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Colletotrichum systematics: Past, present and prospects

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Abstract

Colletotrichum is one of the serious plant pathogens, with worldwide distribution, causing anthracnose in economically important crops. Every year many research papers and reports are published on *Colletotrichum* phylogeny and taxonomy. Many novel *Colletotrichum* species have been described based on morphological characters and multi-locus phylogenetic analysis. There is, however, a need to develop a consensus among researchers on the gene sets to be used in sequence-based identification and resolution of cryptic species of *Colletotrichum*. Though a polyphasic approach is recommended, it is not fully enforced in many publications. In this paper, the methods prevalent in *Colletotrichum* systematics are discussed, which is followed by our suggestions towards developing a stable and reliable classification system for *Colletotrichum*.

Key words – anthracnose – barcoding – identification – morphology – new taxa – polyphasic taxonomy

Introduction

Colletotrichum (*Glomerellaceae, Sordariomycetes*, *Ascomycota*) is one of the top 10 economically important fungal pathogens (Dean et al. 2012). This is based on its perceived scientific and economical importance. *Colletotrichum* species cause anthracnose in diverse host-plants such as fruit-plants, vegetables and ornamentals. The diseases symptoms include, but not limited to, blight, fruit-lesion, fruit-rot and leaf-wilt (Bailey & Jeger 1992, Hyde et al. 2009a, b, 2014, Phoulivong et al. 2010, 2011, Rojas et al. 2010, Su et al. 2011, Cannon et al. 2012, Damm et al. 2012a, b, 2013, Weir et al. 2012, Doyle et al. 2013, Huang et al. 2013, Sharma et al. 2013a, 2014, 2015a, Udayanga et al. 2013). They are responsible for post-harvest fruit rot of agricultural commodities such as apple, banana, chilli, coffee and mango (Bailey & Jeger 1992). Extensive yield loss has been reported due to the damages caused by *Colletotrichum* infection, which substantiates the severity of *Colletotrichum* as a post-harvest pathogen (Prusky 1996, Droby et al. 2011, Snowdon 2010, Swamy 2012). This has implications in plant-quarantine decisions as *Colletotrichum*-infected commodities are not suitable for the import/ export purpose, leading to revenue loss (Chakrabarty et al. 2011). *Colletotrichum* species are cosmopolitan in distribution and exhibit diverse host-associations. Multiple *Colletotrichum* species can infect a host plant genus (*Coffea* – Nguyen et al. 2009, Prihastuti et al. 2009, Silva et al. 2012b; *Mangifera* – Phoulivong et al. 2010, Lima et al. 2013, Sharma et al. 2013a, 2015b) or conversely a single *Colletotrichum*

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species can infect many host plants (*C. boninense* – Moriwaki et al. 2003, Damm et al. 2012a; *C. fructicola* – Prihastuti et al. 2009, Phoulivong et al. 2010, Weir et al. 2012, Sharma et al. 2013a, 2014, Udayanga et al. 2013). Some species of *Colletotrichum* species reportedly infect humans (Cano et al. 2004, Shivaprakash et al. 2011, Figtree et al. 2013, Natarajan et al. 2013).

Colletotrichum systematics: the history

Colletotrichum was originally described under the name *Vermicularia* by Tode (1790), but later it was revised as *Colletotrichum* by Corda (1837). *Colletotrichum* was classified in "Melanconiales" under "Coelomycetes" (Hawksworth, 1983). The epithets *Colletotrichum* and *Vermicularia* were used indiscriminately during the 19th and early 20th centuries for a range of species, which are now classified in *Colletotrichum* (Sutton 1992). *Colletotrichum* is distinguished from *Vermicularia* by the presence of marginal setae as compared to the setae dispersed throughout the conidiomata in *Vermicularia* (Clements & Shear 1931). However, Duke (1928) had earlier demonstrated that conidiomatal structure and form, the presence/ absence of setae and their arrangement within the acervulus are extremely variable and of no taxonomic significance at the genus level. This resulted in transfer of a large number of species from *Vermicularia* to *Colletotrichum* (Duke 1928, Cannon et al. 2012). *Gloeosporium*, a morphologically similar anamorph, also posed problems during identification, and distinguishing it from *Colletotrichum* was tough, as although *Gloeosporium* species did not produce setae, some could generate setae on certain substrates (Baker et al. 1940). Earlier *G. lindemuthianum* was transferred to *Colletotrichum* by Briosi & Cavara (1889). Lately, *G. kaki* Hori has been transferred to *C. horii* (Weir & Johnston 2010) and *G. pedemontanum* has been synonymized as *C. gloeosporioides* (Weir et al. 2012).

Colletotrichum or _Glomerella_: solution to nomenclatural perplexity

Colletotrichum, in its traditional sense, represents anamorphic features, while *Glomerella* has been used to represent its teleomorph. As on 17th August 2016, the term "*Colletotrichum*" produced 771 search results, while the term "*Glomerella*" produced 89 search results in Mycobank (www.mycobank.org). Similar results can also be obtained in the Index Fungorum (http://www.indexfungorum.org). However, these numbers are high as compared to the current number of the accepted species names under *Colletotrichum* (Cannon et al. 2012). There are currently about 150 accepted species of *Colletotrichum* (Cannon et al. 2012, Peng et al. 2012, 2013, Damm et al. 2013, Doyle et al. 2013, Lima et al. 2013, Liu et al. 2013a, b, 2015, Manamgoda et al. 2013, Udayanga et al. 2013, Liu et al. 2016b, Niu et al. 2016, Wang et al. 2016), out of which only 30 species are associated with *Glomerella* stage (Edgerton 1901, Spaulding & Schrenk 1903, Shear & Wood 1913, Petch 1917, Lehman & Wolf 1926, Stevens 1931, Arx & Mueller 1954, Politis 1975, Sutton 1992, Guerber & Correll 2001, Hyde et al. 2009b, Damm et al. 2012a, b, Cannon et al. 2012), indicating at the possible infrequent occurrence of *Glomerella* in nature/ culture media. A comprehensive list for the anamorph-teleomorph connections was provided by Cannon et al. (2012). Nevertheless, the identification of many *Glomerella* species remains uncertain and warrants a revision based on a polyphasic approach (discussed later).

Considering the ambiguity regarding the "preferred name" of pleomorphic fungi, revisions were made in the International Code of Botanical Nomenclature (ICBN; Vienna Code); now known as the International Code of Nomenclature for algae, fungi and plants (ICN; Melbourne Code) in the Eighteenth International Botanical Congress held in Melbourne in July 2011 (Norvell 2011). The Article 59 of the ICN has been modified and it now establishes a code of "one fungus: one name". Thus, all the fungal species exhibiting separate asexual and sexual life cycles will be described with only one formal name. In order to deal with the nomenclatural issues associated with *Colletotrichum*, International Sub-commission on *Colletotrichum* Taxonomy (ISCT) has been established under the International Commission on the Taxonomy of Fungi (ICTF, http://www.fungaltaxonomy.org/subcommissions). The epithet *Colletotrichum* is more preferred (84% based on statistics) as compared to *Glomerella* (Cai & Weir 2012). More information on the history of classification and nomenclature are detailed in a recent review by Cannon et al. (2012).

Colletotrichum taxonomy: species recognition criteria

There are four main species recognition criteria: (1) Biological species recognition criterion advocates the model of inter-sterility between two distinct species. (2) Morphological species recognition criterion advocates the morphological divergence between species. (3) Ecological species recognition criterion advocates the acclimatization of a species to a specific geographical niche. (4) Phylogenetic species recognition criterion advocates the molecular divergence between closely related lineages based on DNA sequence data (Taylor et al. 2000, Giraud et al. 2008, Cai et al. 2011). In case of *Colletotrichum*, formerly identification based on morphology (morphological species recognition criterion) was preferred, but with the development and ease of DNA sequencing technologies, phylogenetic species recognition criterion has become popular. Nevertheless, identification of a fungal species based on morpho-taxonomic characters is not completely reliable without the establishment of the model of inter-sterility (Biological species recognition criterion).

Morpho-taxonomic characters such as shape and size of conidia, setae and appressoria, together with host-specificity were traditionally used to define *Colletotrichum* species (von Arx 1957, Sutton 1980, 1992). Relying only on morphological characteristics of a culture, von Arx (1957) reported eleven *Colletotrichum* species, which increased to 40 based on host-specificity and morphology (Sutton 1980). Description of 40 *Colletotrichum* species along with a key-based identification system for *Colletotrichum* was provided by Sutton (1980), which helps in preliminary identification. Following this trend, around 900 *Colletotrichum* species names were designated by various researchers (Sutton 1992). Species identification and classification based solely on morpho-taxonomic characters is highly prone to errors and, in many cases such as *Colletotrichum* species complexes, unreliable due to the presence of overlapping morphological characters (Cai et al. 2009, Hyde et al. 2009a). Besides, *Colletotrichum* host-association reports are made with partial sampling restricted to a particular host or site/s, not always supplemented with pathogenicity assays; accounting for limited understanding of host-specificity. Diverse lifestyle and survival strategies in *Colletotrichum* is responsible for the high genetic diversity and complexities in the taxonomic placement of the member species of *Colletotrichum*. Only a few species are known to be host-specific, such as *C. musae* (*Musa* sp.), *C. nupharicola* (*Nuphar lutea*), *C. lindemuthianum* (beans). Hence, species recognition solely based on morphology and host-specificity in *Colletotrichum* is not advisable.

Advancements in molecular biology provided new DNA-sequence based identification tools (Bruns et al. 1991, Shenoy et al. 2007a). Some of the initial studies included: identification based on analysis of restriction fragment length polymorphism (RFLP), use of polymerase chain reaction (PCR) based technique to assess the random amplified polymorphic DNA (RAPD) and sequence data of 5.8S ribosomal RNA and flanking internal transcribed spacers 1 & 2 (ITS) region (Welsh & McClelland 1990, White et al. 1990, Williams et al. 1990, Sreenivasprasad et al. 1996). Although ITS/5.8S rRNA gene region offers a good species-level resolution in many fungal groups (Nilsson et al. 2008, Schoch et al. 2012), it offers moderate species resolution in *Colletotrichum* (Cai et al. 2009, Crouch et al. 2009, Damm et al. 2009, 2010, Gazis et al. 2011, Cannon et al. 2012, Sharma et al. 2013b).

Application of a single species recognition criterion in all cases is essentially not possible (Giraud et al. 2008). Thus recent studies highlight the need to identify a secondary barcode for *Colletotrichum* (Sharma et al. 2013a, 2015a) and recommend a polyphasic approach towards characterization of *Colletotrichum* species (Cai et al. 2009, Cannon et al. 2012).

Polyphasic taxonomy

Cai et al. (2009) suggested the parameters/ characters to be incorporated while describing *Colletotrichum* species using a polyphasic approach. Polyphasic taxonomy includes the classification of a fungal species using different parameters such as: morphology (colony morphology, conidia, presence or absence of setae, production of aprèssoria and ascospores), multi-locus sequence data, pathogenicity assay, biochemical testing, secondary metabolite production and utilization of carbon source. Following their recommendations, multi-locus phylogenetic analysis

has become prevalent and many novel species have been described based on morphology, phylogenetic analyses and pathogenicity testing (Damm et al. 2009, 2012a, b, 2013, Doyle et al. 2013, Lima et al. 2013, Liu et al. 2013a, b, Manamgoda et al. 2013, Peng et al. 2013, Sharma et al. 2013a, 2015a, Udayanga et al. 2013, Weir et al. 2012). In a few cases results for biochemical testing have also been provided (Prihastuti et al. 2009). An example of the usefulness of polyphasic approach is the merging of *C. capsici* with *C. truncatum*. *Colletotrichum capsici* was initially described as *Vermicularia capsici* Syd. (Sydow, 1913) in India and epitypified by Shenoy et al. (2007b). However, based on multi-locus analysis using five genes (*act*, *chs1*, *gapdh*, *his3*, ITS) coupled with morphological characterization *C. capsici* was shown to be a synonym of *C. truncatum sensu stricto* within *C. truncatum* species complex (Damm et al. 2009). Similar approach has been employed to resolve *C. acutatum*, *C. boninense*, *C. gloeosporioides* and *C. orbiculare* species complexes (Damm et al. 2012 a, b, 2013, Weir et al. 2012). The biochemical testing and analysis of secondary metabolites synthesized by *Colletotrichum* isolates is not popular in *Colletotrichum* taxonomy. Hence, it is suggested that the parameters recommended by Cai et al. (2009) are employed while characterizing a *Colletotrichum* species.

Need for a secondary barcode

Earlier, *Colletotrichum* species were identified based on morphological characters and mainly ITS sequence data (the fungal barcode region) (Freeman et al. 2000, Martínez-Culebras et al. 2000, Afanador-Kafuri et al. 2003, Cano et al. 2004). In some studies, β-tubulin (*tub2*) sequences have also been used for phylogenetic analysis (Myllys et al. 2002, Than et al. 2008), but use of multi-locus sequence dataset was not prevalent. Thus, the accuracy of species names in many of these reports remain doubtful. In the absence of a reliable secondary barcode marker, researchers are relying more on phylogenetic analysis based on the multi-locus sequence dataset [actin (*act*), calmodulin (*cal*), chitin synthase (*chs1*), glutamine synthase (*gs*), glyceraldehyde 3-phosphate dehydrogenase (*gapdh*), histone (*his3*) and *tub2*] to identify and classify a *Colletotrichum* species. Multigene phylogeny has proven to be beneficial in resolving cryptic species within major species complexes of *Colletotrichum*. However, the selection of the genes used for phylogenetic analysis has varied according to the species complex [*C. acutatum – act*, *chs1*, *gapdh*, *his3*, ITS, *tub2*; *C. boninense – act*, *cal*, *chs1*, *gapdh*, *his3*, ITS, *tub2*; *C. destructivum/ dematium/ truncatum – act*, *chs1*, *gapdh*, *his3*, ITS, *tub2*; *C. gigapsorum – act*, *chs1*, *gapdh*, ITS, tub2; *C. gloeosporioides – act*, *cal*, *chs1*, *gapdh*, ITS and *C. orbiculare – act*, *chs1*, *gapdh*, *gs*, *his3*, ITS, *tub2*] (Damm et al. 2009, 2012 a, b, 2013, 2014, Weir et al. 2012, Liu et al. 2015). Moreover, there is no consensus among researchers working on *Colletotrichum* taxonomy as to which gene markers should be used to define and delimit a species within different species complexes of *Colletotrichum*. Thus it is important to generate an agreement on this issue. It is also important to develop datasets for a secondary barcode marker to accurately identify cryptic species within the major species complexes of *Colletotrichum*. Gene markers such as intronic sequence of 5′ region of the translation elongation factor 1-α (*5′tef1*), ribosomal polymerase largest subunit (*rpb1*) and intergenic spacer region between *apn2* and *Mat1-2* genes (*ApMat*) have been shown to be useful in resolution of clades at *C. gloeosporioides* species complex level (Rojas et al. 2010, Silva et al. 2012a, Doyle et al. 2013, Sharma et al. 2013a). Due to the availability of limited reference dataset in case of *rpb1* and *5′tef1*, their utility in *Colletotrichum* phylogeny has not been fully realized. In addition, presence of large region of homoplastic introns in case of *5′tef1* also limits the usage of this marker at species complex level (Rojas et al. 2010). *ApMat* gene-marker was reported to provide better resolution (Silva et al. 2012a, Doyle et al. 2013, Sharma et al. 2013a, 2015a) as compared to the five gene-markers used by Weir et al. (2012). There are no reported studies on secondary barcode for the other species complexes of *Colletotrichum*, such as *C. acutatum*, *C. boninense*, *C. graminicola* or *C. truncatum*. Establishing a single gene-marker which will serve as a secondary barcode for the species complexes is warranted for the advancement of *Colletotrichum* taxonomy.

Conclusions and future prospects

Rapid and accurate species identification of *Colletotrichum* species is essential, as it plays a crucial role in plant quarantine issues involving export-import of agricultural commodities (Rossman & Palm-Hernández 2008). However, there is no consensus among mycologists and plant pathologists working on *Colletotrichum* on the taxonomic approach and characters to be employed while identifying and describing a new *Colletotrichum* species or pathogen. There is a need for a reliable secondary barcode marker for the accurate identification of *Colletotrichum* species. *ApMat* marker has been projected as a putative secondary barcode for *C. gloeosporioides* species complex (Sharma et al. 2013a, 2015a). Using *ApMat* marker based analysis, seven species within *C. gloeosporioides* species complex (*C. communis*, *C. dianesei*, *C. endomangiferae*, *C. hymenocallidis*, *C. jasmini-sambac*, *C. murrayae*, *C. siamense*), having phylogenetic affinities with *C. siamense sensu stricto* were considered to be part of a separate species complex called as *C. siamense* species complex (Sharma et al. 2015a). These species were previously described as separate species based on their host and ecological diversity, from 2009 to 2014 (Yang et al. 2009, Wikee et al. 2011, Peng et al. 2012, Doyle et al. 2013, Lima et al. 2013, Vieira et al. 2014); but considered as conspecific to *C. siamense* by Weir et al. (2012). Later, Liu et al. (2015) demonstrated that a combination of *ApMat* and *gs* regions is useful for species delimitation of five species (*C. fructivorum*, *C. rhexiae*, *C. kahawae*, *C. temperatum*, and *C. jiangxiense*) which were inseparable using *Apmat* marker only, within *C. gloeosporioides* species complex. To test the hypothesis that *C. siamense s. l.* is a species complex, Liu et al. (2016a) have recently compared the gene trees generated using different gene sets (*ApMat*, *cal*, *gapdh*, *gs*, ITS, *tub2*) and established *C. siamense s. l.* as a single species based on multi-locus GCPSR, pairwise homoplasy index test, coalescent analyses, cross mating and genetic recombination tests. Thus, our search for a secondary barcode for *Colletotrichum* still continues. It is suggested that researchers working on *Colletotrichum* taxonomy consider incorporating certain measures to illustrate a new species as followed in bacterial taxonomy (Lapage et al. 1990, Logan et al. 2009, Sarethy et al. 2014). There are a few parameters which should be set and agreed upon by the consensus of fellow researchers: (1) Minimum number of isolates included in a study; (2) The set of genes to be sequenced and analyzed; (3) Biochemical tests to be performed; (4) Type of phylogenetic analysis to be done; (5) The need for mating compatibility test; (6) Results of pathogenicity testing; and (7) Substrate utilization test. It is hoped that researchers will work hand-in-hand and finalize the parameters for describing novel species of *Colletotrichum*.

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