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# *Colletotrichum* – current status and future directions

P.F. Cannon[1*], U. Damm[2], P.R. Johnston[3], and B.S. Weir[3]

[1]*CABI Europe-UK, Bakeham Lane, Egham, Surrey TW20 9TY, UK and Royal Botanic Gardens, Kew, Richmond TW9 3AB, UK*; [2]*CBS-KNAW Fungal Biodiversity Centre, Uppsalalaan 8, 3584 CT Utrecht, The Netherlands*; [3]*Landcare Research, Private Bag 92170 Auckland, New Zealand*

**Correspondence*: Paul Cannon, p.cannon@cabi.org

**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 BioloMICS web environment.

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

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## INTRODUCTION

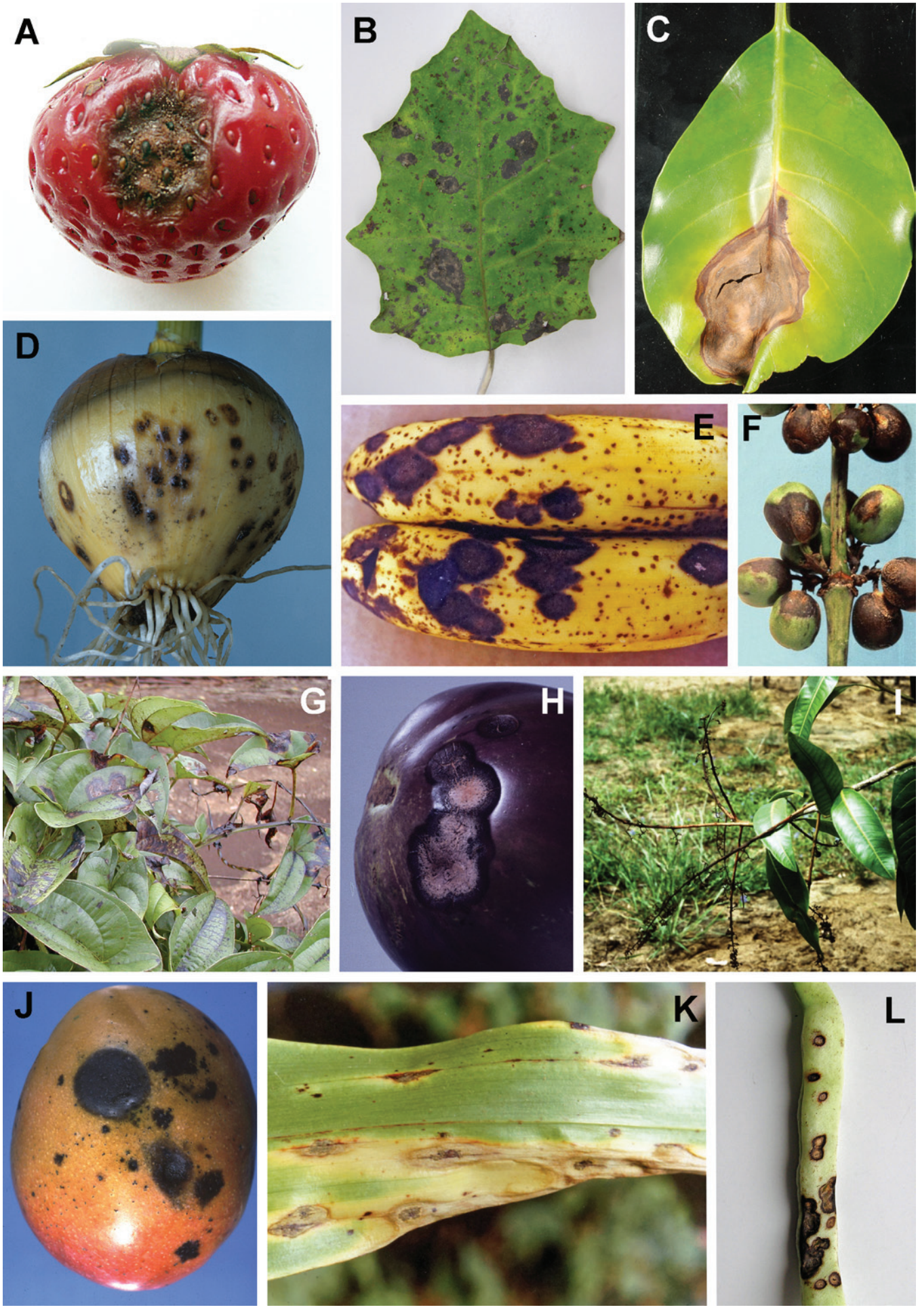
The genus *Colletotrichum* includes a number of plant pathogens of major importance, causing diseases of a wide variety of woody and herbaceous plants. It has a primarily tropical and subtropical distribution, although there are some high-profile species affecting temperate crops. Fruit production is 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, Agrios 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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a further body of research into *Colletotrichum* genetics, pathology and host-parasite interactions. It has been reviewed by Nicholson (1992), Bergstrom & 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 truncatula* to the alfalfa pathogen *C. trifolii* 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, Rodriguez & 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 (Tsuji *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, Réblová *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 complication 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 hemibiotrophic phase (Latunde-Dada 2001, Peres *et al.* 2005, Münch *et al.* 2008), and distinguishing between the two life strategies is problematic. Freeman & Rodriguez (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 pathogencity 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 (Leahy *et al.* 1995, MacKenzie *et al.* 2009). Species are associated widely 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. fioriniae* 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).

**Fig. 1A-L.** (see page 182). Disease symptoms caused by *Colletotrichum* species. The causal organisms have in most cases been identified to species complex level only. A. Anthracnose on strawberry fruit caused by *C. nymphaeae* (acutatum clade). B. Leaf spot of *Brachyglottis repanda* caused by *C. beeveri* (boninense clade). C. Anthracnose symptoms on leaves of *Tecomanthe speciosa* caused by *C. boninense* agg. D. Anthracnose of onion bulb caused by *C. circinans* (dematium clade). E. Anthracnose of banana caused by *C. musae* (gloeosporioides clade). F. Coffee berry disease caused by *C. kahawae* subsp. *kahawae* (gloeosporioides clade). G. Leaf anthracnose of yam caused by *C. gloeosporioides* agg. H. Anthracnose of aubergine (eggplant) fruit caused by *C. gloeosporioides* agg. I. Blossom blight of mango caused by an undetermined *Colletotrichum* sp. J. Anthracnose of mango caused by *C. gloeosporioides* agg. K. Leaf blight of maize caused by *C. graminicola* (graminicola clade). L. Anthracnose of bean pod caused by *C. lindemuthianum* (orbiculare agg.). A, © Ulrike Damm/CBS. B, C, D, H © Landcare Research, New Zealand. E, F, K © Jim Waller/CABI. G © Paul Cannon/CABI. I, J © Barbara Ritchie/CABI. L © Lu Guo-zhong, Dalian, China.

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 between fungus and plant was detected, but greatest pathogen diversity occurred in Central America, which is the centre of origin of the host plant. In a similar study, 90 pathotypes were detected by Mahuku & Riascos (2004) from 200 isolates collected in Central and South America. Greater diversity was detected in the Mesoamerican region compared with Andean populations. Sharma *et al.* (2007) conducted a similar study in north-west India, detecting substantial further diversity with 29 pathogenic races from a pool of 90 isolates, of which 17 had not been reported by Mahuku & Riascos (2004). On a smaller scale, six different races of *C. lindemuthianum* were reported from two counties in the state of Minas Geraes, Brazil (Pinto *et al*. 2012), demonstrating complex population structure within a small area. Heterothallic mating and teleomorph formation were demonstrated for *C. lindemuthianum* by Rodriguez-Guerra *et al*. (2005). This body of research provides indications that the taxon concerned is undergoing rapid evolutionary change.

Variability and evolution at population level have been investigated for other species and species clusters in *Colletotrichum* including *C. acutatum* (*e.g.* Freeman *et al*. 2000, 2001, Denoyes-Rothan *et al.* 2003, Peres *et al*. 2008), *C. cereale* (Crouch *et al*. 2008, 2009d), *C. coccodes* (Ben-Daniel *et al.* 2010), *C. gloeosporioides* (Cisar *et al*. 1994, Cisar & TeBeest 1999), *C. graminicola* (*e.g.* Vaillancourt *et al*. 2000, Chen *et al*. 2002, Valèrio *et al*. 2005), *C. sublineola* (Rosewich *et al*. 1998), *C.* "*truncatum*" (actually a member of the *C. destructivum* clade; Menat *et al.* 2012). This is by no means a comprehensive list of research papers on this topic – a full assessment would justify a further major review.

## 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 (1928), 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*, *Gl. castagnei* 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

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 appressorial 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 nrDNA 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 mtSSU 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 (Prihastuti *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 |
| Sreenivasaprasad *et al.* (1992) | acutatum, gloeosporioides | Strawberry | | ITS |
| Sreenivasaprasad *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 |
| Sreenivasaprasad *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-Figueres (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 |
| Denoyes-Rothan *et al.* (2003) | acutatum, gloeosporioides | Strawberry | | ITS |
| Guerber *et al.* (2003) | acutatum | | USA, New Zealand | GAPDH, GS |
| Martínez-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 *at 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) | acutatum | *Acer platanoides* | USA | ITS, LSU |
| Marcelino *et al.* (2008) | acutatum | Insects | USA | ITS, LSU, TUB2, GAPDH, GS, MAT1-2 |
| Peres *et al.* (2008) | acutatum | *Citrus* | N and S America | ITS, GAPDH |
| Than *et al.* (2008a) | acutatum, truncatum, gloeosporioides | | | ITS, TUB2 |
| Than *et al.* (2008b) | acutatum | | | 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) | acutatum | Strawberry | Spain | ITS |
| MacKenzie *et al.* (2009) | acutatum | | USA, Costa Rica | ITS, GAPDH, GS |
| McKay *et al.* (2009) | acutatum, 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) | acutatum, gloeosporioides | Cranberry | N America | ITS, LSU |
| Prihastuti *et al.* (2009) | gloeosporioides | Coffee | Thailand | ITS, ACT, TUB2, CAL, GS, GAPDH |
| Shivas & Tan (2009) | acutatum | | | ITS, TUB2 |
| Sun & Zhang (2009) | destructivum | | | ITS |
| Talhinhas *et al.* (2009) | acutatum, 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) | acutatum, gloeosporioides | Apple | Brazil | ITS |
| Hemelrijk *et al.* (2010) | acutatum | 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, 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, truncatum | Jasmine | Vietnam | ITS, ACT, TUB2, CAL, GS, GAPDH |
| Xie *et al.* (2010) | acutatum, gloeosporioides | Strawberry | China | ITS |
| Choi *et al.* (2011) | destructivum | | Korea | ITS, ACT, EF1α, GS |
| Faedda *et al.* (2011) | acutatum | Olive | Italy | ITS, TUB2 |
| Gazis *et al.* (2011) | gloeosporioides | *Hevea* species | Peru | ITS, TEF, GPD |
| Liu *et al.* (2011) | coccodes | Potato | | ITS, ACT, GAPDH, TUB2 |
| Rampersad (2011) | gloeosporioides, truncatum | Papaya | Trinidad | ITS, TUB2 |
| Silva-Rojas & Ávila-Quezada (2011) | acutatum, 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 |

**Table 1.** (Continued).

| Publication | Clade | Host taxa | Geographical limits | Loci used |
|---|---|---|---|---|
| Damm *et al.* (2012a) | acutatum | | | ITS, ACT, GAPDH, CHS-1, TUB2, HIS3 |
| Damm *et al.* (2012b) | boninense | | | ITS, ACT, GAPDH, CHS-1, TUB2, HIS3, CAL |
| Silva *et al.* (2012a,b) | gloeosporioides | Coffee | | ITS, ApMAT, Apn15L, MAT1-2, MAT5L, Apn1Ex3, Apn13L, TUB2, GS |
| Weir *et al.* (2012) | gloeosporioides | | | ITS, ACT, GAPDH, CHS-1, TUB2, CAL, GS, SOD2 |
| Yang *et al.* (2012) | genus-wide | *Hemerocallis* | China | ITS, ACT, GAPDH, CHS-1, TUB2 |

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 more than one 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* (= *Stigmatula*; see Cannon 1996) constituted a natural family that did not belong to the *Dothideales*. Chadefaud (1960) introduced (but did not validly publish) the ordinal name *Glomerellales*, including *Glomerella*, *Phyllachora* and two other genera in a non-ranked group "Eu-Glomérellales". 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*. 1995) 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, Castlebury *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*, *Ophiodothella 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 Chadefaud 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. piperata* (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. chamaemori*), which is not closely related to the anthracnose pathogens. *Gnomoniopsis* Berl. has recently been confirmed as a genus of the *Gnomoniaceae* (*Diaporthales*) 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* (*Gnomoniaceae*). Type material has not been traced, and so *Chiloëlla* remains of uncertain affinity. *Ga. montana* (syn. *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*, *Haplothecium 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 *Gloeo. 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

**Table 2.** *Colletotrichum* species with reported *Glomerella* sexual morphs.

| ***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* | | Connection doubtful (see Damm *et al.* 2012b), modern revision needed |
| *Gloeosporium 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. falcatum* | *Ga. tucumanensis* | Carvajal & Edgerton (1944), Politis (1975) | Laboratory culture | *Ga. tucumanensis* | graminicola | |
| *C. fioriniae* | *Ga. fioriniae* | Marcelino *et al.* (2008), Shivas & Tan (2009) | Laboratory mating study | NA | acutatum | |
| *C. fructicola* | Unnamed | Prihastuti *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 |

**Table 2.** (Continued).

| *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* | Petch (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* | Not closely related to any established clade | Identity of this fungus is not completely clarified |
| *C. parsonsii* | 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. piperatum* | *Ga. piperata* | Stoneman (1898) | Laboratory culture | *Ga. cingulata* | gloeosporioides ? | Modern revision needed |
| *C. rhodocyclum* | *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 | |
| *C. taiwanense* | *Ga. septospora* | Sivanesan & Hsieh (1993) | Single-ascospore isolations produced both morphs | NA | | Perhaps does not belong to *Colletotrichum*, modern revision needed |
| Unnamed | *Ga. magna* | Jenkins & Winstead (1964) | Laboratory crossing | NA | Not closely related to any established clade | 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. miyabeana* | Fukushi (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 & Banniza (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 glycines* 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. acutata* 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 taxa has been abolished (Hawksworth 2011). Nevertheless, the need to understand sexual recombination and production in terms of biological strategy (and potentially also economic significance) at species and population level remains clear.

Although currently available data are incomplete, it does appear that some *Colletotrichum* clades have species that form sexual morphs more readily than others. Those where sexual morphs are generated frequently, measured in terms of the proportion of consituent species with known meiotic morphs, include the gloeosporioides and boninense clades. To our knowledge, in contrast, there are no reliable reports of a sexual morph from any taxon within the truncatum 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 Beirn 2009). Mating seems to be rare in the orbiculare clade, with only a small proportion of crosses between *C. lindemuthianum* strains producing fertile progeny (Rodríguez-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 infrageneric clades of fungi has been demonstrated before, *e.g.* by O'Donnell *et al*. (2000) in the *Fusarium graminearum* complex, by Stukenbrock *et al*. (2012) in *Zymoseptoria* 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 rDNA 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: JQ948459; TUB2: JQ950110; ACT: JQ949780; CHS-1: JQ949120; GAPDH: JQ948790; HIS3: JQ949450 | Damm *et al.* (2012a) |
| ***C. acutatum*** | acutatum | IMI 117617 | Holotype | ITS: AF411700 | Vinnere *et al.* (2002) |
| | | CBS 112996, ATCC 56816 | Culture from epitype | ITS: JQ005776; TUB2: JQ005860; ACT: JQ005839; CHS-1: JQ005797; GAPDH: JQ948677; HIS3: JQ005818 | Damm *et al.* (2012a) |
| ***C. aenigma*** | gloeosporioides | ICMP 18608 | Culture from holotype | ITS: JX010244; TUB2: JX010389; ACT: JX009443; CHS-1: JX009774; GAPDH: JX010044; CAL: JX009683; GS: JX010078; SOD2: JX010311 | Weir *et al.* (2012) |
| ***C. aeschynomenes*** | gloeosporioides | ICMP 17673, ATCC 201874 | Culture from holotype | ITS: JX010176; TUB2: JX010392; ACT: JX009483; CHS-1: JX009799; GAPDH: JX009930; CAL: JX009721; GS: JX010081; SOD2: JX010314 | Weir *et al.* (2012) |
| ***C. agaves*** | | CBS 118190 | Morphology congruent with the type | ITS: DQ286221; LSU: DQ286222 | Farr *et al.* (2006) |
| ***C. alatae*** | gloeosporioides | CBS 304.67, ICMP 17919 | Culture from holotype | ITS: JX010190; TUB2: JX010383; ACT: JX009471; CHS-1: JX009837; GAPDH: JX009990; CAL: JX009738; GS: JX010065; SOD2: JX010305 | Weir *et al.* (2012) |
| ***C. alienum*** | gloeosporioides | ICMP 12071 | Culture from holotype | ITS: JX010251; TUB2: JX010411; ACT: JX009572; CHS-1: JX009882; GAPDH: JX010028; CAL: JX009654; GS: JX010101; SOD2: JX010333 | Weir *et al.* (2012) |
| ***C. annellatum*** | boninense | CBS 129826 | Culture from holotype | ITS: JQ005222; TUB2: JQ005656; ACT: JQ005570; CHS-1: JQ005396; GAPDH: JQ005309; HIS3: JQ005483; CAL: JQ005743 | Damm *et al.* (2012b) |
| ***C. anthrisci*** | dematium | CBS 125334 | Culture from holotype | ITS: GU227845; TUB2: GU228139; ACT: GU227943; CHS-1: GU228335; GAPDH: GU228237; HIS3: GU228041 | Damm *et al.* (2009) |
| ***C. aotearoa*** | gloeosporioides | ICMP 18537 | Culture from holotype | ITS: JX010205; TUB2: JX010420; ACT: JX009564; CHS-1: JX009853; GAPDH: JX010005; CAL: JX009611; GS: JX010113; SOD2: JX010345 | Weir *et al.* (2012) |
| ***C. asianum*** | gloeosporioides | MFU 090233, ICMP 18580, CBS 130418 | Culture from holotype | ITS: FJ972612; TUB2: JX010406; ACT: JX009584; CHS-1: JX009867; GAPDH: JX010053; CAL: FJ917506; GS: JX010096; SOD2: JX010328 | Prihastuti *et al.* (2009), Weir *et al.* (2012) |
| ***C. australe*** | acutatum | CBS 116478, HKUCC 2616 | Culture from holotype | ITS: JQ948455; TUB2: JQ950106; ACT: JQ949776; CHS-1: JQ949116; GAPDH: JQ948786; HIS3: JQ949446 | Damm *et al.* (2012a) |
| ***C. axonopodi*** | graminicola? | IMI 279189 | Culture from holotype | ITS: EU554086; Mat1/APN2: FJ377907; APN2: EU364993 | Crouch *et al.* (2009c, d) |
| ***C. beeveri*** | boninense | CBS 128527, ICMP 18594 | Culture from holotype | ITS: JQ005171; TUB2: JQ005605; ACT: JQ005519; CHS-1: JQ005345; GAPDH: JQ005258; HIS3: JQ005432; CAL: JQ005692 | Damm *et al.* (2012b) |
| ***C. boninense*** | boninense | MAFF 305972, CBS 123755 | Culture from holotype | ITS: AB051400, JQ005153; TUB2: JQ005588; ACT: JQ005501; CHS-1: JQ005327; GAPDH: GQ221769, JQ005240; HIS3: JQ005414; CAL: JQ005674 | Moriwaki *et al.* (2003), Damm *et al.* (2012b) |
| ***C. brasiliense*** | boninense | CBS 128501, ICMP 18607 | Culture from holotype | ITS: JQ005235; TUB2: JQ005669; ACT: JQ005583; CHS-1: JQ005409; GAPDH: JQ005322; HIS3: JQ005496; CAL: JQ005756 | Damm *et al.* (2012b) |
| ***C. brassicicola*** | boninense | CBS 101059 | Culture from holotype | ITS: JQ005172; TUB2: JQ005606; ACT: JQ005520; CHS-1: JQ005346; GAPDH: JQ005259; HIS3: JQ005433; CAL: JQ005693 | Damm *et al.* (2012b) |
| ***C. brisbaniense*** | acutatum | CBS 292.67 | Culture from holotype | ITS: JQ948291; TUB2: JQ949942; ACT: JQ949612; CHS-1: JQ948952; GAPDH: JQ948621; HIS3: JQ949282 | Damm *et al.* (2012a) |
| ***C. carthami*** | acutatum | SAPA100011 | Epitype | ITS: AB696998; TUB2: AB696992 | Uematsu *et al.* (2012) |
| ***C. cereale*** **[2]** | graminicola | CBS 129663, KS20BIG | None | ITS: DQ126177, JQ005774; TUB2: JQ005858; ACT: JQ005837; CHS-1: JQ005795; HIS3: JQ005816; SOD2: DQ133277; MAT1-2: DQ131946 | Crouch *et al.* (2006). O'Connell *et al.* (2012) |

**Table 3.** (Continued).

| 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 | SAPA 100010 | Authentic specimen | ITS: AB696999; TUB2: AB696993 | Uematsu *et al.* (2012) |
| | | IMI 364540 | None | ITS: JQ948273; TUB2: JQ949924; ACT: JQ949594; CHS-1: JQ948934; GAPDH: JQ948603; HIS3: JQ949264 | Damm *et al.* (2012a) |
| ***C. circinans*** | dematium | CBS 221.81 | Culture from epitype | ITS: GU227855; TUB2: GU228149; ACT: GU227953; CHS-1: GU228345; GAPDH: GU228247; HIS3: GU228051; LSU: JN940807 | Damm *et al.* (2009), Schoch *et al.* (2012) |
| ***C. clidemiae*** | gloeosporioides | ICMP 18658 | Culture from holotype | ITS: JX010265; TUB2: JX010438; ACT: JX009537; CHS-1: JX009877; GAPDH: JX009989; CAL: JX009645; GS: JX010129; SOD2: JX010356 | Weir *et al.* (2012) |
| ***C. cliviae*** | | CBS 125375 | Culture from holotype | ITS: GQ485607, JX519223; TUB2: GQ849440, JX519249; ACT: GQ856777, JX519240; CHS-1: GQ856722, JX519232; GAPDH: GQ856756; CAL: GQ849464 | Yang *et al.* (2009), this study |
| ***C. coccodes*** | | CBS 369.75 | Culture from neotype | ITS: HM171679, JQ005775; TUB2: JQ005859; ACT: HM171667, JQ005838; CHS-1: JQ005796; GAPDH: HM171673; HIS3: JQ005817; CAL: HM171670; GS: HM171676 | Liu *et al.* (2011), O'Connell *et al.* (2012) |
| ***C. colombiense*** | boninense | CBS 129818 | Culture from holotype | ITS: JQ005174; TUB2: JQ005608; ACT: JQ005522; CHS-1: JQ005348; GAPDH: JQ005261; HIS3: JQ005435; CAL: JQ005695 | Damm *et al.* (2012b) |
| ***C. constrictum*** | boninense | CBS 128504, ICMP 12941 | Culture from holotype | ITS: JQ005238; TUB2: JQ005672; ACT: JQ005586; CHS-1: JQ005412; GAPDH: JQ005325; HIS3: JQ005499; CAL: JQ005759 | Damm *et al.* (2012b) |
| ***C. cordylinicola*** | gloeosporioides | MFU090551, ICMP 18579 | Culture from holotype | ITS: HM470246, JX010226; TUB2: HM470249, JX010440; ACT: HM470234; CHS-1: JX009864; GAPDH: HM470240, JX009975; CAL: HM470237; GS: HM470243, JX010122; SOD2: JX010361 | Phoulivong *et al.* (2010), Weir *et al.* (2012) |
| ***C. cosmi*** | acutatum | CBS 853.73 | Culture from holotype | ITS: JQ948274; TUB2: JQ949925; ACT: JQ949595; CHS-1: JQ948935; GAPDH: JQ948604; HIS3: JQ949265 | Damm *et al.* (2012a) |
| ***C. costaricense*** | acutatum | CBS 330.75 | Culture from holotype | ITS: JQ948180; TUB2: JQ949831; ACT: JQ949501; CHS-1: JQ948841; GAPDH: JQ948510; HIS3: JQ949171 | Damm *et al.* (2012a) |
| ***C. curcumae*** | truncatum | IMI 288937 | Culture from epitype | ITS: GU227893; TUB2: GU228187; ACT: GU227991; CHS-1: GU228383; GAPDH: GU228285; HIS3: GU228089 | Damm et al. (2009) |
| ***C. cuscutae*** | acutatum | IMI 304802 | Culture from holotype | ITS: JQ948195; TUB2: JQ949846; ACT: JQ949516; CHS-1: JQ948856; GAPDH: JQ948525; HIS3: JQ949186 | Damm *et al.* (2012a) |
| ***C. cymbidiicola*** | boninense | 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*** | boninense | 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*** | dematium | CBS 125.25 | Culture from epitype | ITS: GU227819; TUB2: GU228113; ACT: GU227917; CHS-1: GU228309; GAPDH: GU228211; HIS3: GU228015; LSU: JN940809 | Damm *et al.* (2009), Schoch *et al.* (2012) |
| ***C. destructivum*** | destructivum | CBS 149.34 | None | ITS: AJ301942; TUB2: JQ005848; ACT: JQ005827; CHS-1: JQ005785; HIS3: JQ005806 | O'Connell *et al.* (2012) |
| ***C. dracaenophilum*** | | CBS 118199 | Culture from holotype | ITS: DQ286209, JX519222; TUB2: JX519247; ACT: JX519238; CHS-1: JX519230; LSU: DQ286210 | Farr *et al.* (2006), this study |
| ***C. echinochloae*** | graminicola | MAFF 511473 | Culture from holotype | ITS: AB439811; SOD2: AB440153; MAT1-2: AB439820 | Moriwaki & Tsukiboshi (2009), Crouch *et al.* (2009c, d) |

**Table 3.** (Continued).

| Species | Clade | Source material [1] | Status of source material | GenBank accession number(s) | Reference |
|---|---|---|---|---|---|
| ***C. eleusines*** | graminicola | MAFF 511155 | Culture from epitype | ITS: EU554131, JX519218; TUB2: JX519243; ACT: JX519234; CHS-1: JX519226; SOD2: EU554234; APN2: EU365038 | Crouch *et al.* (2009c, d), this study |
| ***C. eremochloae*** | graminicola | CBS 129661 | Culture from holotype | ITS: JQ478447, JX519220; TUB2: JX519245; ACT: JX519236; CHS-1: JX519228; SOD2: JQ478449; Mat1/APN2: JQ478462; APN2: JQ478476 | Crouch & Tomaso-Peterson (2012), this study |
| ***C. falcatum*** | graminicola | CGMCC 3.14187, CBS 147945 | Culture from neotype | ITS: HM171677, JQ005772; TUB2: JQ005856; ACT: JQ005835; CHS-1: JQ005793; HIS3: JQ005814; Mat1/APN2: HM569769; APN2: HM569770 | Prihastuti *et al.* 2010, O'Connell *et al.* (2012) |
| ***C. fioriniae*** | acutatum | EHS 58, CBS 128517, ARSEF 10222 | Culture from holotype | ITS: EF464594, JQ948292; TUB2: EF593325, JQ949943; ACT: JQ949613; CHS-1: JQ948953; GAPDH: EF593344, JQ948622; HIS3: JQ949283; GS: EF593353; MAT1-2: EF593362; LSU: EF464581 | Marcelino *et al.* (2008), Shivas & Tan (2009), Damm *et al.* (2012a) |
| ***C. fructi*** | dematium | CBS 346.37 | Culture from epitype | ITS: GU227844; 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: FJ907441, JX010405; ACT: FJ907426; CHS-1: JX009866; GAPDH: FJ972578, JX010033; CAL: FJ917508; GS: FJ972593, JX010095; SOD2: JX010327 | Prihastuti *et al.* (2009), Weir *et al.* (2012) |
| ***C. fuscum*** | destructivum | CBS 130.57 | None | ITS: JQ005762; TUB2: JQ005846; ACT: JQ005825; CHS-1: JQ005783; HIS3: JQ005804 | O'Connell *et al.* (2012) |
| ***C. gloeosporioides*** | gloeosporioides | IMI 356878, CBS 112999, ICMP17821 | Culture from epitype | ITS: EU371022, JQ005152, JX010152; TUB2: FJ907445, JQ005587, JX010445; ACT: FJ907430, JQ005500, JX009531; CHS-1: JQ005326, JX009818; GAPDH: FJ972582, JQ005239, JX010056; HIS3: JQ005413; CAL: FJ917512, JQ005673, JX009731; GS: FJ972589, JX010085; SOD2: JX010365 | Damm *et al.* (2012b), Weir et al. (2012) |
| ***C. godetiae*** | acutatum | CBS 133.44 | Culture from holotype | ITS: JQ948402; TUB2: JQ950053; ACT: JQ949723; CHS-1: JQ949063; GAPDH: JQ948733; HIS3: JQ949393 | Damm *et al.* (2012a) |
| ***C. graminicola*** | graminicola | CBS 130836, M 1.001 | Culture from epitype | ITS: DQ003110, JQ005767; TUB2: JQ005851; ACT: JQ005830; CHS-1: JQ005788; HIS3: HQ005809; Mat1/APN2: FJ377994; MAT1-2: EU365081 | Du *et al.* (2005), Crouch *et al.* (2009 d), O'Connell *et al.* (2012) |
| ***C. guajavae*** | acutatum | IMI 350839 | Culture from holotype | ITS: JQ948270; TUB2: JQ949921; ACT: JQ949591; CHS-1: JQ948931; GAPDH: JQ948600; HIS3: JQ949261 | Damm *et al.* (2012a) |
| ***C. hanaui*** | graminicola | MAFF 305404 | Culture from holotype | ITS: EU554101, JX519217; TUB2: JX519242; CHS-1: JX519225; SOD2: EU554205; Mat1/APN2: FJ377922; APN2: EU365008 | Crouch *et al.* (2009c, d), this study |
| ***C. hemerocallidis*** | dematium | CDLG5 | Culture from holotype | ITS: JQ400005; TUB2: JQ400019; ACT: JQ399991; CHS-1: Q399998; GAPDH: JQ400012 | Yang *et al.* 2012 |
| ***C. higginsianum*** | destructivum | IMI 349063 | None | ITS: JQ005760; TUB2: JQ005844; ACT: JQ005823; CHS-1: JQ005781; HIS3: JQ005802 | O'Connell *et al.* (2012) |
| ***C. hippeastri*** | boninense | CBS 125376 | Culture from holotype | ITS: GQ485599, JQ005231; TUB2: GQ849446, JQ005665; ACT: GQ856788, JQ005579; CHS-1: GQ856725, JQ005405; GAPDH: GQ856764, JQ005318; HIS3: JQ005492; CAL: GQ849469, JQ005752 | Yang *et al.* (2009), Damm *et al.* (2012b) |
| ***C. horii*** | gloeosporioides | NBRC 7478, ICMP 10492 | Culture from neotype | ITS: GQ329690; TUB2: JX010450; ACT: JX009438; CHS-1: JX009752; GAPDH: GQ329681; CAL: JX009604; GS: JX010137; SOD2: JX010370; TEF1: GQ329693 | Weir & Johnston (2010), Weir *et al.* (2012) |
| ***C. indonesiense*** | acutatum | CBS 127551 | Culture from holotype | ITS: JQ948288; TUB2: JQ949939; ACT: JQ949609; CHS-1: JQ948949; GAPDH: JQ948618; HIS3: JQ949279 | Damm *et al.* (2012a) |
| ***C. jacksonii*** | graminicola | MAFF 305460 | Culture from holotype | ITS: EU554108, JX519216; TUB2: JX519241; ACT: JX519233; CHS-1: JX519224; SOD2: EU554212 | Crouch *et al.* (2009c, d), this study |

**Table 3.** (Continued).

| Species | Clade | Source material [1] | Status of source material | GenBank accession number(s) | Reference |
|---|---|---|---|---|---|
| ***C. jasminigenum*** | truncatum | CGMCC LLTX–01, MFU 10–0273 | Culture from type | ITS: HM131513; TUB2: HM153770; ACT: HM131508; GAPDH: HM131499; CAL: HM131494; GS: 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: JQ948775; HIS3: JQ949435 | Damm *et al.* (2012a) |
| ***C. kahawae* subsp. *ciggaro*** | gloeosporioides | ICMP 18539 | Culture from holotype | ITS: JX010230; TUB2: JX010434; ACT: JX009523; CHS-1: JX009800; GAPDH: JX009966; CAL: JX009635; GS: JX010132; SOD2: JX010346 | Weir *et al.* (2012) |
| ***C. kahawae* subsp. *kahawae*** | gloeosporioides | IMI 319418, ICMP17816 | Culture from holotype | ITS: GU174550, JX010231; TUB2: JX010444; ACT: JX009452; CHS-1: JX009813; GAPDH: GU174562, JX010012; CAL: JX009642; GS: JX010130; SOD2: JX010130 | Weir *et al.* (2012) |
| ***C. karstii*** | boninense | CBS 132134, CORCG6, CGMCC3.14194 | Culture from holotype | ITS: HM585409; TUB2: HM585428; ACT: HM581995; CHS-1: HM582023; GAPDH: HM585391; CAL: HM582013 | Yang *et al.* (2011) |
| ***C. kinghornii*** | acutatum | CBS 198.35 | Culture from holotype | ITS: JQ948454; TUB2: JQ950105; ACT: JQ949775; CHS-1: JQ949115; GAPDH: JQ948785; HIS3: JQ949445 | Damm *et al.* (2012a) |
| ***C. laticiphilum*** | acutatum | CBS 112989, IMI 383015, STE-U 5303 | Culture from holotype | ITS: JQ948289; TUB2: JQ949940; ACT: JQ949610; CHS-1: JQ948950; GAPDH: JQ948619; HIS3: JQ949280 | Damm *et al.* (2012a) |
| ***C. lilii*** | spaethianum | CBS 109214 | Morphology congruent with original description | ITS: GU227810; TUB2: GU228104; ACT: GU227908; CHS-1: GU228300; GAPDH: GU228202; HIS3: GU228006 | Damm *et al.* (2009) |
| ***C. limetticola*** | acutatum | CBS 114.14 | Culture from epitype | ITS: JQ948193; TUB2: JQ949844; ACT: JQ949514; CHS-1: JQ948854; GAPDH: JQ948523; HIS3: JQ949184 | Damm *et al.* (2012a) |
| ***C. lindemuthianum*** | orbiculare | CBS 144.31 | None | ITS: JQ005779; TUB2: JQ005863; ACT: JQ005842; CHS-1: JQ005800; HIS3: JQ005821 | O'Connell *et al.* (2012) |
| ***C. lineola*** | dematium | CBS 125337 | Culture from epitype | ITS: GU227829; TUB2: GU228123; ACT: GU227927; CHS-1: GU228319; GAPDH: GU228221; HIS3: GU228025 | Damm *et al.* (2009) |
| ***C. linicola*** | destructivum | CBS 172.51 | None | ITS: JQ005765; TUB2: JQ005849; ACT: JQ005828; CHS-1: JQ005786; HIS3: JQ005807 | O'Connell *et al.* (2012) |
| ***C. liriopes*** | spaethianum | CBS 119444 | Culture from holotype | ITS: GU227804; TUB2: GU228098; ACT: GU227902; CHS-1: GU228294; GAPDH: GU228196; HIS3: GU228000 | Damm *et al.* (2009) |
| ***C. lupini*** | acutatum | BBA 70884, CBS 109225 | Culture from neotype | ITS: DQ286119, JQ948155; TUB2: JQ949806; ACT: JQ949476; CHS-1: JQ948816; GAPDH: JQ948485; HIS3: JQ949146; Mat1/APN2: DQ174704; TUB1: AJ301948 | Nirenberg *et al.* (2002), Damm *et al.* (2012a) |
| ***C. malvarum*** | orbiculare | LW1 | None | GAPDH: DQ792860 | Liu *et al.* (2007a) |
| ***C. melonis*** | acutatum | CBS 159.84 | Culture from holotype | ITS: JQ948194; TUB2: JQ949845; ACT: JQ949515; CHS-1: JQ948855; GAPDH: JQ948524; HIS3: JQ949185 | Damm *et al.* (2012a) |
| ***C. miscanthi*** | graminicola | MAFF 510857 | Culture from holotype | ITS: EU554121, JX519221; TUB2: JX519246; ACT: JX519237; CHS-1: JX519229; SOD2: EU554224; APN2: EU365028 | Crouch *et al.* (2009c, d), this study |
| ***C. musae*** | gloeosporioides | CBS 116870, ICMP19119 | Culture from epitype | ITS: HQ596292, JX010146; TUB2: HQ596280; ACT: HQ596284, JX009433; CHS-1: JX009896; GAPDH: HQ596299, JX010050; CAL: JX009742; GS: HQ596288, JX010103; SOD2: JX010335 | Su *et al.* (2011), Weir *et al.* (2012) |
| ***C. navitas*** | graminicola | CBS 125086 | Culture from holotype | ITS: GQ919067, JQ005769; TUB2: JQ005853; ACT: JQ005832; CHS-1: JQ005790; HIS3: JQ005811; SOD2: GQ919073; Mat1/APN2: GQ919071; APN2: GQ919069 | Crouch *et al.* (2009a), O'Connell *et al.* (2012) |
| ***C. nicholsonii*** | graminicola | MAFF 511115 | Culture from holotype | ITS: EU554126, JQ005770; TUB2: JQ005854; ACT: JQ005833; CHS-1: JQ005791; HIS3: JQ005812; SOD2: EU554229; Mat1/APN2: FJ377946; APN2: EU365033 | Crouch *et al.* (2009c, d), O'Connell *et al.* (2012) |

**Table 3.** (Continued).

| 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 | Damm *et al.* (2012b) |
| ***C. nupharicola*** | gloeosporioides | CBS 470.96, ICMP 18187 | Culture from holotype | ITS: JX010187; TUB2: JX010398; ACT: JX009437; CHS-1: JX009835; GAPDH: JX009972; CAL: JX009663; GS: JX010088; SOD2: JX010320 | Weir *et al.* (2012) |
| ***C. nymphaeae*** | acutatum | CBS 515.78 | Culture from epitype | ITS: JQ948197; TUB2: JQ949848; ACT: JQ949518; CHS-1: JQ948858; GAPDH: JQ948527; HIS3: JQ949188 | Damm *et al.* (2012a) |
| ***C. oncidii*** | boninense | CBS 129828 | Culture from holotype | ITS: JQ005169; TUB2: JQ005603; ACT: JQ005517; CHS-1: JQ005343; GAPDH: JQ005256; HIS3: JQ005430; CAL: JQ005690 | Damm *et al.* (2012b) |
| ***C. orbiculare*** | orbiculare | LARS 414, 104T, CBS 514.97 | None | ITS: JQ005778; TUB2: JQ005862; ACT: JQ005841; CHS-1: JQ005799; HIS3: JQ005820 | O'Connell *et al.* (2012) |
| ***C. orchidophilum*** | | CBS 632.80 | Culture from holotype | ITS: JQ948151; TUB2: JQ949802; ACT: JQ949472; CHS-1: JQ948812; GAPDH: JQ948481; HIS3: JQ949142 | Damm *et al.* (2012a) |
| ***C. parsonsiae*** | boninense | CBS 128525, ICMP 18590 | Culture from holotype | ITS: JQ005233; TUB2: JQ005667; ACT: JQ005581; CHS-1: JQ005407; GAPDH: JQ005320; HIS3: JQ005494; CAL: JQ005754 | Damm *et al.* (2012b) |
| ***C. paspali*** | graminicola | MAFF 305403 | Culture from holotype | ITS: EU554100, JX519219; TUB2: JX519244; ACT: JX519235; CHS-1: JX519227; SOD2: EU554204; Mat1/APN2: FJ377921; APN2: EU365007 | Crouch *et al.* (2009c, d), this study |
| ***C. paxtonii*** | acutatum | IMI 165753 | Culture from holotype | ITS: JQ948285; TUB2: JQ949936; ACT: JQ949606; CHS-1: JQ948946; GAPDH: JQ948615; HIS3: JQ949276 | Damm *et al.* (2012a) |
| ***C. petchii*** | boninense | CBS 378.94 | Culture from epitype | ITS: JQ005223; TUB2: JQ005657; ACT: JQ005571; CHS-1: JQ005397; GAPDH: JQ005310; HIS3: JQ005484; CAL: JQ005744 | Damm *et al.* (2012b) |
| ***C. phaseolorum*** **[4]** | dematium | CBS 157.36 | Authentic strain | ITS: GU227896; TUB2: GU228190; ACT: GU227994; CHS-1: GU228386; GAPDH: GU228288; HIS3: GU228092 | Damm *et al.* (2009) |
| ***C. phormii*** | acutatum | CBS 118194 | Culture from epitype | ITS: DQ286136, JQ948446; TUB2: JQ950097; ACT: JQ949767; CHS-1: JQ949107; GAPDH: JQ948777; HIS3: JQ949437; LSU: DQ286137 | Farr *et al.* (2006), Damm *et al.* (2012a) |
| ***C. phyllanthi*** | boninense | CBS 175.67 | Culture from holotype | ITS: JQ005221; TUB2: JQ005655; ACT: JQ005569; CHS-1: JQ005395; GAPDH: JQ005308; HIS3: JQ005482; CAL: JQ005742 | Damm *et al.* (2012b) |
| ***C. pseudoacutatum*** | | CBS 436.77 | Culture from holotype | ITS: JQ948480; TUB2: JQ950131; ACT: JQ949801; CHS-1: JQ949141; GAPDH: JQ948811; HIS3: JQ949471 | Damm *et al.* (2012a) |
| ***C. psidii*** | gloeosporioides | CBS 145.29*, ICMP 19120 | Authentic strain | ITS: JX010219; TUB2: JX010443; ACT: JX009515; CHS-1: JX009901; GAPDH: JX009967; CAL: JX009743; GS: JX010133; SOD2: JX010366 | Weir *et al.* (2012) |
| ***C. pyricola*** | acutatum | CBS 128531, ICMP 12924 | Culture from holotype | ITS: JQ948445; TUB2: JQ950096; ACT: JQ949766; CHS-1: JQ949106; GAPDH: JQ948776; HIS3: JQ949436 | Damm *et al.* (2012a) |
| ***C. queenslandicum*** | gloeosporioides | ICMP 1778 | Culture from epitype | ITS: JX010276; TUB2: JX010414; ACT: JX009447; CHS-1: JX009899; GAPDH: JX009934; CAL: JX009691; GS: JX010104; SOD2: JX010336 | Weir *et al.* (2012) |
| ***C. rhombiforme*** | acutatum | CBS 129953 | Culture from holotype | ITS: JQ948457; TUB2: JQ950108; ACT: JQ949778; CHS-1: JQ949118; GAPDH: JQ948788; HIS3: JQ949448 | Damm *et al.* (2012a) |
| ***C. rusci*** | | CBS 119206 | Culture from holotype | ITS: GU227818; TUB2: GU228112; ACT: GU227916; CHS-1: GU228308; GAPDH: GU228210; HIS3: GU228014 | Damm *et al.* (2009) |
| ***C. salicis*** | acutatum | CBS 607.94 | Culture from epitype | ITS: JQ948460; TUB2: JQ950111; ACT: JQ949781; CHS-1: JQ949121; GAPDH: JQ948791; HIS3: JQ949451 | Damm *et al.* (2012a) |

**Table 3.** (Continued).

| Species | Clade | Source material [1] | Status of source material | GenBank accession number(s) | Reference |
|---|---|---|---|---|---|
| ***C. salsolae*** | gloeosporioides | ICMP 19051 | Culture from holotype | ITS: JX010242; TUB2: JX010403; ACT: JX009562; CHS-1: JX009863; GAPDH: JX009916; CAL: JX009696; GS: JX010093; SOD2: JX010325 | Weir *et al.* (2012) |
| ***C. scovillei*** | acutatum | CBS 126529, BBA 70349 | Culture from holotype | ITS: JQ948267; TUB2: JQ949918; ACT: JQ949588; CHS-1: JQ948928; GAPDH: JQ948597; HIS3: JQ949258 | Damm *et al.* (2012a) |
| ***C. sansevieriae*** | | MAFF 239721 | Culture from holotype | ITS: AB212991 | Nakamura *et al.* (2006) |
| ***C. siamense*** | gloeosporioides | MFU 090230, ICMP 18578, CBS 130417 | Culture from holotype | ITS: FJ972613, JX010171; TUB2: FJ907438, 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*** | acutatum | BRIP 28519, CBS 122122 | Culture from holotype | ITS: FJ972601, JQ948276; TUB2: FJ907443, JQ949927; ACT: FJ907428, JQ949597; CHS-1: JQ948937; GAPDH: FJ972580, JQ948606; HIS3: JQ949267; CAL: FJ917510; GS: FJ972591 | Shivas & Tan (2009), Damm *et al.* (2012a) |
| ***C. sloanei*** | acutatum | IMI 364297 | Culture from holotype | ITS: JQ948287; TUB2: JQ949938; ACT: JQ949608; CHS-1: JQ948948; GAPDH: JQ948617; HIS3: JQ949278 | Damm *et al.* (2012a) |
| ***C. spaethianum*** | spaethianum | CBS 167.49 | Culture from epitype | ITS: GU227807; TUB2: GU228101; ACT: GU227905; CHS-1: GU228297; GAPDH: GU228199; HIS3: GU228003; LSU: JN940813 | Damm *et al.* (2009), Schoch et al. (2012) |
| ***C. spinaciae*** | dematium | CBS 128.57 | Morphology congruent with original description | ITS: GU227847; TUB2: GU228141; ACT: GU227945; CHS-1: GU228337; GAPDH: GU228239; HIS3: GU228043 | Damm *et al.* (2009), |
| ***C. sublineola*** **[5]** | graminicola | BPI399463 | Lectotype | ITS: JQ478437; HIS3: JQ005813; SOD2: JQ478453; Mat1/APN2: JQ478466; APN2: JQ478477 | Crouch & Tomaso-Peterson (2012), |
| | | CBS 131301, S3.001 | Culture from epitype | ITS: DQ003114, JQ005771; TUB2: JQ005855; ACT: JQ005834; CHS-1: JQ005792; HIS3: JQ005813; SOD2: DO132051; Mat1/APN2: FJ378029; APN2: EU365121; MAT1-2: DQ002865 | Crouch & Tomaso-Peterson (2012), Crouch *et al.* (2006), O'Connell *et al.* (2012) |
| ***C. tabacum*** | destructivum | CBS 161.53 | None | ITS: JQ005763; TUB2: JQ005847; ACT: JQ005826; CHS-1: JQ005784; HIS3: JQ005805 | O'Connell *et al.* (2012) |
| ***C. tamarilloi*** | acutatum | CBS 129814 | Culture from holotype | ITS: JQ948184; TUB2: JQ949835; ACT: JQ949505; CHS-1: JQ948845; GAPDH: JQ948514; HIS3: JQ949175 | Damm *et al.* (2012a) |
| ***C. theobromicola*** | gloeosporioides | ICMP 18649, CBS 124945 | Culture from neotype | ITS: GU994360, JX010294; TUB2: GU994477, JX010447; ACT: JX009444; CHS-1: JX009869; GAPDH: JX010006; CAL: JX009591; GS: JX010139; SOD2: JX010372; Mat1/APN2: GU994448; APN2: GU994419; TEF1: GU994506 | Rojas *et al.* (2010), Weir *et al.* (2012) |
| ***C. ti*** | gloeosporioides | ICMP 4832 | Culture from holotype | ITS: JX010269; TUB2: JX010442; ACT: JX009520; CHS-1: JX009898; GAPDH: JX009952; CAL: JX009649; GS: JX010123; SOD2: JX010362 | Weir *et al.* (2012) |
| ***C. tofieldiae*** | spaethianum | CBS 495.85 | Morphology congruent with original description | ITS: GU227801; TUB2: GU228095; ACT: GU227899; CHS-1: GU228291; GAPDH: GU228193; HIS3: GU227997; LSU: JN940815 | Damm *et al.* (2009), Schoch *et al.* (2012) |
| ***C. torulosum*** | boninense | CBS 128544, ICMP 18586 | Culture from holotype | ITS: JQ005164; TUB2: JQ005598; ACT: JQ005512; CHS-1: JQ005338; GAPDH: JQ005251; HIS3: JQ005425; CAL: JQ005685 | 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; HIS3: GU228008 | Damm *et al.* (2009) |
| ***C. tropicale*** | gloeosporioides | CBS 124949, ICMP18653 | Culture from holotype | ITS: GU994331, JX010264; TUB2: GU994454, JX010407; ACT: JX009489; CHS-1: JX009870; GAPDH: JX010007; CAL: JX009719; GS: JX010097; SOD2: JX010329; Mat1/APN2: GU994425; APN2: GU994396; TEF1: GU994483 | 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 45525 | 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: JQ949926; ACT: JQ949596; CHS-1: JQ948936; 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: JX009653; 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 |

ARSEF: ARS Collection of Entomopathogenic Fungal Cultures, Ithaca, NY, USA.

BBA: Culture collection of the Biologische Bundesanstalt für Land- und Forstwirtschaft, *Berlin*, Germany.

BPI: Systematic Mycology and Microbiology Laboratory, USDA Agricultural Research Service, Beltsville, MD, USA.

BRIP: Culture Collection of the DPI&F Plant Pathology Herbarium, Indooroopilly, Queensland, Australia.

CBS: Culture collection of the Centraalbureau voor Schimmelcultures, Fungal Biodiversity Centre, Utrecht, The Netherlands.

CGMCC: China General Microbiological Culture Collection Center, Beijing, China.

ICMP: International Collection of Microorganisms from Plants, Landcare Research, Auckland, New Zealand.

IMI: Culture collection of CABI Europe UK Centre, Egham, UK.

M1.001: sourced from Lisa Vaillancourt, University of Kentucky.

MAFF: NIAS Genebank, Microorganism Section, Tsukuba, Japan.

MFU: fungarium of Mae Fah Luang University, Thailand (cultures in BCC (BIOTEC Culture Collection, Thailand).

NBRC: NITE Biological Resource Center, Chiba, Japan.

STE-U: Culture collection of the Department of Plant Pathology, University of Stellenbosch, South Africa.

[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*. (2006) 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 1763), but genes are differential at varying positions in the hierachy 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 (ICNAFP), 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 ICNAFP 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 within 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 shortcoming 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 graminicola clade are much less closely related than those of the *C. 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.*

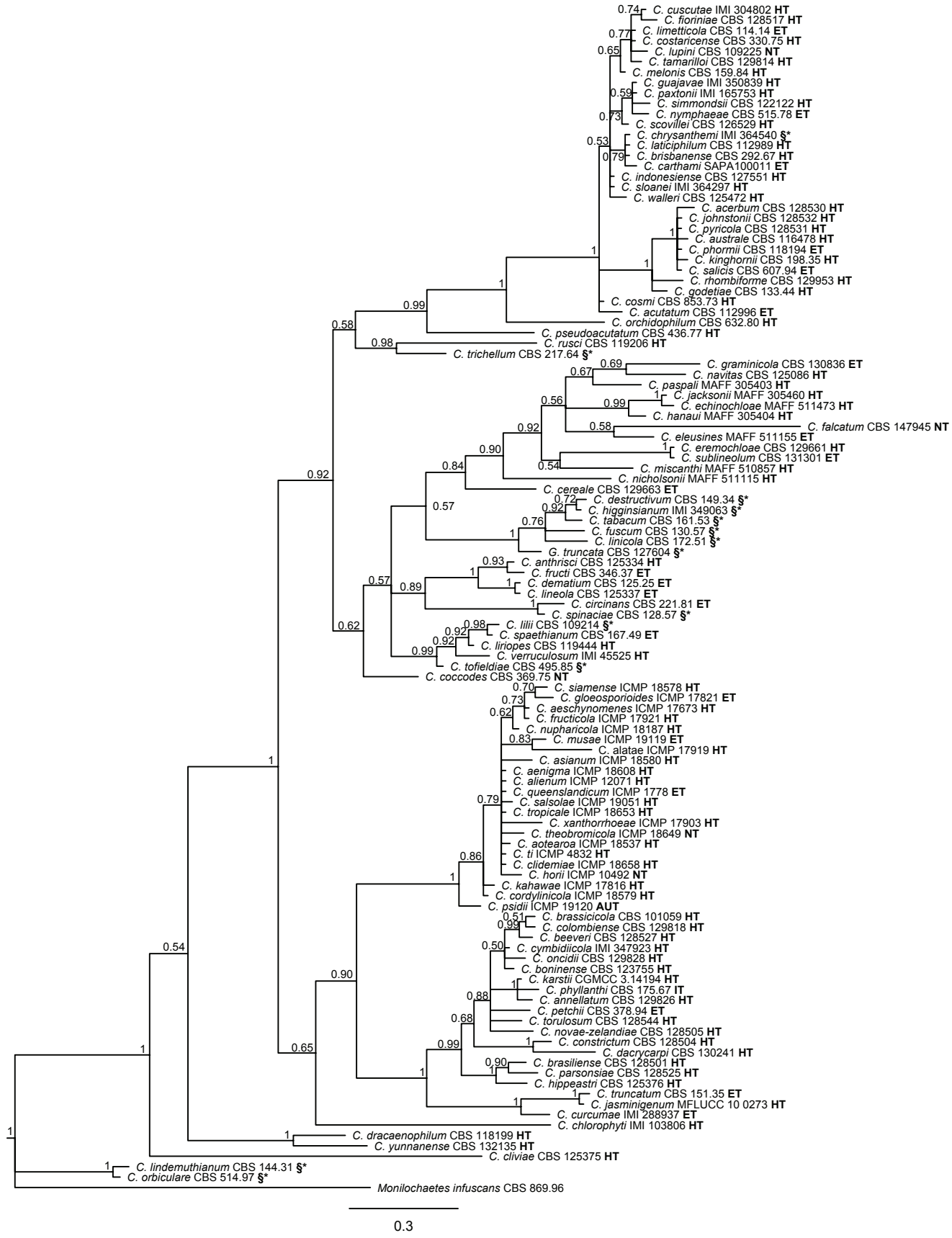


**Fig. 2.** Phylogenetic tree derived from a Bayesian analysis of an alignment of ITS (599 bp) sequences, run for $1\times10^7$ generations with a GTR+I+Γ model of DNA evolution. Species names are followed by culture number, and status of the culture, where HT = ex-holotype, ET = epitype, NT = ex-neotype, IT = ex-isotype, AUT = authentic culture. Sequences from a number of non-validated cultures have been included in order to represent clades that have not yet been subject to revision based on multilocus data. These are indicated by the symbol §*.

*orchidophilum* 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 spaethianum clades and *C. coccodes*. 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


**Fig. 3.** Phylogenetic tree derived from a Bayesian analysis of a partitioned, concatenated alignment of CHS-1 (251 bp), ACT (305 bp), TUB2 (545 bp) and ITS (599 bp) sequences, run for $1\times10^7$ generations with a GTR+I+Γ model of DNA evolution for each partition. The major clades recognised in this paper are indicated. Other details as per Fig. 2.

clade consisting of the larger of the two subclades along with *C. fioriniae*. 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 gloeosporioides 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 gloeosporioides 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 in economic terms, but *C. spinaciae* (a pathogen of *Beta* and *Spinacia*; Gourley 1966, Washington *et al.* 2006) and *C. circinans* (attacking *Allium* species; Hall *et al.* 2007, Kim *et al.* 2008) both cause substantial crop losses under some circumstances. These two plant pathogenic species occupy a well-defined subclade distinct from a separate subclade made up of the putatively saprobic species *C. dematium*, *C. lineola*, *C. fructi* and *C. anthrisci* (Damm *et al.* 2009; Fig. 3). The type species of *Colletotrichum*, *C. lineola*, belongs to the dematium clade; it was described by Corda (1831) but treated as a synonym of *C. dematium* by von Arx (1957) and Sutton (1981). However, research based on newly collected strains from the region of the original collection showed that *C. lineola* and *C. dematium* are separable based on DNA sequence data (Damm *et al*. 2009).

## Destructivum clade

The destructivum clade contains several important plant 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. linicola*. *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).

*Glomerella 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.

## Gloeosporioides clade

The *C. gloeosporioides* species complex has been studied by Weir *et al*. (2012, this issue). It is a well-supported clade (Bayesian posterior probability value 1) 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 subclade (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 teleomorphs 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).

## Orbiculare 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 cluster 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 cluster 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)

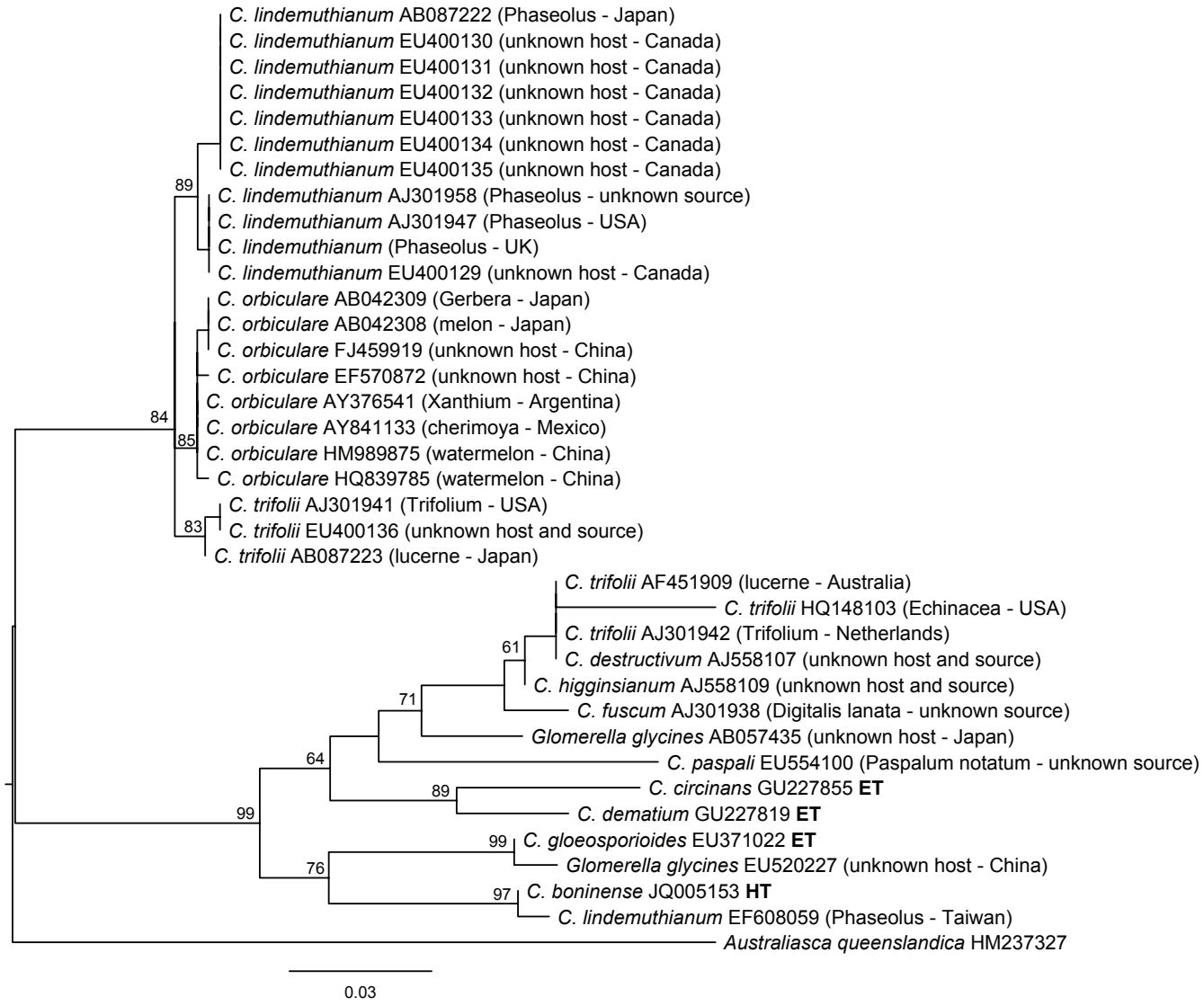


**Fig. 4**. Maximum likelihood phylogeny based on an ITS alignment of GenBank accessions of the *C. lindemuthianum*, *C. orbiculare*, *C. trifolii* and *C. destructivum* species complexes (alignment with ClustalX, 1000 bootstrap replicates, PhyML package).

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 malvarum* 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 to 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*.

*Colletotrichum curcumae* also belongs to this clade, a poorly-known species considered to be the causal agent of turmeric leaf spot disease (*Curcuma longa, Zingiberaceae*; Palarpawar &

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 (Wikee *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. dematium* 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 dematium clade, but forms a sister clade (along with *C. rusci*) 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 *Clivia miniata*, *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.* 2006), 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 capestris*, *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 aound 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 prejudges 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.

A further important activity for the *Colletotrichum* community is to establish a robust phylogeny-based online identification system with barcode reference sequences from ex-type or other verified material that can be queried using Blast tools, as a rigorous alternative to the uncurated data set accessible in GenBank. A preliminary system has already been set up by the CBS-KNAW Fungal Biodiversity Centre based on the multilocus sequence data listed in Table 3 (http://www.cbs.knaw.nl/colletotrichum). In addition to sequences, it will also include morphological and cultural characters and pictures of each species facilitating comprehensive polyphasic identification. Methods used to collect the data are explained, and cultures are listed along with ecological data available. This database will be updated as new taxa are discovered and typifications completed by members of the Subcommission on *Colletotrichum*.

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