Strawberry         | Belgium               | ITS                                           |
| Lopez & Lucas (2010)                | gloeosporioides | Cashew             | Brazil                | LSU                                           |
| Manuel et al. (2010)                | gloeosporioides | Coffee             | Angola                | ITS                                           |
| Nguyen et al. (2010)                | genus-wide    | Coffee             | Vietnam               | ITS, mtSSU                                    |
| Phoulivong et al. (2010)            | gloeosporioides | Tropical fruits    | Laos, Thailand        | ITS, TUB1, TUB2, CAL, ACT, GAPDH              |
| Phuong et al. (2010)                | genus-wide    | Coffee             | Vietnam               | ITS, mtSSU                                    |
| Prihastuti et al. (2010)            | graminicola   | Poaceae            |                       | ITS, APN2/IGS/MAT1                            |
| Rojas et al. (2010)                 | gloeosporioides | Cacao              | S America, China      | ITS, EF1α, TUB2, RPB1, APN2, MAT1-2          |
| Weir & Johnston (2010)              | gloeosporioides | Persimmon          |                       | ITS, GAPDH, EF1α                              |
| Wikee et al. 2010                   | gloeosporioides | Jasmine            | Vietnam               | ITS, ACT, TUB2, CAL, GS, GAPDH                |
| Xie et al. (2010)                   | acetatum, gloeosporioides | Strawberry      | China                 | ITS                                           |
| Choi et al. (2011)                  | destructivum  |                    | Korea                 | ITS, ACT, EF1α, GS                            |
| Faedda et al. (2011)                | acetatum      | Olive              | Italy                 | ITS, TUB2                                     |
| Gazis et al. (2011)                 | gloeosporioides | Hevea species      | Peru                  | ITS, TEF, GPD                                 |
| Liu et al. (2011)                   | cocodes       | Potato             |                       | ITS, ACT, GAPDH, TUB2                         |
| Rampersad (2011)                    | gloeosporioides, truncatum | Papaya         | Trinidad              | ITS, TUB2                                     |
| Silva-Rojas & Ávila-Quezada (2011)  | acetatum, boninense, gloeosporioides | Avocado       | Mexico                | ITS, LSU                                      |
| Yang et al. (2011)                  | genus-wide    | Orchidaceae        | China                 | ITS, ACT, TUB2, CAL, CHS-1, GAPDH             |
| Crouch & Tomaso-Peterson (2012)     | graminicola   | Centipedegrass, sorghum |                       | ITS, APN2/IGS/MAT1-2, SOD2                   |
cluster from strawberry and non-crop species. Crouch et al. (2006, 2009d) distinguished clades within the C. cereale cluster that correlated with pathogenicity, with some causing disease of turfgrasses and others isolated from asymptomatic prairie grasses. Gazis et al. (2011) compared Amazonian populations of endophytic taxa belonging to the C. gloeosporioides cluster associated with two species of Hevea, the cultivated H. brasiliensis and the non-cultivated H. guianensis. Higgins et al. (2011) studied Colletotrichum endophytes from grass and non-grass hosts in tropical forest in Panama, recovering some genetically distinct taxa via direct sequence from surface-sterilised grass tissue that were not detected using cultural methods. They also observed that many taxa were detected from less than one more grass host genus, corroborating observations by Lu et al. (2004) and Arnold & Lutzoni (2007) that the commonest tropical endophytes appear to be host generalists. However, the ITS sequences used to define OTUs in all these studies are too conservative to reflect all speciation events (Crouch et al. 2009b, Gazis et al. 2011). Several endophyte taxa isolated from cacao in Panama by Rojas et al. (2010) were thought to comprise part of the background endophytic community in the Panamanian forest ecosystem, but most strains studied came from crop plants and their status as native species needs further investigation.

All of the studies of Colletotrichum associated with non-crop plants detailed above demonstrate considerable diversity of taxa. Despite preliminary evidence that host specificity is less in native tropical forest ecosystems compared with managed environments, the sheer number of habitats (in the form of leaves, fruits etc.) that remain unsampled indicate the likelihood that overall species-level diversity of the genus is still significantly under-represented.

**PHYLOGENETIC POSITION**

Colletotrichum, as an asexual fungal genus, was included in morphological classifications of the Ascomycota as its sexual genus Glomerella. Successive editions of the *Dictionary of the Fungi* until edn 6 (Ainsworth, 1971) listed Glomerella as a member of the Phyllachoraceae in the order Sphaeriales. The Phyllachoraceae was originally described by Theissen & Sydow (1915) as part of the Dothideales. Petrak (1924) concluded that Phyllachora, Polystigma and Physalosporina (= Stigmata; see Cannon 1996) constituted a natural family that did not belong to the Dothideales. Chadeaufa (1960) introduced (but did not validly publish) the ordinal name Glomerellales, including Glomerella, Phyllachora and two other genera in a non-ranked group “Eu-Glomerellales”. Barr (1976) introduced (but again did not validly publish) the ordinal name Phyllachorales, in which was included a disparate set of families with the Phyllachoraceae subsumed into the Melogrammataceae. Glomerella was accepted as part of that assemblage. Seven years later, Barr (1983) validated the ordinal name Phyllachorales but did not explicitly alter its composition. The same year, Hawksworth et al. (1983) placed Glomerella in its traditional position in the Phyllachoraceae, but treated the family as the only representative of the Polystigmatales, yet another name that appears not to have been validly published. Edition 8 of the *Dictionary of the Fungi* (Hawksworth et al. 1985) adopted a similar classification, though the ordinal name Polystigmatales was replaced by Phyllachorales.

Glomerella had long been considered to be an outlier within the Phyllachoraceae due to its non-stromatic nature (Cannon 1991). The family name Glomerellaceae was first published (invalidly) by Locquin (1984), in a general account of the fungi in which no fewer than 278 new families were introduced. Locquin’s work was generally ignored, until preliminary sequence-based studies along with ontogenetic research (Uecker 1994) confirmed that Glomerella and Phyllachora did not belong to the same order of fungi. The Glomerellaceae was adopted in the 9th edition of the *Dictionary of the Fungi* with an uncertain position within the Sordariomycetidae (Kirk et al. 2001), and in the 10th edition as an unplaced taxon within the Hypocreomycetidae (Kirk et al. 2008).

The first attempts to place Glomerella/Colletotrichum within a molecular phylogenetic system were published by Illingworth et al. (1991) and Berbee & Taylor (1992), using 18S rDNA sequences. Although the number of taxa sampled was insufficient to provide reliable placement, the samples of C. gloeosporioides included in these studies were shown to cluster with members of the Hypocreales. Most subsequent phylogenetic studies included Glomerella/Colletotrichum only as outgroups, or to provide an overall framework for the phylogeny of unrelated groups (e.g. Zhang & Blackwell 2002, Castelbury et al. 2004, Huhndorf et al. 2004).

There is very little information available on sequences from the Phyllachoraceae sensu stricto. Winka & Eriksson (2000) found that two 18S rDNA sequences from Phyllachora species clustered in the Sordariomycetidae clade, while Glomerella cingulata was considered to be more closely related to the Hypocreomycetidae. Wanderlei-Silva et al. (2003) also published a study based on 18S rDNA, that claimed that the Phyllachoraceae was polyphyletic. In this work, core taxa clustered with the Sordariales, Ophidiocystis vaccinii clustered within the Xylariales, and Glomerella/Colletotrichum was shown as a sister group to the Hypocreales.

Zhang et al. (2006) confirmed the phylogenetic position of Glomerella within the Hypocreomycetidae, and provided a Latin
diagnosis for the *Glomerellaceae*. A sister taxon relationship with *Verticillium* was recovered (Zhang et al. 2006), but this clustering appears to be an artefact of limited taxa sampling. Subsequent investigations assigned *Verticillium* to the *Plectosphaerellaceae* (Zare et al. 2007, Cannon et al. 2012), following the conclusions of Zare et al. (2000). The phylogenetic position of the *Glomerellaceae* was further elucidated by Réblová et al. (2011) in a study using ITS, LSU, SSU and rpb2 genes. In this work, the *Glomerellaceae* occupied a common clade with two newly recognised families, the *Australiascaceae* and *Reticulascaceae*. They accordingly validated the order *Glomerellales* (first introduced by Chadeauf 1960 but without a Latin diagnosis) for the three families. Based on SSU data, Réblová et al. (2011) showed that the *Glomerellales* occupied a well-supported clade that included the *Hypocreales*, *Microascales* and the *Plectosphaerellaceae*, equivalent to the *Hypocreomycetidae* as delimited by Zhang et al. (2006). Similar results were obtained with LSU sequence data, although the separation of the *Hypocreomycetidae* was not supported by bootstrap analysis or posterior probability measures (Réblová et al. 2011). This is probably not the final word in elucidation of the phylogenetic position of *Colletotrichum*, but the *Glomerellales* clade is well supported despite significant morphological differences between the three families included.

**SEXUAL MORPHS AND SEXUAL-ASEXUAL CONNECTIONS**

In common with many other fungal pathogens, the *Colletotrichum* asexual morph is most commonly associated with disease symptoms, with the sexual morph tending to develop on moribund or dead host tissues (Sutton 1992). *Colletotrichum* sexual morphs are therefore under-studied in comparison with the asexual stages. This lack of attention to the sexual morphs is compounded by the need to identify species from cultures, the preparation of which may keep compatible strains separate. This makes it difficult to assess the prominence of the *Glomerella* stages in nature compared with their asexual morphs.

*Colletotrichum* sexual morphs were first described by Stoneman (1898) in the genus *Gnomoniopsis* Stoneman, in a comprehensive and well-illustrated account of the development of anthracnose diseases in the USA. Four species were described in full, all of which were linked to previously described asexual morphs; *Gn. cingulata* (anamorph *Gloeosporium cingulatum*, from *Ligustrum vulgare*), *Gn. pipera* (asexual *Gl. piperatum*, from *Capsicum annuum*), *Gn. cincta* (asexual *Colletotrichum cinctum*, from the orchids *Maxillaria picta* and *Oncidium sp.*) and *Gn. rubicola* (.asexual *C. rubicola*, from *Rubus strigosus*). A fifth species, given the name *Gnomoniopsis? vanillae* (asexual *Colletotrichum* sp., from *Vanilla*) was also described in a preliminary manner. All of the species accepted were linked to their asexual morphs by cultural methods in the laboratory.

Von Schrenk & Spaulding (1903) pointed out that Stoneman’s genus was a later homonym of *Gnomoniopsis* Berl. (Berlese 1893; type *Gn. chamaemorii*), which is not closely related to the anthracnose pathogens. *Gnomoniopsis* Berl. has recently been confirmed as a genus of the *Gnomoniaceae* (Díaporthales) rather than the *Glomerellaceae* (Sogonov et al. 2008). Von Schrenk and Spaulding (1903) accordingly proposed the name *Glomerella* for the anthracnose-causing species, making new combinations for the four species definitely accepted by Stoneman in her genus and adding a fifth, *Glomerella rufomaculans*, considered to be the causal agent of bitter rot of apple (see also Du et al. 2005). The type of *Gnomoniopsis* Stonem. was not originally specified, and nor was that of *Glomerella*. The earliest lectotypification of *Glomerella* appears to be by Clements & Shear (1931), who designated *Ga. cingulata* as type. This choice has been accepted by subsequent authors, most notably by von Arx & Müller (1954) and von Arx (1987).

A comprehensive monograph for *Glomerella* has never been published. The broadest treatment to date is by von Arx & Müller (1954), at a similar level of detail to the revision of *Colletotrichum* three years later by von Arx (1957b). Von Arx & Müller recognised only five species, two of which are poorly known and cannot be confirmed as belonging to *Glomerella*.

Those excluded by us from von Arx & Müller’s concept of *Glomerella* include *Ga. guevinae* (syn. *Chiloëlla guevinae*), which has ascospores that are covered in a gelatinous sheath and are much smaller than those of typical *Glomerella* species. No asexual morph has been seen. Sydow (1928) suggested that *Chiloëlla* has affinities with *Physalospora* (*Hyponectriaceae*) or *Plagiostoma* (*Gromoniaceae*). Type material has not been traced, and so *Chiloëlla* remains of uncertain affinity. *Ga. montana* (*Physalospora montana, Phyllachora montana*) was considered by Parbery (1964) to have affinities with a small group of *Phyllachora* species on montane grasses with sexual morphs that mature on dead plant tissues. Authentic material of the species in *K* conforms with this interpretation. Von Arx & Müller (1954) did find the type material to be in association with old *Colletotrichum* fruit-bodies, but there is no demonstrated connection between the morphs.

The three species treated by von Arx & Müller (1954) that definitely belong to *Glomerella* are the type *Ga. cingulata*, *Ga. tucumanensis* and *Ga. amenti*. *Glomerella tucumanensis* is widely accepted as the sexual morph of *Colletotrichum falcatum*, the cause of red rot of sugarcane. Work by Sutton (1968) and Crouch et al. (2009c) confirm this species as a distinct and apparently host-specific pathogen using both morphological and molecular criteria. *Glomerella amenti* (syn. *Phyllachora amenti, Haploethecium amenti*) was described from flower stalks and bracts of the arctic-alpine species *Salix reticulata*, an unexpected habitat for a species of *Glomerella*, but its phylogenetic position has been reassessed (Damm et al. 2012a), and confirmed as a synonym of *C. salicis*, a member of the *C. acutatum* clade.

*Glomerella cingulata* is now widely recognised as a species aggregate and the sexual counterpart to the *C. gloeosporioides* aggregate, although the connection has not been explicitly proved, and the link at species level may well be incorrect. As far as we are aware, type material of *Ga. cingulata* has not been examined in modern times (though a possible authentic specimen is preserved in BPI). Similarly, the identity of *Gloeosporium cingulatum* Atk., with which *Ga. cingulata* was linked by Stoneman (1898), has not been critically reassessed, and the conidia of *Gloeoc. cingulatum* as illustrated by Stoneman could also belong to the *C. acutatum* clade.

Shear & Wood (1907) and Edgerton (1908) considered that at least several of the putatively host-specific taxa described by Stoneman (1898) as species of *Gnomoniopsis* were conspecific, although they did not include material ascribed to *Ga. cingulata* in their studies. The equation of the name *Ga. cingulata* with the species aggregate rather than the fungus causing disease of *Ligustrum* was further established in works by Dastur (1920) and Small (1921, 1926), which focused on cross-inoculation experiments.

Since the name *Glomerella cingulata* was originally published, unnecessary or poorly justified taxa proliferated for the same reason...
| **Colletotrichum species** | **Glomerella species** | **Reference** | **Method** | **Teleomorph placement (von Arx & Müller 1954)** | **Current clade** | **Notes** |
|---------------------------|------------------------|---------------|------------|-----------------------------------------------|------------------|-----------|
| C. "acutatum"             | Ga. acutata            | Guerber & Correll (2001), Damm et al. (2012a) | Laboratory crossing | NA | acutatum | Teleomorph type a hybrid between C. acutatum and C. fioriniae |
| C. annellatum             | Unnamed                | Damm et al. (2012b) | Developed on SNA medium and sterile plant stem in culture | NA | boninense |
| C. boninense              | Unnamed                | Damm et al. (2012b) | Developed on SNA and OA medium | NA | boninense |
| C. brassicicola           | Unnamed                | Damm et al. (2012b) | Developed on sterile plant stem in culture | NA | boninense |
| C. cinctum                | Ga. cincta             | Stoneman (1898) | Laboratory culture | Ga. cingulata | | |
| Glgeosporium cingulatum   | Ga. cingulata          | Stoneman (1898) | Laboratory culture of sterilised bean stem, single-ascospore cultures | Ga. cingulata | gloeosporioides ? | Identity and placement uncertain, modern revision needed |
| C. cliviae                | Unnamed                | Yang et al. (2011) | Developed on PDA medium | NA | | Not closely related to any established clade |
| C. constrictum            | Unnamed                | Damm et al. (2012b) | Developed on SNA medium and sterile plant stem in culture | NA | boninense |
| C. cymbidiicola           | Unnamed                | Damm et al. (2012b) | Developed on SNA medium and sterile plant stem in culture | NA | boninense |
| C. destructivum           | Ga. glycines           | Manandhar et al. (1986) | Laboratory culture | Ga. cingulata | destructivum | Identification of both morphs doubtful, modern revision needed |
| C. falcum                 | Ga. tucumanensis       | Carvajal & Edgerton (1944), Politis (1975) | Laboratory culture | Ga. tucumanensis | graminicola |
| C. fioriniae              | Ga. fioriniae          | Marcotino et al. (2008), Shivas & Tan (2009) | Laboratory mating study | NA | acutatum |
| C. fructicola             | Unnamed                | Pethasturi et al. (2009) | Laboratory culture | NA | gloeosporioides |
| C. gloeosporioides        | Ga. cingulata          | e.g. Cisar et al. (1994), Cisar & TeBeest (1999) | Co-occurrence on host, laboratory mating study | Ga. cingulata | gloeosporioides | Connection unlikely to be correct, placement uncertain |
| C. glycines               | Ga. glycines           | Lehman & Wolf (1926) | Culture of both morphs | Ga. cingulata | truncatum | Treated as an independent species by von Arx (1987). Connection doubtful, modern revision needed |
| C. gossypii               | Ga. gossypii           | Edgerton (1909) | Laboratory culture | Ga. cingulata | gloeosporioides | Modern revision needed |
| C. graminicola            | Ga. graminicola        | Politis (1975), Vaillancourt & Hanau (1991, 1992) | Laboratory mating study | NA | graminicola |
| C. "heveae"               | Ga. phyllanthi         | Pai et al. (1970) | Developed on PDA medium | NA | boninense | Connection based on wrong identification of the anamorph, see C. phyllanthi |
| C. ignotum                | Unnamed                | Rojas et al. (2010) | Laboratory culture | NA | gloeosporioides |
| C. karstii                | Unnamed                | Yang et al. (2011), Damm et al. (2012b) | Developed on SNA and PDA medium | NA | boninense |
| C. lagenarium             | Ga. lagenaria          | Stevens (1931) | CMA culture with UV irradiation | Ga. cingulata | orbiculare ? | Modern revision needed |
| Colletotrichum species | Glomerella species | Reference | Method | Teleomorph placement (von Arx & Müller 1954) | Current clade | Notes |
|------------------------|--------------------|-----------|--------|---------------------------------------------|--------------|-------|
| C. lindemuthianum      | Ga. lindemuthiana  | Shear & Wood (1913), Rodríguez-Guerra et al. (2005) | Laboratory culture or laboratory crossing | Ga. cingulata | orbiculare | Modern revision needed |
| Gloeosporium lycopersici | Ga. lycopersici | Krüger (1913) | Laboratory culture, inoculated tomato fruits | Ga. cingulata | acutatum | Synonym of C. salicis |
| C. mume                | Ga. mume           | Hemmi (1920) | Laboratory culture | Ga. cingulata | | Modern revision needed |
| C. musae               | Ga. musarum        | Pitch (1917) | Present on same piece of host tissue | Ga. cingulata | gloeosporioides | Connection needs further research: see Weir et al. (2012) |
| C. orchidearum         | Unnamed            | Yang et al. (2011) | Developed on PDA medium | Ga. cingulata | | Identity of this fungus is not completely clarified |
| C. parsonsi           | Unnamed            | Damm et al. (2012b) | Developed on SNA medium | NA | boninense | |
| C. petchii             | Unnamed            | Damm et al. (2012b) | Developed on sterile plant stem in culture | NA | boninense | |
| C. phomoides           | Ga. phomoides      | Swank (1953) | Both morphs developing from single-conidium isolate | Ga. cingulata | dematium ? | Modern revision needed |
| C. phormii             | Ga. phormii        | Hennings (1898), Farr et al. (2006), Damm et al. (2012a) | Developed on leaves | Ga. phacidiomorpha and Ga. cingulata | acutatum | Also see Kinghorn (1936) and von Arx (1987), misapplied as Ga. phacidiomorpha |
| C. phyllanthi          | Ga. phyllanthi     | Pai et al. (1970), Damm et al. (2012b) | Based on type specimen (dried culture) and description (living culture sterile) | NA | boninense | Anamorph and teleomorph based on same type |
| C. piperata            | Ga. piperata       | Stoneman (1898) | Laboratory culture | Ga. cingulata | gloeosporioides ? | |
| C. rhodocyclus         | Ga. phacidiomorpha | Kinghorn (1936) | Developed on the surface of living leaves, not in culture | Ga. cingulata | acutatum | Synonym of C. phormii, name Ga. phacidiomorpha misapplied (Farr et al. 2006) |
| C. rhombiforme         | Unnamed            | Damm et al. (2012a) | Developed on sterile plant stem in culture | NA | acutatum | |
| C. rubicola            | Ga. rubicola       | Stoneman (1898) | Single-conidium isolations produced both morphs | Ga. cingulata | acutatum ? | Modern revision needed |
| C. salicis             | Ga. salicis        | Damm et al. (2012a) | Developed on sterile plant stem in culture | Ga. amenti, Ga. cingulata | acutata | Ga. amenti forms no anamorph according to Arx and Müller (1954) |
| C. sublineolum         | Unnamed            | Vaillancourt & Hanau (1992) | Laboratory mating study | NA | graminicola | Perhaps does not belong to Colletotrichum, modern revision needed |
| C. taiwanesense        | Ga. septospora     | Skanesan & Hsieh (1993) | Single-ascospore isolations produced both morphs | NA | | The anamorph has been referred to as "C. magna" (e.g., Redman et al. 1999) but the name does not appear to have been formally published. Modern revision needed |
| Unnamed                | Ga. magna          | Jenkins & Winstead (1964) | Laboratory crossing | NA | Not closely related to any established clade | |
| Unnamed                | Ga. miyabeana      | Fukushima (1921), Johnston & Jones (1997) | Found on stems and leaves of Salix purpurea var. angustifolia and on sterilised pieces of willow stem in culture | Ga. cingulata | acutatum | Synonym of C. salicis, treated as Ga. miyabeana by von Arx (1957b, 1987) |
| Unnamed                | Ga. truncata       | Armstrong-Cho & Barniza (2006) | Pairing of anamorph isolates | NA | destructivum | Anamorph misidentified as C. truncatum (Latunde-Dada & Lucas 2007, Damm et al. 2009) |
as did those for *Colletotrichum gloeosporioides*, i.e. assumed host specificity. Von Arx & Müller provided a long list of 117 synonyms belonging to at least 42 independent taxa (they did not distinguish between homotypic synonyms and taxa in different genera with the same epithet). As with previous work on *C. gloeosporioides*, the contribution of Von Arx & Müller provided a valuable foundation for later investigations. Subsequent research has identified further distinct *Glomerella* taxa, and currently around 30 species of *Colletotrichum* are known to have (or have at least been claimed to have) *Glomerella* sexual morphs. They are listed in Table 2.

There has been little morphology-based comparison of the sexual taxa, and differential characters cited by researchers seem restricted to ascospore shape and size, with individual taxa showing wide variation and exhibiting overlapping ranges. For example, Lehman & Wolf (1926) described the ascospores of *Glomerella cingulata* as ranging between 13 and 43 µm (though chiefly 19–28 µm) in length. Elsewhere, von Arx & Müller (1954) gave measurements for *Ga. cingulata* of 9–30 × 3–8 µm (mostly 12–24 × 4–7 µm). Comparative study has certainly been compromised by the excessively wide species concept for *Ga. cingulata*. However, the ascospores of *Ga. tucumanensis* were described as larger than the norm for *Ga. cingulata* by von Arx & Müller (1954). Guerber & Correll (2001) established that ascospores of *Ga. acutatum* were smaller and somewhat less strongly pointed than those of *Ga. cingulata*, but qualified their conclusions as the strains studied of the latter species were too few to establish clear boundaries between the two taxa based on these criteria. Future study may identify further diagnostic morphology-based characters for the sexual morph of *Colletotrichum*, particularly when viewed in light of modern phylogenetic species concepts.

Assessment of historical asexual-sexual connections in *Colletotrichum* is very problematic. Many of the claimed links are not based on authentic material, thereby casting doubt on the identities of both morphs. Some are based on little more than juxtaposition on diseased plant samples. Even when the connections are well-researched and use correctly identified material (for the time), the identity of the holomorph may not be easy to establish using modern phylogenetic methods. Some of the information in Table 2 must therefore be considered as more of historic than scientific value.

The substantial changes in *Colletotrichum* species delimitation made possible by molecular systematic analysis mean that many asexual-sexual connections need further study, and in most cases the sexual names are not typified according to modern practice. From a nomenclatural perspective, the need for this work is now less critical as the requirement for separate naming of asexual and sexual morphs more readily than others. Those where sexual morphs are generated frequently, measured in terms of the proportion of constituent species with known meiotic morphs, include the gloeosporioides and boninensis clades. To our knowledge, in contrast, there are no reliable reports of a sexual morph from any taxon within the truncatatum clade. In other groups, such as the graminicola clade, individual species are well known to produce sexual morphs (e.g. *C. falcatum*, *C. graminicola*), but others seem to form them rarely or not at all (Crouch and Beirm 2009). Mating seems to be rare in the orbiculare clade, with only a small proportion of crosses between *C. lindemuthianum* strains producing fertile progeny (Rodriguez-Guerra et al. 2005).

The mechanisms of recombination and sexual production in *Colletotrichum* are still inadequately understood. Classical genetic research on mating systems in strains identified as *Glomerella cingulata* (e.g. Olive 1951, Wheeler 1954) indicated that both homothallic and heterothallic isolates exist, although their modern taxonomic placement within the gloeosporioides clade is not known. Despite documented heterothallic behaviour, only one mating type idiomorph has been recovered from population-level screening in a number of studies (e.g. Chen et al. 2002, Du et al. 2005, Crouch et al. 2008).

In a number of species, sexual production has only been documented in laboratory crosses (see Table 2), and the role of mating in natural populations is unclear. Fertile sexual morphs were produced resulting from what is now considered to be interspecific hybridisation of strains within the *C. acutatum* clade (Guerber & Correll 2001, Damm et al. 2012a), and this phenomenon may be widespread. Hybridisation between taxa within infragenetic clades of fungi has been demonstrated before, e.g. by O’Donnell et al. (2000) in the *Fusarium graminearum* complex, by Stukkenbrock et al. (2012) in *Zygomycetes* and by Turner et al. (2010, 2011) in *Neurospora*. In the *Neurospora* example, fertile progeny were produced from geographically isolated strains but not from sympatric isolates, suggesting that reproductive barriers evolve at a local level and can be overcome following long-distance dispersal of conidia. Not all of the strains used to produce sexual morphs in the acutatum clade (Guerber & Correll 2001) have been analysed using multilocus sequence technology, so we cannot say whether similar mechanisms are operating in *Colletotrichum*.

Mating-type gene sequences have been shown to be good markers for phylogenetic analysis. To date, they have been studied in the acutatum, graminicola, gloeosporioides and orbiculare clades (e.g. Du et al. 2005, García-Serrano et al. 2008, Marcelino et al. 2008, Crouch et al. 2009, Moriwaki & Tsukiboshi 2009, Rojas et al. 2010).

**TYPIFICATION**

Communication of information relating to *Colletotrichum* species has been seriously compromised in the past by misidentification, misapplication of names and grossly differing species concepts. Many of these problems were caused by uncritical use of species names on the assumptions that (a) all species are host-specific and (b) that only one species of *Colletotrichum* (or at least only one species with similar gross morphology) parasitises each host genus. Many older *Colletotrichum* names lack type specimens that are suitable for molecular analysis, and do not have authentic living strains preserved in culture collections. Because the nomenclatural Code (now entitled the International Code of Nomenclature for Algae, Fungi and Plants; Hawksworth 2011) now allows for the designation of epitypes, modern sequenceable collections can be used as substitutes for the original material. An epitype should have morphological, cultural and pathological characteristics similar to those described in the original publication, originate from the same geographical region and host, and preserve (where at all possible) application of the name in concord with modern usage (Cannon et al. 2008). Many currently used names of *Colletotrichum* now have epitypes designated (e.g. Cannon et al. 2008, Than et al. 2008, Damm et al. 2009, 2012a, b, Su et al. 2011, Weir et al. 2012).
Table 3 summarises the nucleotide sequences associated with type or other representative strains of Colletotrichum species, which we recommend as reference data to aid researchers and plant health practitioners in species identification. Some widely used species names included in Table 3 are of uncertain taxonomic application, as they have not been recently revised or their typification is in doubt. In some of these cases, strains and/or sequences are included in Table 3 that represent the species as generally accepted by modern authors (not necessarily taxonomists), and might thus be appropriate material on which to base epitypes or neotypes in order to preserve current application of the names. We cite these also in Table 3, but stress strongly that they do not have formal nomenclatural status and they should not be taken to be endorsed as authentic. These exceptions are indicated by the marker "none" in the column labelled "status of source material".

These data form the framework for an online identification system for Colletotrichum species, hosted by the Centraalbureau voor Schimmelcultures but administered by the recently formed Colletotrichum subcommission of the International Commission on Taxonomy of Fungi (ICTF, http://www.fungaltaxonomy.org/), which is in turn a body under the auspices of both the International Mycological Association (http://www ima-mycology.org/) and the International Union of Microbiological Societies (http://www iums.org/). This database can be accessed at http://www.cbs.knaw.nl/Colletotrichum/. The database will be updated periodically to include reference sequences for novel taxa and for species that have been subjected to modern phylogeny-based revision.

**SPECIES CONCEPTS AND BARCODING**

Our understanding of Colletotrichum species and the processes by which they have evolved has undergone several step changes over the years. The first part of this review focuses on the unreliability of host-based diagnosis, and the lack of resolution of taxonomic systems based firstly on morphological features, and latterly by ITS DNA sequences. Here, we concentrate on the changes of the last 10 years, with rapid moves to species definition based on multilocus analysis, knowledge gains from molecular plant/fungus interaction studies, and the synergies with wider genetic research.

At the beginning of the century, concern was expressed at the wide constituent genetic variation between taxa of Colletotrichum recognised at the species level, and the varying utility of species concepts in the eyes of pathologists (Cannon et al. 2000). Some species, such as *C. gloeosporioides*, were defined partially by ITS sequence, but were primarily considered to represent morphological taxa. These were known to encompass extensive genetic variation, but were maintained for utilitarian reasons. *Colletotrichum kahawae* on the other hand was thought at the time to represent a single clonal population causing a specific, devastating disease of coffee berries. That species has recently been redefined with a broader circumscription (Weir et al. 2012).

In *Colletotrichum*, species definition based on ITS sequence has proved unsatisfactory, that gene fragment being too evolutionarily conservative to distinguish between taxa that can be recognised using other genes and gene combinations (e.g. Du et al. 2005, Crouch et al. 2009b, Gazis et al. 2009). This is of some concern, as the ITS region is widely used for species definition in the Fungi (e.g. Begerow et al. 2010, Druzhinina et al. 2005, Eberhardt 2010, Kelly et al. 2011), and has recently been proposed as a universal barcode sequence (Schoch et al. 2011, 2012).

ITS was proposed as the primary fungal barcode marker for various reasons, including pragmatism – the number of existing fungal ITS sequences is far greater than that for any other gene. Many other genes/gene fragments have been used for diagnostic purposes in the Fungi, especially beta-tubulin (TUB2) and calmodulin (e.g. for *Aspergillus* and *Penicillium*; Samson et al. 2007, Peterson 2008, Houbraken et al. 2011), TEF1 (for *Fusarium*; Geiser et al. 2004, O’Donnell et al. 2009) and COX1 (for *Penicillium*; Seifert et al. 2007).

Many other molecular markers have wide diagnostic potential for the Fungi, including most of those currently used for phylogenetic analysis in *Colletotrichum* (see Table 3). Further candidates are being considered. Aguileta et al. (2008) identified no fewer than 246 single-copy orthologous gene clusters in an optimally performing gene set, from analysis of 21 fungal genomes. Several widely used markers, including TUB2 and TEF1, were not included within their list of best-performing genes, and are probably unsuitable as universal fungal markers due to the presence of paralogs (James et al. 2006, Walker et al. 2012). Building on this work, Schmitt et al. (2009) developed primer sets for MCM7 and Tsr1, two of the most phylogenetically informative sequences identified by Aguileta et al. (2008). MCM7 has been shown to work effectively in widely divergent fungal groups within the Ascomycota (Schmitt et al. 2009, Raja et al. 2011). Walker et al. (2012) evaluated two further single-copy protein-encoding genes, FG1093 and MS204 that also have potential in fungal diagnostics.

The prospect of a single short universally amplifiable DNA sequence being diagnostic for all organisms (or even all species within a major taxonomic group) is enticing, but unrealistic. This does not mean that data from single loci such as ITS do not have wide application, for example in environmental sequencing (e.g. Buée et al. 2009) or analysis of historical specimens (e.g. Brock et al. 2009, Dentinger et al. 2010b). There is also evidence that ITS sequences alone can constitute useful barcode markers for some groups of the Basidiomycota (e.g. Kõljalg et al. 2005, Dentinger et al. 2011). It is not clear whether this apparent difference in utility of ITS-based diagnostics between ascomycetous and basidiomycetous fungi reflects different speciation patterns or variation in species concepts.

Comparison of a phylogenetic tree of Colletotrichum species derived from ITS sequences alone and one generated from multilocus data (Figs 2, 3) confirms that ITS resolves major clades well, though does not reflect their higher-order topology accurately in all cases. However, posterior probability support is lacking within many of the major clades, especially those containing *C. acutatum* and *C. gloeosporioides* and their respective relatives. A robust sequence-based identification system for Colletotrichum species must therefore use an alternative molecular marker, or a combination of markers.

Performance analysis of the genes used in a multilocus analysis of the *C. acutatum* clade (Damm et al. 2012a) indicates that the two most diagnostic markers are TUB2 and GAPDH, which resolved all 29 subclades. These were equated by those authors to species. In contrast, ITS sequences could only resolve 11 of the 29 taxa within the clade. TUB2 performed marginally better than GAPDH due to a larger overall number of bp differences, but even so, some clades differed only by one bp in the TUB2 sequence. An identification system based on this gene alone would therefore be vulnerable to sequencing error, suggesting that data from multiple loci should be used.
**Table 3. Authentic sequences for accepted Colletotrichum species.**

| Species                  | Clade          | Source material [1] | Status of source material | GenBank accession number(s) | Reference                          |
|--------------------------|----------------|--------------------|---------------------------|----------------------------|------------------------------------|
| C. acerbum               | acutatum       | CBS 128530, ICMP 12921 | Culture from holotype     | ITS: JQ048459; TUB2: JQ050110; ACT: JQ049780; CHS-1: JQ049120; GAPDH: JQ049780; HIS3: JQ049450 | Damm et al. (2012a)                 |
| C. acutatum              |                | IMI 117617         | Holotype                  | ITS: JQ005776; TUB2: JQ005800; ACT: JQ005339; CHS-1: JQ005797; GAPDH: JQ049877; HIS3: JQ050188 | Vinnere et al. (2002)               |
|                          |                | CBS 112966, ATCC 56816 | Culture from epitype     | ITS: JX010244; TUB2: JX010389; ACT: JX010440; CHS-1: JX010761; SOD2: JX010311 | Weir et al. (2012)                  |
| C. aerigma               | gloeosporioides | ICMP 18608         | Culture from holotype     | ITS: JQ010576; TUB2: JQ010580; ACT: JQ010597; CHS-1: JQ010603; SOD2: JX010311 | Weir et al. (2012)                  |
| C. aescynomenes          | gloeosporioides | ICMP 17673, ATCC 201874 | Culture from holotype     | ITS: JX010176; TUB2: JX010382; ACT: JX009483; CHS-1: JX009799; SOD2: JX010341 | Weir et al. (2012)                  |
| C. agaves                |                | CBS 118190         | Morphology congruent with the type | ITS: JX005222; TUB2: JX005656; ACT: JX005570; CHS-1: JX005396; SOD2: JX010314 | Farr et al. (2006)                  |
| C. alatae                | gloeosporioides | CBS 304.67, ICMP 17919 | Culture from holotype     | ITS: JQ010190; TUB2: JQ010382; ACT: JQ009417; CHS-1: JQ009337; GAPDH: JQ009990; CAL: JQ009683; GS: JX010078; SOD2: JX010311 | Weir et al. (2012)                  |
| C. alienum               | gloeosporioides | ICMP 12071         | Culture from holotype     | ITS: JQ010251; TUB2: JQ010411; ACT: JQ009572; CHS-1: JQ009882; GAPDH: JQ009990; CAL: JQ009654; GS: JX010081; SOD2: JX010311 | Weir et al. (2012)                  |
| C. aenigma               | gloeosporioides | ICMP 18608         | Culture from holotype     | ITS: JQ005222; TUB2: JQ005666; ACT: JQ005570; CHS-1: JQ005396; SOD2: JX010314 | Damm et al. (2012b)                |
| C. anthrisci             | dematiaceous   | CBS 123334         | Culture from holotype     | ITS: GU227845; TUB2: GU228139; ACT: GU227943; CHS-1: GU228335; GAPDH: GU228237; HIS3: GU228041 | Damm et al. (2009)                  |
| C. aotea                | gloeosporioides | ICMP 18537         | Culture from holotype     | ITS: JX010205; TUB2: JX010420; ACT: JX009853; CHS-1: JX009353; GAPDH: JX010055; CAL: JX009611; GS: JX010096; SOD2: JX010333 | Weir et al. (2012)                  |
| C. australe              | boninense      | CBS 116478, HKUCC 2616 | Culture from holotype     | ITS: JQ005235; TUB2: JQ005669; ACT: JQ005837; CHS-1: JQ005409; SOD2: JX010314 | Damm et al. (2012b)                |
| C. brassicicola          | boninense      | CBS 128527, ICMP 128594 | Culture from holotype     | ITS: JQ005172; TUB2: JQ005606; ACT: JQ005345; GAPDH: JQ005258; HIS3: JQ005532; CAL: JQ005929 | Damm et al. (2012b)                |
| C. brasiliense           | boninense      | MAFF 305972, CBS 130418 | Culture from holotype     | ITS: AB051400; JQ005172; TUB2: JQ005606; ACT: JQ005345; GAPDH: JQ005258; HIS3: JQ005532; CAL: JQ005929 | Prihastuti et al. (2009), Weir et al. (2012) |
| C. brassicola            | boninense      | CBS 128501, ICMP 128501 | Culture from holotype     | ITS: JQ005235; TUB2: JQ005606; ACT: JQ005345; GAPDH: JQ005258; HIS3: JQ005532; CAL: JQ005929 | Weir et al. (2012)                  |
| C. brisbaneensis         | boninense      | CBS 101099         | Culture from holotype     | ITS: JQ005172; TUB2: JQ005606; ACT: JQ005345; GAPDH: JQ005258; HIS3: JQ005532; CAL: JQ005929 | Damm et al. (2012b)                |
| C. carthami              | acutatum       | CBS 292.67         | Culture from holotype     | ITS: JQ048281; TUB2: JQ049942; ACT: JQ049612; CHS-1: JQ049782; GAPDH: JQ049822 | Damm et al. (2012a)                |
| C. cereale [2]           | graminicola?   | CBS 129663, KS20BIG | None                      | ITS: JQ049998; TUB2: JQ049999 | Uematsu et al. (2012)               |

[1] [Reference]
| Species              | Clade         | Source material [1] | Status of source material | GenBank accession number(s) | Reference               |
|----------------------|---------------|---------------------|---------------------------|-----------------------------|-------------------------|
| C. chlorophyti       | IMI 103806    | Culture from holotype | ITS: GU227894; TUB2: GU228188; ACT: GU227992; CHS-1: GU228384; GAPDH: GU228286; HIS3: GU228090 | Damm et al. (2009)        |
| C. chrysanthemi [3]  | acutatum      | Authentic specimen   | ITS: AB969999; TUB2: AB969993 | Uematsu et al. (2012)       |
| C. chrysanthemi      | IMI 364540    | None                | ITS: JQ948273; TUB2: JQ949924; ACT: JQ949594; CHS-1: JQ949394; GAPDH: JQ948603; HIS3: JQ949264 | Damm et al. (2012a)       |
| C. circinans         | CBS 221.81    | Culture from holotype | ITS: GU227855; TUB2: GU228149; ACT: GU227953; CHS-1: GU228345; GAPDH: GU228247; LSU: JQ940807 | Damm et al. (2009), Schoch et al. (2012) |
| C. clidemiae         | ICMP 18658    | Culture from holotype | ITS: JQ005174; TUB2: JQ005608; ACT: JQ005522; CHS-1: JQ005348; GAPDH: JQ005261; HIS3: JQ005435; CAL: JQ005695 | Damm et al. (2012b)       |
| C. cliviae           | CBS 125375    | Culture from holotype | ITS: GO85607; JX519223; TUB2: GO849440, JX519249; ACT: GO856777, JX519240; CHS-1: GO856722, JX519232 | Weir et al. (2012)        |
| C. cocodes           | CBS 369.75    | Culture from holotype | ITS: HM171679; JQ005575; TUB2: JQ005589; ACT: HM171667; JQ005383; CHS-1: JQ005796; GAPDH: HM171673; HIS3: HM171670; GS: HM171676 | Yang et al. (2009), this study |
| C. colombiene        | CBS 128918    | Culture from holotype | ITS: JQ005817; TUB2: JQ005608; ACT: JQ005522; CHS-1: JQ005348; GAPDH: JQ005261; HIS3: JQ005435; CAL: JQ005695 | Weir et al. (2012)        |
| C. constrictum       | CBS 128504, ICMP 12941 | Culture from holotype | ITS: JQ005238; TUB2: JQ005672; ACT: JQ005568; CHS-1: JQ005542; GAPDH: JQ005235; HIS3: JQ005349; CAL: JQ005794 | Damm et al. (2012b)       |
| C. cordylinicola     | MFU090551, ICMP 18579 | Culture from holotype | ITS: HM470246; JQ005575; TUB2: HM470249, JX010440; ACT: HM470234; CHS-1: JX009984; GAPDH: HM470240, JX009975; HIS3: HM470237; GS: HM470243, JX010122; CAL: HM470237, JX010122 | Phoulivong et al. (2010), Wei et al. (2012) |
| C. cosmi             | CBS 853.73    | Culture from holotype | ITS: JQ948274; TUB2: JQ94925; ACT: JQ949395; CHS-1: JQ948935; GAPDH: JQ948604; HIS3: JQ949265 | Damm et al. (2012a)       |
| C. costaricense      | CBS 330.75    | Culture from holotype | ITS: JQ948180; TUB2: JQ949831; ACT: JQ949501; CHS-1: JQ949848; GAPDH: JQ948510; HIS3: JQ949171 | Damm et al. (2012a)       |
| C. curcumae          | IMI 288937    | Culture from holotype | ITS: GU227893; TUB2: GU228187; ACT: GU227991; CHS-1: GU228384; GAPDH: GU228286; HIS3: GU228090 | Damm et al. (2009)        |
| C. cuscutae          | IMI 304802    | Culture from holotype | ITS: JQ948919; TUB2: JQ948946; ACT: JQ949516; CHS-1: JQ948966; GAPDH: JQ948525; HIS3: JQ949186 | Damm et al. (2012a)       |
| C. cymbidicola       | IMI 347923    | Culture from holotype | ITS: JQ005166; TUB2: JQ005600; ACT: JQ005514; CHS-1: JQ005340; GAPDH: JQ005253; HIS3: JQ005427; CAL: JQ005687 | Damm et al. (2012b)       |
| C. dacrycarpi        | CBS 130241, ICMP 19107 | Culture from holotype | ITS: JQ005236; TUB2: JQ005670; ACT: JQ005584; CHS-1: JQ005410; GAPDH: JQ005323; HIS3: JQ005497; CAL: JQ005757 | Damm et al. (2012b)       |
| C. dematium          | CBS 125 25    | Culture from holotype | ITS: GU227893; TUB2: GU228113; ACT: GU227917; CHS-1: GU228309; GAPDH: GU228211; HIS3: GU228015 | Damm et al. (2009), Schoch et al. (2012) |
| C. destructivum      | CBS 149.34    | None                | ITS: AJ301942; TUB2: JQ005584; ACT: JQ005827; CHS-1: JQ005785; HIS3: JQ005806 | O’Connell et al. (2012)   |
| C. dracenophilum     | CBS 118199    | Culture from holotype | ITS: DQ285201; JX519222; TUB2: JX519247; ACT: JX519238; CHS-1: JX519230; LSU: DQ285210 | Fair et al. (2006), this study |
| C. echinochloae      | MAFF 511473   | Culture from holotype | ITS: AB940153; SOD2: AB439820 | Moriwaki & Tsukiboshi (2009), Crouch et al. (2009c, d) |
| Species             | Clade          | Source material [1] | Status of source material | GenBank accession number(s) | Reference                                      |
|---------------------|----------------|--------------------|--------------------------|-----------------------------|------------------------------------------------|
| C. eleusines        | graminicola    | MAFF 511155        | Culture from epitype     | ITS: EU554131, JX519243, ACT: JX519234; CHS-1: JX519226; SOD2: EU554234; APN2: EU650308 | Crouch et al. (2009c, d), this study          |
| C. eremochloae      | graminicola    | CBS 126611         | Culture from holotype    | ITS: JQ047847, JX519220, TUB2: JX519245; ACT: JX519236; CHS-1: JX519228; SOD2: JQ047849; Mat1/APN2: JQ047862; APN2: JQ047846 | Crouch & Tomaso-Peterson (2012), this study |
| C. falcatum         | graminicola    | CGMCC 3.14187, CBS 147945 | Culture from neotype    | ITS: HM171677, JX005772; TUB2: JQ005856; ACT: JQ005835; CHS-1: JQ005793; HIS3: JQ005814; Mat1/APN2: H569769; APN2: H569770 | Prihastuti et al. 2010, O'Connell et al. (2012) |
| C. floriniae        | acutatum       | EHS 58, CBS 128517, ARSEF 10222 | Culture from holotype  | ITS: EF454594, JQ494292; TUB2: EF933325, JQ494943; ACT: JQ494913; CHS-1: JQ494953; GAPDH: EF93344, JQ494922; HIS3: JQ494928; GS: EF93353; MAT1-2: EF93362; LSU: EF454581 | Marcelino et al. (2008), Shivas & Tan (2009), Damm et al. (2012a) |
| C. fructicola       | dematioid      | CBS 346.37         | Culture from epitype     | ITS: GU228744, TUB2: GU228138; ACT: GU227942; CHS-1: GU228334; GAPDH: GU228236; HIS3: GU228040 | Damm et al. (2009)                              |
| C. fructicola       | gloeosporioides| MFU090228, ICMP 18581*, CBS 130416 | Culture from holotype  | ITS: FJ972603, JX010165; TUB2: FJ907445; ACT: FJ907430; CHS-1: JQ009866; GAPDH: FJ972578; HIS3: FJ972593; SOD2: JX010038; APN2: JX010040; | Prihastuti et al. (2009), Weir et al. (2012) |
| C. fructicola       | destruectivum  | CBS 130.57         | None                     | ITS: JQ005762; TUB2: JQ005846; ACT: JQ005851; CHS-1: JQ005783; HIS3: JQ005804 | O'Connell et al. (2012)                         |
| C. fructicola       | gloeosporioides| IMI 359878, CBS 112999, ICMP17821 | Culture from epitype   | ITS: EU371022, TUB2: JQ005767; ACT: JQ005851; CHS-1: JQ005783; HIS3: JQ005804; GAPDH: FJ972578; HIS3: JQ005804; SOD2: JX010038 | Damm et al. (2012a), Weir et al. (2012) |
| C. fusum            | destructivum   | CBS 130.57         | None                     | ITS: JQ005762; TUB2: JQ005846; ACT: JQ005851; CHS-1: JQ005783; HIS3: JQ005804 | O'Connell et al. (2012)                         |
| C. graminicola      | graminicola    | CBS 130836, M 1.001 | Culture from epitype     | ITS: DG003110, TUB2: JQ005767; ACT: JQ005851; CHS-1: JQ005783; HIS3: JQ005804; GAPDH: FJ972578; HIS3: JQ005804; SOD2: JX010038 | Damm et al. (2012a)                              |
| C. guajavae         | acutatum       | IMI 350839         | Culture from epitype     | ITS: JQ049402; TUB2: JQ050033; ACT: JQ049402; CHS-1: JQ049402; GAPDH: JQ049373; HIS3: JQ049393 | Damm et al. (2012a)                              |
| C. hanai            | graminicola    | MAFF 305404        | Culture from holotype    | ITS: EU554101, TUB2: JQ050013; ACT: JQ049402; CHS-1: JQ049402; GAPDH: JQ049373; HIS3: JQ049393 | Crouch et al. (2009c, d), this study          |
| C. hemerocalidis    | dematioid      | CDLG5              | Culture from holotype    | ITS: JQ040019; TUB2: JQ040019; ACT: JQ040019; CHS-1: JQ040019; GAPDH: JQ040019 | Yang et al. 2012                                |
| C. higginsianum     | destructivum   | IMI 340833         | None                     | ITS: JQ057602; TUB2: JQ050584; ACT: JQ050581; CHS-1: JQ050584; HIS3: JQ050584; GAPDH: JQ050584 | O'Connell et al. (2012)                         |
| C. hippostrai       | boninense      | CBS 125376         | Culture from holotype    | ITS: GQ856599; TUB2: GQ856599; ACT: GQ856599; HIS3: GQ856599; GAPDH: GQ856599; CHS-1: GQ856599; MAT1-2: GQ856599 | Yang et al. (2009), Damm et al. (2012b) |
| C. horii            | gloeosporioides| NBRC 7478, ICMP 10492 | Culture from neotype    | ITS: GQ326692; TUB2: JX010450; ACT: JQ009438; CHS-1: JQ009752; GAPDH: GQ326692; HIS3: GQ326692; SOD2: JX010450; TEF1: GQ326692 | Weir & Johnston (2010), Weir et al. (2012) |
| C. indonesiense     | acutatum       | CBS 127551         | Culture from holotype    | ITS: JQ494828; TUB2: JQ494828; ACT: JQ494828; CHS-1: JQ494828; GAPDH: JQ494828 | Damm et al. (2012a)                              |
| C. jacksonii        | graminicola    | MAFF 305404        | Culture from holotype    | ITS: EU554108, TUB2: JX519241; ACT: JX519241; CHS-1: JX519241; SOD2: EU554212 | Crouch et al. (2009c, d), this study          |
| Species            | Clade         | Source material [1] | Status of source material | GenBank accession number(s)                  | Reference                      |
|--------------------|---------------|---------------------|---------------------------|---------------------------------------------|---------------------------------|
| **C. jasminigenum**| truncatum     | CGMCC LLTX–01, MFU  | Culture from type         | ITS: HM131513; TUB2: HM153770; ACT: HM131508; GAPDH: HM131499; CAL: HM131494; FS: HM131504 | Wikee et al. 2010            |
| **C. johnstonii**  | acutatum      | CBS 128532, ICMP 12926 | Culture from holotype     | ITS: JQ948444; TUB2: JQ950095; ACT: JQ949765; CHS-1: JQ949105; GAPDH: JQ949106; FS: JQ949435 | Damm et al. (2012a)          |
| **C. kahawae**     | subsp. ciggaro| ICMP 18539           | Culture from holotype     | ITS: JQ174550; TUB2: JQ101032; ACT: JQ10444; CHS-1: JQ109800; GAPDH: JQ109866; CAL: JQ109835; FS: JQ101032; SOD2: JQ100103 | Weir et al. (2012)        |
| **C. kahawae**     | subsp. kahawae| IMI 319418, ICMP 17516 | Culture from holotype     | ITS: HM58409; TUB2: HM58542; ACT: CHS-1: JQ109813; GAPDH: GU174562; FS: JQ101030; SOD2: JQ1001103 | Weir et al. (2012)        |
| **C. karstii**     | boninense     | CBS 132134, CORCG6, CGMCC3.14194 | Culture from holotype | ITS: JQ948289; TUB2: JQ949105; ACT: JQ949610; CHS-1: JQ949115; GAPDH: JQ949119; FS: JQ949280 | Yang et al. (2011)         |
| **C. kinghornii**  | acutatum      | CBS 198.35           | Culture from holotype     | ITS: JQ948454; TUB2: JQ949105; ACT: JQ949775; CHS-1: JQ949115; GAPDH: JQ949119; FS: JQ949280 | Damm et al. (2012a)          |
| **C. laticiphilum**| acutatum      | CBS 11289, IMI 383015, STE-U 5303 | Culture from holotype | ITS: JQ948454; TUB2: JQ949105; ACT: JQ949775; CHS-1: JQ949115; GAPDH: JQ949119; FS: JQ949280 | Damm et al. (2012a)          |
| **C. lilii**       | spaethianum   | CBS 109214           | Morphology congruent with original description | ITS: GU227810; TUB2: GU228104; ACT: GU228798; CHS-1: GU228300; GAPDH: GU228022; FS: GU228066 | Damm et al. (2009)         |
| **C. limetticola** | acutatum      | CBS 114.14           | Culture from epitype       | ITS: JQ948193; TUB2: JQ949844; ACT: JQ949514; CHS-1: JQ948584; GAPDH: JQ948523; FS: JQ949184 | Damm et al. (2012a)          |
| **C. lindemuthianum| orbiculare    | CBS 144.31           | None                       | ITS: JQ005779; TUB2: JQ005583; ACT: JQ005584; HF: JQ005585; HIS3: JQ005586 | O'Connell et al. (2012)       |
| **C. lineola**     | dematium      | CBS 128532           | Culture from epitype       | ITS: GU227829; TUB2: GU228123; ACT: GU227927; CHS-1: GU228319; GAPDH: GU228221; FS: GU228025 | Damm et al. (2009)         |
| **C. linicola**    | destructivum  | CBS 172.51           | None                       | ITS: JQ005765; TUB2: JQ005584; ACT: JQ005584; HIS3: JQ005586 | O'Connell et al. (2012)       |
| **C. liripes**     | spaethianum   | CBS 119444           | Culture from holotype     | ITS: GU227804; TUB2: GU228098; ACT: GU228792; CHS-1: GU228319; GAPDH: GU228198; FS: GU228000 | Damm et al. (2009)         |
| **C. lupini**      | acutatum      | BBA 70884, CBS 109225 | Culture from neotype      | ITS: DQ286119; TUB2: JQ949155; ACT: JQ949808; ACT: JQ94976; CHS-1: JQ94816; GAPDH: JQ948482; FS: JQ949146; MA1/AN2: DQ174704; TUB1: A.J901948 | Nirenberg et al. (2002), Damm et al. (2012a) |
| **C. malvarum**    | orbiculare    | LW1                  | None                       | GAPDH: JQ984992; FS: JQ005786; HIS3: JQ005786 | Damm et al. (2009)         |
| **C. melonis**     | acutatum      | CBS 159.84           | Culture from holotype     | ITS: JQ948194; TUB2: JQ949845; ACT: JQ949515; CHS-1: JQ948585; GAPDH: JQ948524; FS: JQ949185 | Damm et al. (2012a)          |
| **C. miscanthi**   | graminicola   | MAFF 510857          | Culture from holotype     | ITS: EU545121; JX519221; TUB2: JX519246; ACT: JX519237; CHS-1: JX519229; SOD2: EU554224; APN2: EU555028 | Crouch et al. (2009c, d), this study |
| **C. musae**       | graminicola   | CBS 125086           | Culture from holotype     | ITS: GG919007; TUB2: JQ005879; ACT: JQ005853; CHS-1: JQ005790; HIS3: JQ005811; SOD2: GG919073; MA1/AN2: GG919017; APN2: GG919069 | Crouch et al. (2009a), O'Connell et al. (2012) |
| **C. navitas**     | graminicola   | MAFF 51115           | Culture from holotype     | ITS: EU545126; JQ005770; TUB2: JQ005854; ACT: JQ005833; CHS-1: JQ005791; HIS3: JQ005812; SOD2: EU545229; MA1/AN2: F377946; APN2: EU555033 | Crouch et al. (2009c, d), O'Connell et al. (2012) |
| Species Clade       | Source material [1] | Status of source material | GenBank accession number(s) | Reference                                |
|---------------------|--------------------|--------------------------|-----------------------------|------------------------------------------|
| C. novae-zelandiae  | boninense          | CBS 128505, ICMP 12944   | Culture from holotype       | ITS: JQ005228; TUB2: JQ005662; ACT: JQ005576; CHS-1: JQ005402; GAPDH: JQ005315; HIS3: JQ005489; CAL: JQ005749 |
| C. nupharicola      | gloeosporioides    | CBS 470.96, ICMP 18187   | Culture from holotype       | ITS: JX010187; TUB2: JX010398; ACT: JX009437; CHS-1: JX009835; GAPDH: JX009972; CAL: JX009863; GS: JX010088; SOD2: JX010320 |
| C. nymphaeae        | acutatum           | CBS 515.78               | Culture from holotype       | ITS: JQ484197; TUB2: JQ498848; ACT: JQ494518; CHS-1: JQ484858; GAPDH: JQ48527; HIS3: JQ494188 |
| C. oncidii          | boninense          | CBS 129828               | Culture from holotype       | ITS: JQ005169; TUB2: JQ005603; ACT: JQ005517; CHS-1: JQ005343; GAPDH: JQ005256; HIS3: JQ005430; CAL: JQ00590 |
| C. orbiculare       | orbiculare         | LARS 414, 104T, CBS 514.97 | None                        | ITS: JQ005778; TUB2: JQ005862; ACT: JQ005841; CHS-1: JQ005799; HIS3: JQ005820 |
| C. orchidophilum    | boninense          | CBS 6 32.80              | Culture from holotype       | ITS: JQ484151; TUB2: JQ494802; ACT: JQ494572; CHS-1: JQ48481; HIS3: JQ494142 |
| C. parsnsiae        | boninense          | CBS 128525, ICMP 18990   | Culture from holotype       | ITS: JQ005233; TUB2: JQ005667; ACT: JQ00581; CHS-1: JQ005407; GAPDH: JQ005320; HIS3: JQ005430; CAL: JQ00590 |
| C. paspali          | graminicola        | MAFF 305403              | Culture from holotype       | ITS: EU554100; TUB2: JX519244; ACT: JX519235; CHS-1: JX519227; SOD2: EUE554204; MAT1/APN2: FJ379212; APN2: EU365007 |
| C. paxtonii         | acutatum           | IMI 165753               | Culture from holotype       | ITS: JQ484285; TUB2: JQ499936; ACT: JQ494946; CHS-1: JQ484815; HIS3: JQ494276 |
| C. petchii          | boninense          | CBS 378.94               | Culture from holotype       | ITS: JQ005223; TUB2: JQ005657; ACT: JQ005571; CHS-1: JQ005397; GAPDH: JQ005310; HIS3: JQ005484; CAL: JQ005744 |
| C. phaeoerorum [4]  | dematiun            | CBS 157.36               | Authentic strain           | ITS: GU227896; TUB2: GU228190; ACT: GU227994; CHS-1: GU228386; GAPDH: GU228288; HIS3: GU226902 |
| C. phormii          | acutatum           | CBS 118 194              | Culture from holotype       | ITS: DQ228136; TUB2: JQ494846; ACT: JQ494097; ACT: JQ4949767; CHS-1: JQ4949107; GAPDH: JQ494777; HIS3: JQ494937; LSU: D2296137 |
| C. phyllanthi       | boninense          | CBS 175.67               | Culture from holotype       | ITS: JQ005221; TUB2: JQ005655; ACT: JQ005569; CHS-1: JQ005395; GAPDH: JQ005308; HIS3: JQ005484; CAL: JQ005742 |
| C. pseudoacutatum   | CBS 436.77         | Culture from holotype    | ITS: JQ494803; TUB2: JQ495013; ACT: JQ494801; CHS-1: JQ494914; GAPDH: JQ494811; HIS3: JQ494571 |
| C. psidii           | gloeosporioides    | CBS 145.29*, ICMP 19120  | Authentic strain           | ITS: JX010219; TUB2: JX010443; ACT: JX009515; CHS-1: JX009901; GAPDH: JX009967; CAL: JX009743; GS: JX010132; SOD2: JX010386 |
| C. pyricola         | acutatum           | CBS 128531, ICMP 12924   | Culture from holotype       | ITS: JQ48445; TUB2: JQ495046; ACT: JQ494976; CHS-1: JQ494106; GAPDH: JQ494776; HIS3: JQ494946 |
| C. queenslandicum   | gloeosporioides    | ICMP 1778                | Culture from holotype       | ITS: JX010276; TUB2: JX010414; ACT: JX009477; CHS-1: JX009899; GAPDH: JX009934; CAL: JX009691; GS: JX010104; SOD2: JX010336 |
| C. rhombiforme      | acutatum           | CBS 129853               | Culture from holotype       | ITS: JQ48457; TUB2: JQ495018; ACT: JQ494978; CHS-1: JQ494118; GAPDH: JQ494788; HIS3: JQ494448 |
| C. rusci            | acutatum           | CBS 119206               | Culture from holotype       | ITS: GU227818; TUB2: GU228112; ACT: GU227916; CHS-1: GU228308; GAPDH: GU228210; HIS3: GU228014 |
| C. salicis          | acutatum           | CBS 607.94               | Culture from holotype       | ITS: JQ48460; TUB2: JQ495011; ACT: JQ494781; HIS3: JQ494121; GAPDH: JQ487791; HIS3: JQ494515 |

**Reference:**
- Damm et al. (2012b)
- Weir et al. (2012)
- Damm et al. (2012a)
- Crouch et al. (2009c, d), this study
- O’Connell et al. (2012)
- Farr et al. (2006), Damm et al. (2012a)
- Damm et al. (2012b)
- Damm et al. (2012a)
- Damm et al. (2012b)
- Damm et al. (2012a)
- Weir et al. (2012)
- Damm et al. (2012a)
- Damm et al. (2012a)
- Damm et al. (2009)
- Damm et al. (2012a)
| Species            | Source material [1] | Status of source material | GenBank accession number(s)                      | Reference                                      |
|--------------------|--------------------|----------------------------|-------------------------------------------------|------------------------------------------------|
| C. salsoleae       | ICMP 19051         | Culture from holotype      | ITS: JX010242, TUB2: JX010403, ACT: JX009562, CHS-1: JX009863; GAPDH: JX009916; CAL: JX009968; GS: JX010093; SOD2: JX010325 | Weir et al. (2012)                            |
| C. scovillei       | CBS 126529, BBA 70349 | Culture from holotype     | ITS: JQ48267, TUB2: JQ49918, ACT: JQ495858, CHS-1: JQ498928; GAPDH: JQ49597; HS3: JQ49298 | Damm et al. (2012a)                           |
| C. sansevieriae    | MAFF 239721        | Culture from holotype      | ITS: AB212991                                   |                                              |
| C. siamense        | MFU 090230, ICMP 18578, CBS 130417 | Culture from holotype | ITS: FJ972613, TUB2: FJ907443, JX010404; ACT: FJ907423; CHS-1: JX009865; GAPDH: FJ972575, JX009924; CAL: FJ917505; GS: FJ972596, JX010094; SOD2: JX010326 | Prihastuti et al. (2009), Weir et al. (2012) |
| C. simmondsii      | BRIP 28519, CBS 122122 | Culture from holotype     | ITS: FJ972601, TUB2: FJ907443, JQ948276; ACT: FJ907428, JQ949597; CHS-1: JQ948937; GAPDH: FJ972580, JX010340; GS: FJ972591 | Shivas & Tan (2009), Damm et al. (2012a)     |
| C. sloanei         | IMI 364297         | Culture from holotype      | ITS: JQ498287, TUB2: JQ499308, ACT: JQ499608, CHS-1: JQ498948; GAPDH: JQ498177, HS3: JQ499278 | Damm et al. (2012a)                           |
| C. spaethianum     | CBS 167.49         | Culture from epitype       | ITS: GU227807, TUB2: GU228101; ACT: GU227905; CHS-1: GU228297; GAPDH: GU228199; HS3: GU228003; LSU: JN490813 | Damm et al. (2009), Schoch et al. (2012)     |
| C. spinaciae       | CBS 128.57         | Morphology congruent with original description | ITS: GU227847, TUB2: GU228141; ACT: GU227945; CHS-1: GU228337; GAPDH: GU228239; HS3: GU228043 | Damm et al. (2009)                            |
| C. sublineola [5]  | BPI399463          | Lectotype                  | ITS: JQ478437, HS3: JQ005513; SOD2: JQ478453; APN1: JQ478466; APN2: JQ478477 | Crouch & Tomaso-Peterson (2012), Crouch (2012), O'Connell et al. (2012) |
| C. tabacum         | CBS 161.53         | None                       | ITS: JQ005763, TUB2: JQ005847; ACT: JQ005828; CHS-1: JQ005858; HIS3: JQ010094 | O'Connell et al. (2012)                       |
| C. tamarilloi      | CBS 129814         | Culture from holotype      | ITS: JQ498184, TUB2: JQ498935; ACT: JQ499605, CHS-1: JQ498845; GAPDH: JQ498147, HS3: JQ499715 | Damm et al. (2012a)                           |
| C. theobromicola   | ICMP 18649, CBS 124945 | Culture from neotype     | ITS: GU994360, TUB2: GU994477, JQ005855; ACT: JQ005834; CHS-1: JQ005792; HIS3: JQ005913; SOD2: DO132051; Mat1/APN2: FJ378029; APN2: EU365121; MAI: JQ029865 | Crouch & Tomaso-Peterson (2012), Crouch et al. (2006), O'Connell et al. (2012) |
| C. trifolii        | ICMP 18586         | Culture from holotype      | ITS: JX010242, TUB2: JX010403; ACT: JX009562; CHS-1: JX009863; GAPDH: JX009916; CAL: JX009968; GS: JX010093; SOD2: JX010325 | Weir et al. (2012)                            |
| C. tofieldiae      | CBS 495.85         | Morphology congruent with original description | ITS: GU227801, TUB2: GU228095; ACT: GU227899; CHS-1: GU228291; GAPDH: GU228193; HS3: GU227997; LSU: JN490815 | Damm et al. (2009), Schoch et al. (2012)     |
| C. torulosum       | CBS 128544, ICMP 18586 | Culture from holotype     | ITS: JQ005164, TUB2: JQ005338; ACT: JQ005338; CHS-1: JQ005338; GAPDH: JQ005251 | Damm et al. (2012b)                           |
| C. trichellum      | CBS 217.64         | Morphology congruent with original description | ITS: GU227812, TUB2: GU228106; ACT: GU227910; CHS-1: GU228302; GAPDH: GU228204 | Damm et al. (2009)                            |
| C. tropicalis      | ICMP 18653         | Culture from holotype      | ITS: GU994331, TUB2: GU994454, JX010407; ACT: JX009489; CHS-1: JX009870; GAPDH: JX010007; CAL: JX009719; GS: JX010097; SOD2: JX010329; Mat1/APN2: GU994425; APN2: GU994396 | Rojas et al. (2010), Weir et al. (2012)       |

*Table 3. (Continued).*
| Species | Clade | Source material [1] | Status of source material | GenBank accession number(s) | Reference |
|---------|-------|---------------------|--------------------------|----------------------------|-----------|
| C. truncatum | truncatum | CBS 151.35 | Culture from epitype | ITS: GU227862; TUB2: GU228156; ACT: GU227960; CHS-1: GU228352; GAPDH: GU228254; HIS3: GU228058; LSU: JN940819 | Damm et al. (2009), Schoch et al. (2012) |
| C. verruculosum | spaethianum | IMI 45252 | Culture from holotype | ITS: GU227806; TUB2: GU228100; ACT: GU227904; CHS-1: GU228296; GAPDH: GU228198; HIS3: GU228002 | Damm et al. (2009) |
| C. walleri | acutatum | CBS 125472 | Culture from holotype | ITS: JQ948275; TUB2: JQ949266; ACT: JQ949596; CHS-1: JQ949396; GAPDH: JQ948605; HIS3: JQ949266 | Damm et al. (2012a) |
| C. xanthorrhoeae | gloeosporioides | BRIP 45094, ICMP 17903, CBS127831 | Culture from holotype | ITS: GU048667, GU174551, JX010261; TUB2: JX010448; ACT: JX009478; CHS-1: JX009823; GAPDH: GU174563, JX009927; CAL: JX010653; GS: JX010138; SOD2: JX010369; TEF1: GU174575 | Hyde et al. (2009), Weir & Johnston (2010), Weir et al. (2012) |
| C. yunnanense | | CGMCC AS3.9167, CBS 132135 | Culture from holotype | ITS: EF369490; TUB2: JX519248; ACT: JX519239; CHS-1: JX519231 | Liu et al. (2007b), this study |

[1] Where possible, all taxa are represented by sequences from type or other authentic material. For some however, the necessary research to identify such cultures and/or to designate epitype material is not complete, especially for species within the destructivum and orbiculare clades. To be able to generate robust phylogenetic trees for the entire genus (Figs 2, 3) that include all of the major clades, we have used sequences from some strains that have been used to represent the relevant species (mostly in recent literature) but which do not currently have any special nomenclatural status. Their details are included in Table 3 for reference, and can be recognised with "none" in the type status column. It may be that some or all of these strains will be designated as epitypes in the future, but for the present it should not be assumed that they represent the species as originally circumscribed.

[2] KS20BIG was one of four epitypes designated by Crouch et al. (2006) for C. cereale; the application of the name needs to be more precisely established.

[3] Preliminary multilocus analysis suggests that C. chrysanthemi may not be a synonym of C. carthami as stated by Uematsu et al. (2012).

[4] These sequences derive from one of two authentic but not genetically identical strains; the species was not epitypified as neither of them are now fertile.

[5] A further collection from which a culture was obtained (CBS 131301) was designated as an epitype by Crouch et al. (2008) and recognised as representative of the species also by Du et al. (2005) and Crouch et al. (2009d). It was subsequently confirmed as closely similar to the lectotype based on multilocus DNA sequence analysis (Crouch & Tomaso-Peterson 2012).
Multilocus phylogenies are now typically used as the primary basis on which to describe new species of *Colletotrichum* (see Table 1) and the trend is to include more and more sequences into the analyses. One might conclude that phylogenetic signal is strongly correlated with the number of characters (in this case base pairs) included in the analysis, a position first advanced nearly 250 years ago (Adanson 1783), but genes are differential at varying positions in the hierarchy of taxa. Inclusion of multiple genes that resolve at similar positions in the hierarchy can therefore increase the size (not to mention the cost) of the data set without clarifying the phylogenetic signal. This is highly relevant to species diagnosis, as was observed by Min & Hickey (2007) in a study of mitochondrial genes from 31 fungi of widely varying taxonomic position to determine the optimum sequence length for robust identification. Research by Dentinger et al. (2010a) showed that both bootstrap support and Bayesian posterior probability values were eroded in a multilocus ATP6/LSU/RPB1 analysis of *Boletus* species compared with an analysis based on RPB1 alone. Similar results were obtained by Walker et al. (2012) in a study on two genera of the *Diaporthales*. They found in an analysis of *Ophiognomonia* species that adding TEF1 sequence data to any combination of three of the other loci used (ITS, Tub2, FG1093 and MS204) decreased support and increased the number of tree topologies recovered. Our own preliminary studies on *Colletotrichum* (data not shown) also indicate that in some circumstances, increasing the number of loci may decrease phylogenetic performance, although the effect is minor. Taken together, these data suggest that the recent fungal phylogenetic “arms race”, whereby a steadily increasing number of loci are analysed in concert, may add complexity but not improve insight.

**MAJOR CLADES**

Phylogenetic analysis of the genus *Colletotrichum* reveals that it comprises nine major clades, as well as a number of small clusters and isolated species (Figs 2, 3). There is currently no universally accepted process for naming clades and reconciling them with the traditional taxonomic categories of the International Code of Nomenclature for Algae, Fungi and Plants (ICNAPF), although the draft PhyloCode (http://www.ohio.edu/phylocode/) represents a major step in this direction. Formal recognition of infrageneric categories within *Colletotrichum* is highly desirable. This is for phylogenetic reasons, in that the genus contains many monophyletic subunits with common characteristics (not least in spore morphology). There are also pragmatic reasons for defining such categories, for example to allow linkage to the immense historical body of pathological literature in which the fungal subjects are not assignable to currently accepted species.

Use of the strictly hierarchical infrageneric nomenclature system in the ICNAPF is a possible way to assign formal names to species groups within *Colletotrichum*. However, although the Code allows for extra categories to be interspersed between the three formal ranks (subgenus, section and series), their adoption implies an equality of taxa at the same rank that is not reconcilable with evolutionary processes. We therefore favour a formal (or at least semi-formal) clade-based nomenclature system.

In this paper, we refer to 119 *Colletotrichum* species (Table 3) that collectively encompass almost all of the known phylogenetic variety in the genus, most of them belonging to one of the nine major clades. Additionally, there is a number of small clusters and isolated species, which we believe to represent independent evolutionary units, but which are insufficiently well known to justify formal nomenclatural recognition. Throughout this paper, we refer to these clades using the specific epithet of the first-recognised (or historically most prominent) of their constituent species -- for example the *acutatum* clade is the monophyletic unit containing *C. acutatum* and its close relatives (see Fig. 3). An obvious shortscoming of this system is that there is no objective method of deciding which is the basal node of the named clade. In the case of the *acutatum* clade, we have decided that the clade has *C. orchidophilum* as its sister taxon, because the ingroup taxa are much more closely related to each other than to *C. orchidophilum* or *C. pseudoacutatum*, but there are arguments for extending the clade to include this species, and indeed also *C. pseudoacutatum*.

The species in the *geminicola* clade are much less closely related than those of the *acutatum* clade; the decision for combining them was made rather on the basis of common morphology and host family. The process is to some extent subjective, so while we commend adoption of the nine clades detailed below as formal entities, we hope that clade definition and recognition will be taken on as a task by the new ICTF Subcommission on *Colletotrichum*.

In this paper, reference to the term clade indicates that we are confident that the associated information can be referred to our formal clades (or to species within the clades). We also refer on occasion to informal groupings of taxa, generally as species clusters. In these circumstances, we may know that the knowledge is associated with a particular species group, but are unsure as to its constituent taxa, or to the phylogenetic extent it represents. This frequently occurs when attempting to relate information from pathology papers to our new phylogeny.

Several of the clades indicated in Fig. 3 represent the species complexes as defined by Crouch et al. (2009c, d), Damm et al. (2012a, b, this issue), and Weir et al. (2012, this issue). While these four complexes can be confirmed as monophyletic, the assemblage of curved-spored species from herbaceous hosts studied by Damm et al. (2009) can be seen to be polyphyletic; the species included in that research are placed in three of the formal clades we recognise here, with additional outliers.

In this section, we provide an overview of the nine *Colletotrichum* clades that we recognise. Several additional individual species and small clusters are recognised that do not fall into clear clades (see Fig. 3). The phylogenetic tree presented as Fig. 3 provides a comprehensive visual overview of phylogenetic diversity within *Colletotrichum* as treated in the current literature, but it seems likely that there are further outlying taxa that have not yet been sampled, or for which phylogenetic positions have not been fixed effectively. For example, the tea pathogen *C. theae-sinensis* (Moriwaki et al. 2002, Yoshida & Takeda 2006) has unusually small conidia and may well fall outside of *Colletotrichum* as outlined in Fig. 3. Although Moriwaki et al. (2002) included a strain of *C. theae-sinensis* in phylogenies derived from rDNA datasets, the relevant sequence data from that study are not found in public sequence repositories. Based on these rDNA sequence data, Moriwaki and colleagues suggested that *C. theae-sinensis* might constitute a sister group to the genus, a prediction that needs to be tested further.

**Acutatum clade**

The *acutatum* clade is defined as a collective of *Colletotrichum acutatum* and 29 closely related species (see Fig. 3), with *C.
orchidophillum as sister taxon. The clade, along with a small number of outlying taxa, forms a sister taxon to a combination of the destructivum, graminicola and spathianum clades and C. cocodes. Two principal subclades may be detected within the acutatum clade, containing 19 and nine species respectively, and C. acutatum sensu stricto is resolved as an outlier of a
Colletotrichum – current status and future directions

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clade consisting of the larger of the two subclades along with **C. floriniae**. The acutatum clade can be effectively resolved using ITS sequence data alone (Fig. 2). The major subclades are also distinguishable using ITS alone, but the analysis reveals little or no internal structure within the subclades. A comprehensive account of its constituent species can be found as Damm et al. (2012a).
Boninense clade

The boninense clade contains 17 species as defined here (see Fig. 3). It forms a sister taxon to the gleosporioidae clade, and our multilocus analysis reveals three subclades containing 12, three and two species respectively. Colletotrichum boninense sensu stricto falls within the largest subclade. The nodal structure is complex and we do not see good reason to name the subclades formally. The ITS tree (Fig. 2) shows that the boninense clade can be detected effectively using this single locus, but it is resolved as a sister clade to the truncatum rather than the gleosporioidae clade. The clade has been revised in detail by Damm et al. (2012b).

Dematium clade

The dematium clade contains the type species of the genus, Colletotrichum lineola, and was investigated by Damm et al. (2009), as part of a study of Colletotrichum species with curved conidia. As defined by ourselves, the dematium clade contains six species (Fig. 3) and forms a sister clade to a superclade consisting of the acutatum, destructivum, graminicola and spaethianum clades, along with five further outlying taxa. In the ITS tree (Fig. 2) the clade is fairly well resolved with a Bayesian posterior probability value of 0.89, but the structure of the superclade referred to above is less well defined. An additional species, C. hemerocallidis, closely related to C. dematium, was described just before finishing this review (Yang et al. 2012).

Colletotrichum dematium and C. truncatum (often referred to under its synonym C. capsici) have been confused historically (Sutton 1981), but are found to occupy distinct clades, with the latter species belonging to a small clade near the base of the multilocus phylogeny (Fig. 3). Strains of the six species included in the dematium clade appear to be characteristic of temperate environments, though the sample size for several of the species is inadequate to allow definite conclusions as to their climatic range. In general, members of the dematium clade are not significant pathogens, but to date has not been studied in depth using molecular methods. Economically significant constituent taxa include Colletotrichum destructivum, C. fuscum, C. higginsianum and C. lineola. Colletotrichum destructivum is considered to be pathogenic on lucerne (alfalfa; Medicago sativa) and soybean (Glycine max) (Manandhar et al. 1986, Latunde-Dada et al. 1999), and has also been reported to parasitise a range of unrelated plants including species in the Brassicaceae, Cuscutaceae, Lamiaceae and Solanaceae (reviewed in Hyde et al. 2009a). Colletotrichum higginsianum is known as a pathogen of Brassicaceae (Huser et al. 2009) that is responsible for crop losses in northern temperate climates, and was found to be related to C. destructivum by O’Connell et al. (2004). The fungus is of particular significance as the subject of a whole-genome analysis project, and is increasingly studied as a model for host/pathogen interactions because of its pathogenicity to the model plant Arabidopsis thaliana (Birker et al. 2009, Huser et al. 2009, Kleeman et al. 2012, O’Connell et al. 2012). Colletotrichum higginsianum was reported to be synonymous with C. destructivum by Sun & Zhang (2009) based on ITS sequence similarity, but multilocus phylogenies of strains provisionally accepted as representative of C. higginsianum and C. destructivum indicate that these two species are distinct entities (O’Connell et al. 2012 and Fig. 3 of this study). Thus, although formal taxonomic work with authentic types is still pending, it appears that as with other Colletotrichum groups, the ITS sequence is not sufficiently differential within the destructivum clade to act as a species-level marker in isolation.

Colletotrichum fuscum is a pathogen of Digitalis and Nemesia (Scrophulariaceae; Tomioka et al. 2001). ITS and multilocus data place this species within the destructivum clade (Moriwaki et al. 2002, Cannon et al. 2008; Figs 2, 3), but more detailed information on its taxonomy and phylogenetic relationships is needed. Similarly, C. linicola was shown to belong in this clade based on ITS2/D2 rDNA sequences (Latunde-Dada & Lucas 2007), and preliminary multilocus studies indicate that the species is clearly distinct from others belonging to the destructivum clade (O’Connell et al. 2012; Fig. 2).

Glogerella truncata was described as the teleomorph of C. truncatum (Armstrong-Cho & Banniza 2006, Menat et al. 2012), but the strains studied (from lentil (Lens culinaris) in Canada) belong to the destructivum rather than the truncatum clade (Damm et al. 2009; O’Connell et al. 2012; Figs 2, 3). The name G. truncata remains valid and legitimate to represent a taxon within the destructivum clade despite the misidentification of its anamorph, but assuming that no earlier synonyms are discovered, it will require a new name now that separate binomials for teleomorph and anamorph are prohibited (Hawksworth 2011) to avoid homonymy with C. truncatum.

An outline whole-genus multilocus phylogeny (O’Connell et al. 2012) shows that the destructivum clade is monophyletic and distinct from other clades within Colletotrichum. This is confirmed by our present multilocus study (Fig. 3), with the destructivum clade being resolved as a sister taxon to the combined graminicola and spaethianum clades, and it is also clearly resolved using ITS data alone (Fig. 2). However, none of the strains sequenced in these studies is derived from type or authentic material for the names used, and further research is required to elucidate species concepts and correct nomenclature.

Gleosporioidae clade

The C. gleosporioides species complex has been studied by Weir et al. (2012, this issue). It is a well-supported clade (Bayesian posterior probability value 1.0) on a very long branch and shows few differences in the gene loci studied between most of the 22 species included. However it is a diverse clade in terms of morphology and includes a number of important plant pathogens. Weir et al. (2012) recognised two subclades within the species complex based on an
eight-locus analysis, both of which were supported by Bayesian posterior probability values of 1. They were named as the kahawae and musae clades. Only one of these, the kahawae clade, can be detected unequivocally in our multigene phylogeny (Fig. 3), while the musae clade as recognised by Weir et al. (2012) has a Bayesian posterior probability value of only 0.59. This is a result of the limited number of loci that could be included in the genus-wide alignment. The subclades cannot be effectively distinguished using ITS sequence data alone (see Fig. 2).

Graminicola clade

The Colletotrichum species associated with grasses form a well-defined monophyletic clade, the species of which possess characteristic widely falcate conidia. It is the only major clade that appears to be composed (at least largely) of host-specific taxa (Crouch & Beirn 2009), although further research may confirm that the orbiculare clade shares this characteristic. Multilocus analyses (Fig. 3) revealed two major subclades within the graminicola clade, in agreement with studies published by Crouch et al. (2009c, d). One, represented only by a single strain in Fig. 3, contains the plurivorous taxon Colletotrichum cereale. This is a diverse taxon in phylogenetic terms and there is evidence of significant gene flow between the various constituent populations (Crouch, in litt. Aug. 2012). Colletotrichum cereale is associated with grasses with C3 (cool-season) photosynthetic pathways as either pathogens or endophytes (Crouch et al. 2009d). The second subclade affects C4 (warm-season) grasses including several economically important cereal crops (Crouch et al. 2009a) and comprises a number of apparently host-specific species, not all of which have been described to date (Crouch et al. 2009c, Prihastuti et al. 2010). Several of the species included in the graminicola clade are of major importance, including C. falcatum on sugarcane (Saccharum), C. graminicola on maize (Zea) and C. sublineola on Sorghum species. Colletotrichum cereale and C. eremochloae are pathogens of cultivated turfgrasses (Crouch & Beirn 2009). Research has demonstrated the inadequacy of ITS sequences to differentiate between species within this group (Crouch et al. 2009b), and multigene analyses to date do not clearly resolve relationships within the major suboclade (Crouch et al. 2009c, Fig. 3). The biology and evolution of the clade was reviewed by Crouch & Beirn (2009), focusing on the genetics, biology and epidemiology of the three best-researched species, C. falcatum, C. graminicola and C. sublineola. The first two of these species are essentially homothallic, while C. sublineola may be strictly heterothallic (Vaillancourt & Hanau 1992, Vaillancourt et al. 2000).

With the exception of C. falcatum, the telemorphs of these species have never been encountered in nature (Crouch & Beirn 2009). A whole-genome analysis of a strain of C. graminicola has recently been completed (O’Connell et al. 2012) and this work is now being extended to include further strains from grass hosts (http://www.ars.usda.gov/pandp/docs.htm?docid=22211).

Oribiculare clade

The orbiculare clade contains several important pathogen assemblages. It has been studied in a preliminary fashion from a molecular phylogenetic perspective, but has not been the subject of a recent formal revision. The orbiculare clade is thought to include the species Colletotrichum lindemuthianum, C. malvarum, C. orbiculare and C. trifolii (Liu et al. 2007). Multilocus phylogenies using provisionally identified strains of C. lindemuthianum and C. orbiculare (Fig. 3) show that the orbiculare group occupies a basal clade of Colletotrichum, and that separation of these taxa from Colletotrichum at generic level cannot at present be ruled out. Members of the orbiculare clade as it is currently understood share some morphological features including conidia that are not curved and are relatively short and broad, and small appressoria with simple outlines (Sutton 1980). It must be pointed out that none of these taxa has been adequately typified and linked to authentic sequences. There are in fact separate concepts in the literature for three of the species currently placed within the orbiculare clade (see below), which contributes in no small way to confusion over their identity.

As pointed out by Cannon et al. (2000), Mordue (1971) considered C. lindemuthianum to have relatively long narrow conidia with a very large size range. Mordue’s illustration shows a species that would be placed in the gloeosporioides clade based on morphological data by most authors. Sutton (1980) described and illustrated C. lindemuthianum with short, broad and rounded conidia – typical of those here included in the orbiculare clade (Fig. 3). The confusion presumably arose due to the frequent occurrence of fungi from the gloeosporioides clade on host plants belonging to the Fabaceae. A similar confusion seems to exist for C. orbiculare; the species as described and illustrated by Baxter et al. (1983) has much longer conidia than those of the taxon as defined by other authors, and again it seems possible that strains of the gloeosporioides clade parasitising cucurbits were misidentified. Until both species names are properly typified using modern methods, confusion is likely to continue. As far as we can tell, all of the sequence-based research (bar a single sequence derived from a Taiwanese strain that is certainly misidentified; see Fig. 4) and probably a large majority of pathology reports using the names C. lindemuthianum and C. orbiculare refer to the short-spored taxa belonging to the orbiculare clade. As such, it would be highly appropriate to fix application of these species names to allow their continued use in this manner. Approximately half of the ITS sequences of strains identified as C. trifolii are placed in the destructivum rather than the orbiculare clade (see Fig. 4). Further research is needed before the most appropriate typification can be made; however the original description (Bain & Essary 1906) gives conidial dimensions and shape that are typical of the orbiculare clade.

The orbiculare clade was recognised as a monophyletic unit by Sherriff et al. (1994) and Johnston & Jones (1997) using LSU sequence analysis, Sreenivasaprasad et al. (1996) using ITS data, and Farr et al. (2006) using both gene sequences. A preliminary phylogenetic analysis based only on existing ITS sequences curated by GenBank (Fig. 4) demonstrates that the orbiculare clade is a sister taxon to the whole of the rest of the genus Colletotrichum. This result is consistent with previous research findings. For example, an ITS tree constructed by Yang et al. (2009) showed the orbiculare clade as a sister to C. cliviae, with the combined clade sister to C. yunnanense and C. dracaenophilum, but the clade comprising all three taxa was supported by bootstrap values below 50. Liu et al. (2007) published a phylogenetic analysis of the orbiculare clade, based on GAPDH and GS sequences; this also indicated that the orbiculare group is monophyletic, and that C. lindemuthianum, C. malvarum and C. trifolii form separate clades from a paraphyletic C. orbiculare.

As with other Colletotrichum clades, ITS data do not appear to be sufficiently variable for species level diagnostics within the orbiculare assemblage. However, ITS data do indicate (Fig. 4)
that C. lindemuthianum is a separate lineage from C. orbiculare and C. trifolii, and that it might comprise more than one taxon. An analysis of C. lindemuthianum rDNA data by Balardin et al. (1999) showed that Phaseolus pathogens may occur in numerous subordinate clades within the lindemuthianum subclade. The number of sequences available is too small for confidence, but it does appear that C. lindemuthianum is specific to Phaseolus. However, none of the sequence data or strains used by Balardin et al. (1999) is available through public databases or collections; therefore these conclusions require further evaluation. There are no full ITS sequences from Colletotrichum malvaceum available from public databanks, but a study using ITS2/LSU (Bailey et al. 1996) indicated that Colletotrichum species from Malvaceae occupy at least three subclades within the overall orbiculare clade.

Spaethianum clade

The spaethianum clade receives strong support in both the multilocus and ITS-only analyses (Figs 2, 3). It contains only five species as currently circumscribed, four of which are associated with petaloid monocot plants, and none appears to have economic importance. Its phylogenetic significance is as a sister group to the graminicola clade. The spaethianum clade was recognised as a distinct assemblage by Damm et al. (2009) in their work on the non-grass associated species of Colletotrichum with curved conidia. Four of the five species in this assemblage have complex appressoria, but the clade does not otherwise have diagnostic characteristics in morphological terms.

Truncatum clade

The truncatum clade includes only one major species, C. truncatum (also frequently referred to as C. capsici; Damm et al. 2009), which is reported as an economically destructive pathogen of many tropical crops including legumes and solanaceous plants. The truncatum clade occupies a sister position to the combined C. gloeosporioides and C. boninense clade according to our multilocus analysis (Fig. 3), but to the boninense clade only in the ITS-only analysis (Fig. 2). Conidial morphology in the truncatum group is quite different from that found in the gloeosporioides and boninense clades (Damm et al. 2012b, Weir et al. 2012), providing evidence to support the old hypothesis (Sreenivasaprasad et al. 1996) that the evolution of conidial form followed a complex pattern in Colletotrichum.
Ghurde 1988). The third member of the clade is C. jasminigenum, which was described as a new species causing leaf and blossom anthracnose disease on Jasminum sambac in Vietnam (Wike et al. 2011).

**Other taxa**

Our multilocus tree (Fig. 3) includes various species that are isolated in phylogenetic terms, or form small clusters that do not justify recognition as major clades.

The most important of these species in economic terms is *Colletotrichum coccodes*. This is primarily a pathogen of Solanaceae (potato and tomato), but also survives well in soil and is reported as an associate of a wide range of crops including strawberry (Buddie et al. 1999, Heilmann et al. 2006). *Colletotrichum coccodes* was recently epitypified (Liu et al. 2011). The species is known to be variable in genetic terms (Ben-Daniel et al. 2010). It has been researched into as a potential biocontrol agent for *Abutilon theophrasti* (Dauch et al. 2006). *Colletotrichum coccodes* has distinctive conidia that are straight, have acute ends and are often slightly constricted in the mid portion. Our multilocus analysis (Fig. 3) places it as a sister taxon to the destructivum/spaethianum/graminicola clade. In our ITS-only tree (Fig. 2) it occupies the same position, although the posterior probability values are inadequate to confirm its phylogeny from this gene fragment alone.

*Colletotrichum trichellum* was placed into synonymy with *C. dematiyum* by von Arx (1957), though it was treated as a separate, apparently host-limited species by Sutton (1962, 1981) based on the degree of curvature of the conidia. ITS-only and multilocus phylogenetic analyses (Figs 2, 3) indicate that this species does not belong to the dematiyum clade, but forms a sister clade (along with *C. nusci*) with the acutatum clade.

Three poorly-known species occupy basal positions in the ITS-only and multilocus phylogenetic trees (Figs 2, 3). *Colletotrichum cliviae* (from anthracnose of *Olivia miniat*, Amaryllidaceae; Yang et al. 2009) appears to constitute a monophyletic lineage that is a sister clade to the entire genus apart from the orbiculare clade. *Colletotrichum yunnanense* and *C. dracaenophilum* together form a small clade that is basal to the entire genus apart from the combined orbiculare and *C. cliviae* clade. *Colletotrichum dracaenophilum* is a stem pathogen of *Dracaena* species (Asparagaceae; Farr et al. 2008), while *C. yunnanense* was isolated as an endophyte of *Buxus* (Buxaceae; Liu et al. 2007b). According to their publishing authors, all three species have unusually large conidia. *Colletotrichum yunnanense* and *C. cliviae* have complex appressoria; those of *C. dracaenophilum* were not recorded by the describing authors.

**WHERE DO WE GO FROM HERE?**

What more can we learn about *Colletotrichum* systematics? Several of the major clades have not yet been analysed comprehensively using multilocus technologies. The phylogenetic position of a large part of the species described is still unknown; these species would have to be recollected and epitypified. However, linking new strains to old species is difficult and there are hundreds of "forgotten species" with little information among them. We should therefore focus on clarifying the identity of well-known species that are commonly used and of *Glomerella* species in order to synonymise them in *Colletotrichum*. New species have been discovered regularly over the last five years (including some that are highly distinct in phylogenetic terms) and novel taxa will doubtless continue to appear. Studies of *Colletotrichum* from wild plants would be likely to be particularly fruitful, and provide insights into the taxa currently known from crops and ornamentals. It would be presumptuous even to speculate that the overall systematic framework for the genus cannot be improved.

Future innovations are likely to focus increasingly on understanding populations and host/parasite relationships, and on using increasingly sophisticated analyses of whole genomes. It is only then that we are likely to begin to understand *Colletotrichum* species in their evolutionary context, rather than as cultures in collections. The first major output in this new era of *Colletotrichum* research has now been published (O’Connell et al. 2012), devoted to a comparison of the genomes and transcriptomes of two individual strains of *Colletotrichum*, one each from *C. graminicola* (from *Zea mays*, Poaceae) and *C. higginsianum* (from *Brassica* *caespries*, *Brassicaceae*). Overall genome size and chromosome number was found to be broadly similar, but substantial differences were noted between the two taxa in intrachromosomal organisation and in their suites of pathogenicity-related genes. These last were shown to be a reflection of differing host cell wall characteristics; cell walls of *Poaceae* contain higher quantities of hemicellulose and phenolic compounds, while those of *Brassicaceae* are richer in pectins. The two species were estimated as diverging around 47 M years ago, well after the divergence of their host clades.

Recent changes to the newly renamed *International Code of Nomenclature for Algae, Fungi and Plants* (Hawksworth 2011), especially those Articles relating to registration of names and the abolition of the dual nomenclature system for *Fungi*, mark a further step away from the inflexible application of the rules of date priority towards a consensus approach for choosing between competing names. In response to these historic changes, the International Subcommission on *Colletotrichum* Taxonomy has been set up within the framework of the International Commission on the Taxonomy of Fungi (http://www.fungaltaxonomy.org/). Its remit will be to promote nomenclatural stability for the genus, develop consensus phylogenies, and develop a list of protected names for key taxa that cannot be overturned by the rediscovery of obscure earlier names within the historical literature. An important part of this work is to ensure that all currently accepted species of *Colletotrichum* are adequately typified, with epitypes or neotypes linked to cultures where original type material is lost or inadequate for modern phylogenetic placement, or where no authentic original cultures have been preserved.

In the context of moving to a single name system for these fungi, probably few would argue for the retention of *Glomerella* (the later, sexual genus name with priority until the Melbourne nomenclatural congress in 2011) over *Colletotrichum* (the earlier, asexual name), but it will be the responsibility of the Subcommission to weigh the arguments for each and to recommend one or the other. Technically, we are aware that our publication prejudices this issue, but the transfer of such a large number of the names of multiple well-known economically important species currently accepted as *Colletotrichum* to *Glomerella* would cause chaos amongst the user community. The issues of synonymy between anamorph and teleomorph at the species level are complex (as exemplified by our knowledge of the identities of *Glomerella* *acutata* (Damm et al. 2012a) and *Ga. cingulata* (Weir et al. 2012), and it will in most cases be more practical to assign protected status to the asexual species names rather than go through the formal nomenclatural conservation procedures.
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