Reviews, Critiques and New Technologies

# Diversity and evolution of *Fusarium* species in the *Gibberella fujikuroi* complex

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The *Gibberella fujikuroi* complex (GFC) is a monophyletic taxon that includes an assemblage of *Fusarium* species with similar and overlapping morphological traits that complicates their differentiation. Most of the species in this complex are associated with devastating diseases of many economically important plants. They also produce a remarkably wide range of secondary metabolites or mycotoxins that contaminate food/feed worldwide and can subsequently cause a variety of diseases in humans and animals. Recent developments in molecular systematics have revealed that the *Gibberella fujikuroi* complex includes at least 50 distinct species or phylogenetic lineages. Of these, 34 species have been formally described using morphological characters, 10 have been also described based on sexual fertility and at least 20 species produce one or more mycotoxins. Here, we review the most important criteria for recognising and defining *Fusarium* species in the *Gibberella fujikuroi* complex. We also consider the diversity within this complex, specifically from an evolutionary point of view. We, therefore, discuss the morphological, biological and phylogenetic diversity in the *Gibberella fujikuroi* complex, by reviewing these properties together with aspects such as mycotoxicology, geographic distribution and host/substrate preference of the various *Fusarium* species with respect to their phylogeny.

**Key words:** *Gibberella fujikuroi* species complex, biogeography, host association, mycotoxins, species recognition

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## Introduction

The genus *Fusarium* represents one of the most important groups of ascomycetous fungi. Its members are distributed across the globe where they are responsible for huge economic losses due to reductions in harvest yields and/or the quality of staple foods (Nelson *et al*., 1983; Leslie and Summerell, 2006). At least 80% of all cultivated plants are associated with at least one disease caused by a *Fusarium* species (Leslie and Summerell, 2006). Various *Fusarium* species cause destructive diseases on cereal grains (White, 1980; Parry *et al*., 1995; Nyvall *et al*., 1999; Goswami and Kistler, 2004), some are responsible for vascular wilts or root rots on many important vegetable, ornamental and field crops (Kraft *et al*., 1981; Linderman, 1981; Nelson *et al*., 1981), while others produce cankers on soft- and hardwood trees (Bloomberg, 1981; Dwinell *et al*., 1981, 2001; Wingfield *et al*., 2008). Recently, *Fusarium* species have emerged as human pathogens where they are associated with deeply invasive infections of immunocompromised patients (Nelson *et al*., 1994; Nucci and Anaissie, 2002; Summerbell, 2003; Dignani and Anaissie, 2004). *Fusarium* species are further notorious for producing mycotoxins that contaminate food/feed worldwide (reviewed by Marasas *et al*., 1984; Joffe, 1986; Chelkowski, 1989; Desjardins, 2006), the consumption of which may lead to various serious human and animal

diseases, reduced productivity in livestock and even death if prolonged exposure occurs (D'Mello *et al*., 1999; Placinta *et al*., 1999; Morgavi and Riley, 2007).

Since its establishment in 1809 by Link, the genus *Fusarium* has received much attention in the scientific literature. A significant portion of these studies dealt with taxonomic issues (see Leslie and Summerell, 2006), which for the most part have been dominated by the use of morphology to differentiate species and groups or sections. In the nineties, with the increased utility of DNA-based methods, it rapidly became clear that the morphology-based classifications greatly un-derestimate the true diversity in the genus. The use of DNA sequence information for separating species has, therefore, revolutionised *Fusarium* taxonomy and it is now widely accepted that taxa previously thought to represent single sections or species are actually species complexes consisting of numerous distinct taxa (e.g. O'Donnell, 2000; O'Donnell *et al*., 2000a, 2004). Currently, one of the best-studied species complexes is the *Gibberella fujikuroi* complex (GFC), which includes numerous mycotoxigenic and/or phytopatho-genic species. In this paper, we review the taxonomy of the GFC and its species, as well as the various criteria used for defining species in the complex. We also consider the GFC from an evolutionary point of view, where we specifically address geographic distribution, interacttions with plant hosts and mycotoxin pro-duction.

**Taxonomy of the GFC**

The term "*Gibberella fujikuroi* complex" refers to the monophyletic taxon that broadly corresponds to the Section *Liseola*, but that also accommodates certain species originally classified in other *Fusarium* sections (Fig. 1) (Nirenberg and O'Donnell, 1998; O'Donnell *et al*., 1998, 2000b; Geiser *et al*., 2005). Section *Liseola* was established by Wollenweber and Reinking (1935) based on the morphology of three species (*F. moniliforme*, *F. lactis*, *F. neoceras*) and their varieties that produce macroconidia in sporodochia or pionnotes, microconidia in false heads and/or chains and no chlamydospores (Snyder and Hansen, 1945; Leslie and Summerell, 2006). Later, Snyder and Hansen (1945) argued that the production of microconidia borne in chains is an unstable character that is inappropriate for reliably separating species and varieties in this section. As a result, they lumped together all of Wollenweber and Reinking's species and recognised only *F. moniliforme* as a member of Section *Liseola*. Booth (1971) used the morphology of conidiogenous cells to separate *F. moniliforme* from its variety *F. moniliforme* var. *subglutinans*. In 1983, Nelson and colleagues introduced a system that bridged all the *Fusarium* classification systems existing at that time (Nelson *et al*., 1983; Leslie and Summerell, 2006) and recognised four species (*F. anthophilium*, *F. moniliforme*, *F. proliferatum* and *F. subglutinans*) in the Section *Liseola*. They differentiated these based on shape and production of microconidia in chains and/or false heads from polyphialides and/or monophialides. Following this system, and the use of some additional morphological traits (e.g. production of sterile coiled hyphae, pseudochlamydospores), as well as relying on molecular and biological traits, various other *Fusarium* species in the GFC were subsequently described (Rheeder *et al*., 1996; Klittich *et al*., 1997; Nirenberg and O'Donnell, 1998; Nirenberg *et al*., 1998; Aoki *et al*., 2001; Marasas *et al*., 2001; Britz *et al*., 2002b; Zeller *et al*., 2003).

In the 1990s, advances in technology have made the use of DNA sequence information more readily accessible for classification purposes and a range of DNA-based methods were then applied to characterise the GFC species. These include genomic finger-printing techniques such as electrophoretic karyotyping (Xu *et al*., 1995), random amplified polymorphic DNA (RAPD) (Voigt *et al*., 1995; Viljoen *et al*., 1997), polymerase chain reaction (PCR) restriction fragment length polymorphism (RFLP) analysis of specific genes (Steenkamp *et al*., 1999; Mirete *et al*., 2003) and amplified fragment length poly-morphism (AFLP) analysis (Marasas *et al*., 2001; Zeller *et al*., 2003). For the purposes of direct sequence analysis, various genomic regions have been evaluated as taxonomic markers (O'Donnell and Ciglenik, 1997; O'Donnell *et al*., 1998, 2000b; Steenkamp *et al*., 1999, 2000a; Schweigkofler *et al*., 2004), including the

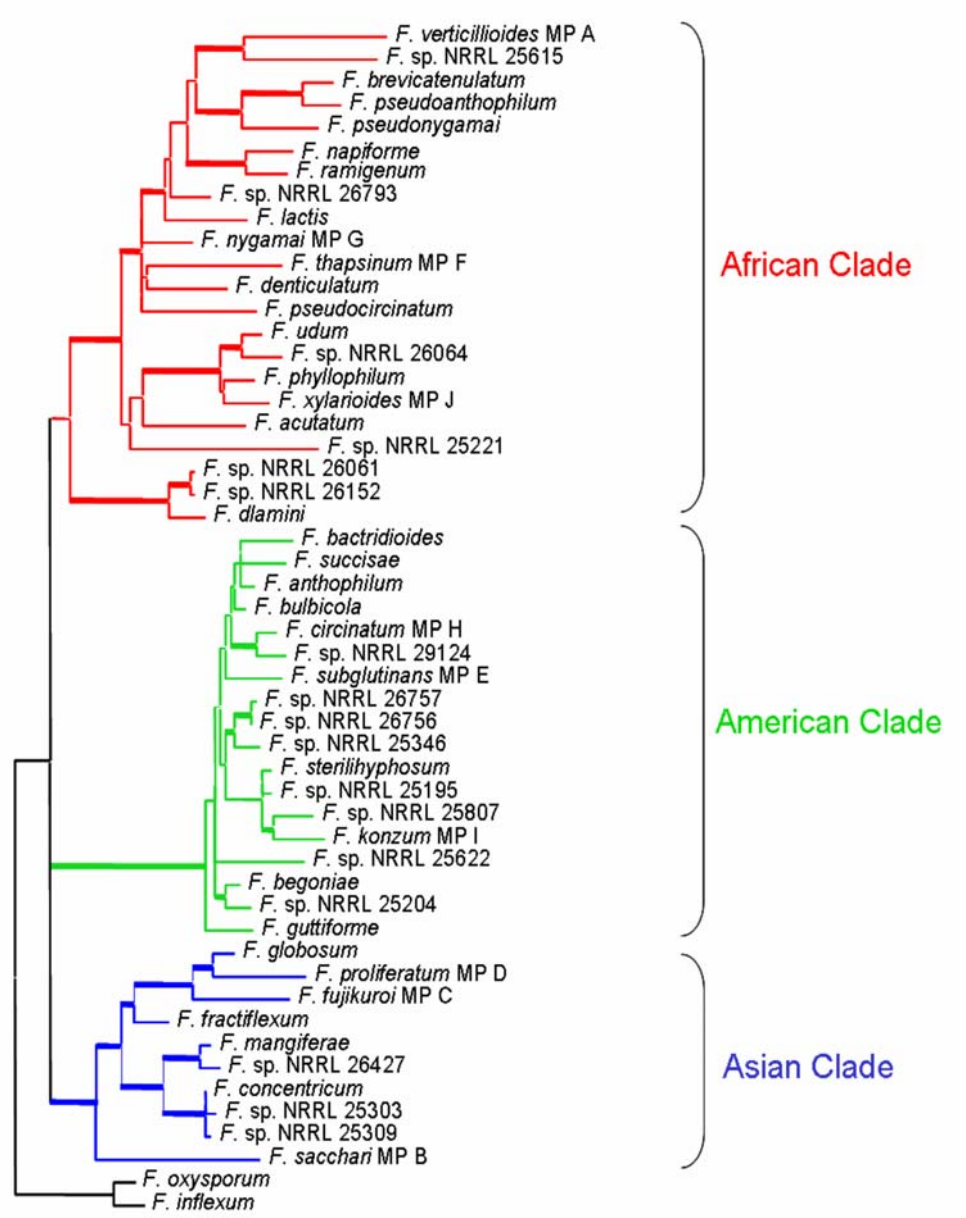



**Fig. 1.** A maximum likelihood phylogeny of *Fusarium* species in the GFC (*Gibberella fujikuroi* complex) based on combined sequence information for the genes encoding translation elongation factor 1 alpha (TEF) and beta-tubulin. All the members of the three well-established clades (O'Donnell *et al*., 1998, 2000b) are included, with the exception of *F. andiyazi* as its phylogenetic affinity remains to be determined. Thick branches are supported by bootstrap values >70% as previously reported (O'Donnell *et al*., 1998, 2000b; Geiser *et al*., 2005). MP A-J indicates the mating populations in the complex and the tree is rooted with *F. oxysporum* and *F. inflexum.*

ribosomal RNA (rRNA) internal transcribed spacer (ITS) widely used for other fungi (Bruns *et al*., 1991; Seifert *et al*., 1995). However, this region has been proven ineffective for classifying *Fusarium* species, due to the presence of two divergent and non-orthologous copies of the ITS2 region in most *Fusarium* species examined (Waalwijk *et al*., 1996; O'Donnell and Ciglenik, 1997; O'Donnell *et al*., 1998). Instead, the gene encoding the translation elongation factor 1-alpha (TEF) has become the marker of choice as it is a single-copy gene that is highly informative among closely related species (Geiser *et al*., 2004).

During the course of the last decade, application of DNA-based methods and phylogenetic analyses of multiple genomic regions have revealed the non-monophyletic nature of many of the *Fusarium* sections, including the section *Liseola* (e.g. O'Donnell *et*

*al*., 1998, 2000b). It is now widely accepted that the GFC includes species previously accommodated in other sections. For example, certain chlamydospore-forming species, that were classified in the Section *Dlaminia* by some workers (Kwasna *et al*., 1991), are now accepted as part of the GFC (O'Donnell *et al*., 1998, 2000b). The GFC also includes a number of species that were previously classified in the *Discolor*, *Elegans* and *Lateritium* sections (Wollenweber, 1934; Booth, 1971; Gerlach and Nirenberg, 1982; Nelson *et al*., 1983; O'Donnell and Cigelnik, 1997; O'Donnell *et al*., 1998, 2000b; Geiser *et al*., 2005). However, a particular set of morphological synapomorphies (shared derived characters) has not yet been identified for the clade and its existence is still supported only by multigene phylogenies (O'Donnell and Cigelnik, 1997; O'Donnell *et al*., 1998, 2000b; Geiser *et al*., 2005).

**Recognising species in the GFC**

To recognise and define species in the GFC, various operational species concepts have been applied. Although a variety of genetic, ecological and biological traits and properties may be used for this purpose (Rojas, 1992; Mayden, 1997) only Morphological Species Recognition, Biological Species Recognition and Phylogenetic Species Recognition (MSR, BSR and PSR, respectively; Taylor *et al*., 2000) have contributed significantly to the classification of *Fusarium* species in the GFC. Of these, the MSR was the most widely used and has dominated *Fusarium* taxonomy since its establishment in 1809. Based on this recognition system, species are primarily identified using shape and size of macroconidia and microconidia, while other characters such as the aerial arrangement of microconidia, morphology of conidiogenous cells and presence/absence of chlamydospores are also used (Booth, 1971; Gerlach and Nirenberg, 1982; Nelson *et al*., 1983; Leslie and Summerell, 2006). The MSR also takes into account physiological characters such as growth rates at different temperatures, host associations, and secondary metabolite production (Nelson *et al*., 1983). Based on the MSR, the GFC currently includes 34 morphospecies (O'Donnell *et al*., 1998, 2000b; Nirenberg and O'Donnell, 1998; Nirenberg *et al*., 1998; Aoki *et al*., 2001; Marasas *et al*., 2001; Britz *et al*., 2002b; Zeller *et al*., 2003; Geiser *et al*., 2005). However, the overall shortage of diagnostic morphological characters complicates separation of similar species and description of new species. This is particularly true for the various species known to be part of the GFC that still await description (O'Donnell *et al*., 1998; 2000b). Therefore, application of the MSR is typically associated with underestimation of the true *Fusarium* diversity. Nevertheless, the MSR remains an integral part of all *Fusarium* species descriptions and allows the sorting of isolates for final species diagnosis using BSR and PSR (Leslie and Summerell, 2006).

In terms of BSR, two fungi belong to the same species if they are sexually compatible and able to enter a teleomorph stage during which sexual fruiting structures bearing fertile progeny are produced (reviewed by Taylor *et al*., 2000; Coyne and Orr, 2004). Sexually fertile strains of the GFC are heterothallic (reviewed by Desjardins, 2003), except for *F. sacchari* that is sometimes apparently homothallic or self-fertile (Britz *et al*., 1999). All sexually fertile strains of the GFC produce a teleomorph in the genus *Gibberella*, which was first described by Fries in 1822 based on its blue/purple perithecia with hyaline/pale yellow ascospores that are straight or curved with 1–3 septa (Samuels *et al*., 2001; Desjardins, 2003). To facilitate the use of BSR for identifying GFC species, extensive population studies have been conducted for selecting hermaphrodite or female-fertile strains of opposite mating type to be used as tester strains in diagnostic sexual crosses (Klittich and Leslie, 1992; Klaasen and Nelson, 1996; Britz *et al*., 1998, 1999; Zeller *et al*., 2003; Lepoint *et al*., 2005). These tests have been simplified by the introduction of PCR-based techniques for scoring mating type (Covert *et al*., 1999; Kerényi *et al*., 1999; Steenkamp *et al*., 2000b). Currently, the GFC includes ten well-characterised biological species or so-called mating populations (MP) that have been designated MP A to MP J (Kuhlman, 1982; Leslie, 1991, 1995; Klittich and Leslie, 1992; Klaasen and Nelson, 1996; Klittich *et al*., 1997; Britz *et al*., 1999, 2002a; Samuels *et al*., 2001; Zeller *et al*., 2003; Geiser

*et al*., 2005; Lepoint *et al*., 2005; Leslie *et al*., 2005a).

Application of BSR for GFC classification purposes has four major disadvantages. First, sexual fruiting structures are known for about 20% of the recognised species in this complex, rendering the BSR useless for diagnosing the vast majority of the known GFC species. Second, populations of many of the species in this complex are characterised by unequal relative frequencies of occurrence of the two mating types (Leslie and Summerell, 2006). For example, Britz *et al*., (2002b) found that the majority of the *F. mangiferae* and *F. sterilihyphosum* isolates they examined were of a single mating type and in such cases, extensive sampling is required in order to ensure that isolates of opposite mating type are identified. Third, the occurrence of hermaphrodite strains in many GFC populations is limited (Kuhlman, 1982; Leslie and Summerell, 2006), which can potentially result in the scoring of sexual crosses as incompatible, even though the interacting individuals represent members of the same biological species. Finally, the results of sexual compatibility tests are not always clear-cut because different species of the GFC apparently have the ability to interbreed. Examples of these are *F. fujikuroi* and *F. proliferatum* (Leslie *et al*., 2004b) and *F. circinatum* and *F. subglutinans* (Desjardins *et al*., 2000; Steenkamp *et al*., 2001). However, despite these shortcomings, the single most important advantage of using the BSR for classifying *Fusarium* species is that it provides a means of measuring the amount of variation associated with morphology, DNA sequence, and physiology within a well-defined species, thus allowing a better understanding of the boundaries between species, especially those thought to be reproducing mainly asexually.

The PSR determines the hierarchical evolutionary relationships between species based on DNA sequence information and interprets them in terms of classification systems (Davis, 1996). Of the known versions of the PSR (reviewed by Avise and Ball, 1990; Luckow, 1995; Davis, 1996, 1997; Mayden, 1997), a modified version of Nixon and Wheeler's (1990) diagnostic PSR (O'Donnell *et al*., 1998) have been used most extensively in the GFC (O'Donnell *et al*., 1998, 2000b; Steenkamp *et al*., 1999, 2000a; Aoki *et al*., 2001; Geiser *et al*., 2005). According to this version of the PSR, species represent the smallest group of populations or lineages that can be diagnosed by an exclusive combination of fixed apomorphies or attributes that include information on their morphology, sexual behaviour and phylogenetic affinities (Nixon and Wheeler, 1990; O'Donnell *et al*., 1998). To apply this version of the PSR, phylogenetic analyses that are based on the combined DNA sequence information for various gene regions (e.g. nuclear 28S rRNA, small subunit of the mitochondrial (mtSSU) rRNA, β-tubulin, histone *H3*, calmodulin and TEF) have been used (O'Donnell *et al*., 1998, 2000b; Steenkamp *et al*., 1999, 2000a; Aoki *et al*., 2001; Geiser *et al*., 2005). These studies showed that the GFC includes at least 50 distinct phylogenetic species or lineages (Fig. 1), which roughly correspond to those recognised using MSR and BSR. However, the resolving power of PSR far outweighs that of MSR and BSR. For example, PSR facilitates separation of biological species known to be capable of interbreeding in the laboratory (see above). Also, PSR allows identification of the various distinct phylogenetic species that make up individual morphospecies (Nirenberg and O'Donnell, 1998; Nirenberg *et al*., 1998; O'Donnell *et al*., 1998, 2000b; Steenkamp *et al*., 1999, 2000a, 2002; Aoki *et al*., 2001; Britz *et al*., 2002b).

Although it is possible to recognise all known *Fusarium* species in the GFC by applying only PSR, the application of this operational concept alone is impractical and it may yield results that are not biologically meaningful (e.g. Coyne and Orr, 2004; Dayrat, 2005). Therefore, the PSR is generally used in combination with MSR and BSR, when recognising *Fusarium* species in the GFC (Klittich *et al*., 1997; Zeller *et al*., 2003). Typically in these situations, the PSR is based on the data for multiple unlinked genomic regions (O'Donnell *et al*., 1998, 2000b; Taylor *et al*., 2000), while additional morphological, physiological and ecological data for MSR and

data on reproductive behaviour for BSR are also included and evaluated. The majority of the current GFC species definitions and descriptions are based on such polyphasic or integrative taxonomic approaches that incurporate various types of data (Klittich *et al*., 1997; Marasas *et al*., 2001; Zeller *et al*., 2003; Dayrat, 2005; Will *et al*., 2005). This integrative approach also extends to routine species identifications where applications of single diagnostic procedures such as the analysis of the TEF-barcoding region (Geiser *et al*., 2004) or the examination of morphological structures are not sufficient for unambiguous diagnoses (Leslie and Summerell, 2006; Dayrat, 2005; Will *et al*., 2005).

**Phylogenetic clades of the GFC**

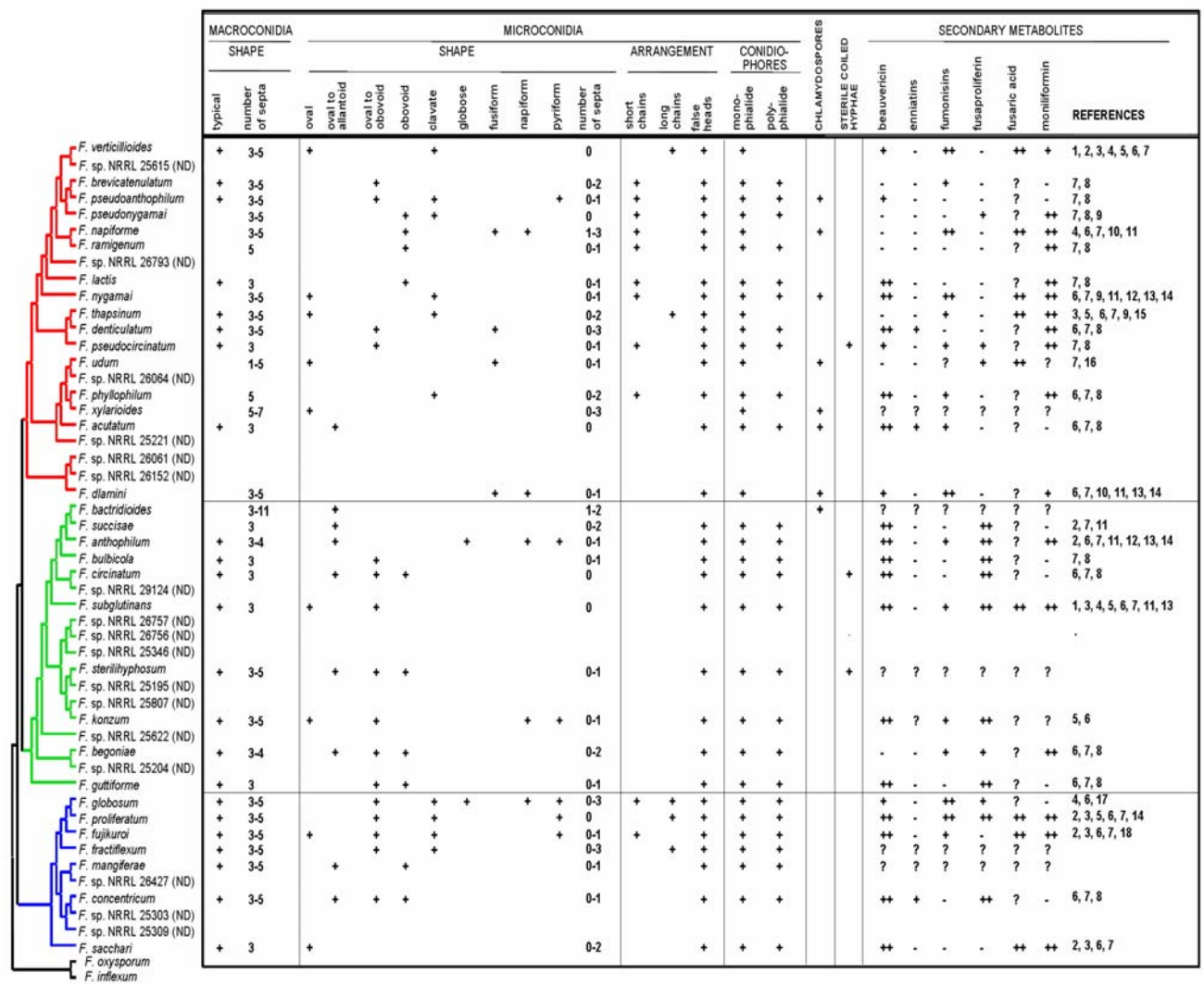
Based on multigene phylogenies, the *Fusarium* species in the GFC (O'Donnell *et al*., 1998, 2000b) can be separated into three large clades (Fig. 1). To explain the existence of these clades, the authors formulated a biogeographic hypothesis based on the origins of the plant hosts from which the respective *Fusarium* species included in their study were isolated. Accordingly, these clades were referred to as the "African", "American" and "Asian" clades (Fig. 1) (O'Donnell *et al*., 1998). In the following section, the morphology, mycotoxicology and host/substrate associations for the known members of each clade are briefly reviewed.

***The "African Clade"***

The so-called "African Clade" is the largest of the three clades with 23 phylogenetic lineages, of which four represent biological species (Fig. 1). These include *F. verticillioides* (MP A), *F. thapsinum* (MP F), *F. nygamai* (MP G) and *F. xylarioides* (MP J), which are the anamorphs of *G. moniliformis*, *G. thapsina*, *G. nygamai* and *G. xylarioide*s, respectively (Klittich and Leslie, 1992; Leslie, 1995; Klaasen and Nelson, 1996; Klittich *et al*., 1997; Geiser *et al*., 2005; Lepoint *et al*., 2005). *Gibberella indica*, the sexual state of *F. udum*, has been observed, but has not been recognised as an MP due to the lack of sufficiently fertile female tester isolates (Rai and Upadhyay, 1982). Also, *F. pseudonygamai* has been mentioned by Leslie *et al*. (2007) as possibly representing a new MP. Of the 19 remaining "African Clade" phylogenetic lineages, 13 represent formally described *Fusarium* species for which only the anamorphs are known and 6 await description.

Amongst the agriculturally important pathogens (*F. verticillioides*, *F. denticulatum*, *F. thapsinum*, *F. nygamai*, *F. lactis*, *F. phyllophilum*, *F. udum*, *F. xylarioides*) included in the clade, *F. verticillioides* is the best known (Booth, 1971; Gerlach and Nirenberg, 1982; Burgess and Trimboli, 1986; Michailides *et al*., 1994, 1996; Clark *et al*., 1995; Nelson *et al*., 1995; Klittich *et al*., 1997; Nirenberg and O'Donnell, 1998; Leslie and Summerell, 2006). This cosmopolitan pathogen of maize causes seedling blight as well as seed, root, stalk and ear rot (White, 1980; Kommedahl and Windels, 1981; Parry, 1995). It also produces various mycotoxins including fusarins (Marasas *et al*., 1984; Faber and Scott, 1989), fusaric acid (Marasas *et al*., 1984; Bacon *et al*., 1996), trace levels of moniliformin (Marasas *et al*., 1984, 1986; Leslie *et al*., 1996) and beauvericin (Leslie *et al*., 2004a). It is, however, most notorious for producing very high levels of fumonisins, specifically fumonisin $B_1$ (Gelderblom *et al*., 1988; Thiel *et al*., 1991; Nelson *et al*., 1993; Marasas, 2001; Desjardins, 2006). This mycotoxin causes equine leukoencephalomalacia (Kellerman *et al*., 1990), porcine pulmonary edema (Harrison *et al*., 1990), hepatocarcinoma in rodents (Gelderblom *et al*., 1991) and has been implicated in the high incidences of human oesophageal cancer in various areas of the world (reviewed by Marasas, 2001). *Fusarium verticillioides* has also been identified as an opportunistic pathogen in human infections (Hennequin *et al*., 1997; Guarro *et al*., 2000).

Morphologically, *F. verticillioides* is characterised by oval to club shaped microconidia produced in long chains that are borne only on monophialides (Fig. 2; Nelson *et al*., 1983). It is these monophialides that distinguishes it from species such as *F. proliferatum* and *F. fujikuroi*, which reside in the "Asian Clade" and that produce chains from polyphialides (Leslie and Summerell, 2006). Although, *F. verticillioides* and *F. thapsinum* have previously been considered as the same




| | MACROCONIDIA SHAPE | | MICROCONIDIA SHAPE | | | | | | | | | | ARRANGEMENT | | | CONIDIO-PHORES | | CHLAMYOSPORES | STERILE COILED HYPHAE | SECONDARY METABOLITES | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | typical | number of septa | oval | oval to allantoid | oval to obovoid | obovoid | clavate | globose | fusiform | napiform | pyriform | number of septa | short chains | long chains | false heads | mono-phialide | poly-phialide | | | beauvericin | enniatins | fumonisins | fusaproliferin | fusaric acid | moniliformin | REFERENCES |
| F. verticillioides | + | 3-5 | + | | | | + | | | | | 0 | | + | + | + | | | | + | - | ++ | - | ++ | + | 1, 2, 3, 4, 5, 6, 7 |
| F. sp. NRRL 25615 (ND) | | | | | | | | | | | | | | | | | | | | | | | | | | |
| F. brevicatenulatum | + | 3-5 | | | + | | | | | | | 0-2 | + | | + | + | + | | | - | - | + | - | ? | - | 7, 8 |
| F. pseudoanthophilum | + | 3-5 | | | + | | + | | | | + | 0-1 | + | | + | + | + | + | | + | - | - | - | ? | - | 7, 8 |
| F. pseudonygamai | | 3-5 | | | | + | + | | | | | 0 | + | | + | + | + | | | - | - | - | + | ? | ++ | 7, 8, 9 |
| F. napiforme | | 3-5 | | | | + | | | + | + | | 1-3 | + | | + | + | | + | | - | - | ++ | - | ++ | ++ | 4, 6, 7, 10, 11 |
| F. ramigenum | | 5 | | | | + | | | | | | 0-1 | + | | + | + | + | | | - | - | - | - | ? | ++ | 7, 8 |
| F. sp. NRRL 26793 (ND) | | | | | | | | | | | | | | | | | | | | | | | | | | |
| F. lactis | + | 3 | | | | + | | | | | | 0-1 | + | | + | + | + | | | ++ | - | - | - | ? | ++ | 7, 8 |
| F. nygamai | | 3-5 | + | | | | + | | | | | 0-1 | + | | + | + | + | + | | ++ | - | ++ | - | ++ | ++ | 6, 7, 9, 11, 12, 13, 14 |
| F. thapsinum | + | 3-5 | + | | | | + | | | | | 0-2 | | + | + | + | | | | - | - | + | - | ++ | ++ | 3, 5, 6, 7, 9, 15 |
| F. denticulatum | + | 3-5 | | | + | | | | + | | | 0-3 | | | + | + | + | | | ++ | + | - | - | ? | ++ | 6, 7, 8 |
| F. pseudocircinatum | + | 3 | | | + | | | | | | | 0-1 | + | | + | + | + | | + | + | - | + | + | ? | ++ | 7, 8 |
| F. udum | | 1-5 | + | | | | | | + | | | 0-1 | | | + | + | | + | | - | - | ? | + | ++ | ? | 7, 16 |
| F. sp. NRRL 26064 (ND) | | | | | | | | | | | | | | | | | | | | | | | | | | |
| F. phyllophilum | | 5 | | | | | + | | | | | 0-2 | + | | + | + | + | | | ++ | - | + | - | ? | ++ | 6, 7, 8 |
| F. xylarioides | | 5-7 | + | | | | | | | | | 0-3 | | | | + | | + | | ? | ? | ? | ? | ? | ? | |
| F. acutatum | + | 3 | | + | | | | | | | | 0 | | | + | + | + | + | | ++ | + | + | - | ? | - | 6, 7, 8 |
| F. sp. NRRL 25221 (ND) | | | | | | | | | | | | | | | | | | | | | | | | | | |
| F. sp. NRRL 26061 (ND) | | | | | | | | | | | | | | | | | | | | | | | | | | |
| F. sp. NRRL 26152 (ND) | | | | | | | | | | | | | | | | | | | | | | | | | | |
| F. dlamini | | 3-5 | | | | | | | + | + | | 0-1 | | | + | + | | + | | + | - | ++ | - | ? | + | 6, 7, 10, 11, 13, 14 |
| F. bactridioides | | 3-11 | | + | | | | | | | | 1-2 | | | | | | + | | ? | ? | ? | ? | ? | ? | |
| F. succisae | | 3 | | + | | | | | | | | 0-2 | | | + | + | + | | | ++ | - | - | ++ | ? | - | 2, 7, 11 |
| F. anthophilum | + | 3-4 | | + | | | | + | | + | + | 0-1 | | | + | + | + | | | ++ | - | + | ++ | ? | ++ | 2, 6, 7, 11, 12, 13, 14 |
| F. bulbicola | + | 3 | | | + | | | | | | | 0-1 | | | + | + | + | | | ++ | - | - | ++ | ? | - | 7, 8 |
| F. circinatum | + | 3 | | + | + | + | | | | | | 0 | | | + | + | + | | + | ++ | - | - | ++ | ? | - | 6, 7, 8 |
| F. sp. NRRL 29124 (ND) | | | | | | | | | | | | | | | | | | | | | | | | | | |
| F. subglutinans | + | 3 | + | | + | | | | | | | 0 | | | + | + | + | | | ++ | - | + | ++ | ++ | ++ | 1, 3, 4, 5, 6, 7, 11, 13 |
| F. sp. NRRL 26757 (ND) | | | | | | | | | | | | | | | | | | | | | | | | | | |
| F. sp. NRRL 26756 (ND) | | | | | | | | | | | | | | | | | | | | | | | | | | |
| F. sp. NRRL 25346 (ND) | | | | | | | | | | | | | | | | | | | | | | | | | | |
| F. sterilihyphosum | + | 3-5 | | + | + | + | | | | | | 0-1 | | | + | + | | | + | ? | ? | ? | ? | ? | ? | |
| F. sp. NRRL 25195 (ND) | | | | | | | | | | | | | | | | | | | | | | | | | | |
| F. sp. NRRL 25807 (ND) | | | | | | | | | | | | | | | | | | | | | | | | | | |
| F. konzum | + | 3-5 | + | | | + | | | | + | + | 0-1 | | | + | + | + | | | ++ | ? | + | ++ | ? | ? | 5, 6 |
| F. sp. NRRL 25622 (ND) | | | | | | | | | | | | | | | | | | | | | | | | | | |
| F. begoniae | + | 3-4 | | + | + | + | | | | | | 0-2 | | | + | + | + | | | - | - | + | + | ? | ++ | 6, 7, 8 |
| F. sp. NRRL 25204 (ND) | | | | | | | | | | | | | | | | | | | | | | | | | | |
| F. guttiforme | + | 3 | | | + | + | | | | | | 0-1 | | | + | + | + | | | ++ | - | - | ++ | ? | - | 6, 7, 8 |
| F. globosum | + | 3-5 | | | + | | + | + | | + | + | 0-3 | + | + | + | + | + | | | + | - | ++ | + | ? | - | 4, 6, 17 |
| F. proliferatum | + | 3-5 | | | + | | + | | | | + | 0 | | + | + | + | + | | | ++ | - | ++ | ++ | ++ | ++ | 2, 3, 5, 6, 7, 14 |
| F. fujikuroi | + | 3-5 | + | | + | | + | | | | + | 0-1 | + | | + | + | + | | | ++ | - | + | - | ++ | ++ | 2, 3, 6, 7, 18 |
| F. fractiflexum | + | 3-5 | | | + | | + | | | | | 0-3 | | + | + | + | + | | | ? | ? | ? | ? | ? | ? | |
| F. mangiferae | + | 3-5 | | + | | + | | | | | | 0-1 | | | + | + | + | | | ? | ? | ? | ? | ? | ? | |
| F. sp. NRRL 26427 (ND) | | | | | | | | | | | | | | | | | | | | | | | | | | |
| F. concentricum | + | 3-5 | | + | + | + | | | | | | 0-1 | | | + | + | + | | | ++ | + | - | ++ | ? | - | 6, 7, 8 |
| F. sp. NRRL 25303 (ND) | | | | | | | | | | | | | | | | | | | | | | | | | | |
| F. sp. NRRL 25309 (ND) | | | | | | | | | | | | | | | | | | | | | | | | | | |
| F. sacchari | + | 3 | + | | | | | | | | | 0-2 | | | + | + | + | | | ++ | - | - | - | ++ | ++ | 2, 3, 6, 7 |
| F. oxysporum | | | | | | | | | | | | | | | | | | | | | | | | | | |
| F. inflexum | | | | | | | | | | | | | | | | | | | | | | | | | | |

**Fig. 2.** Comparison of the morphological traits and mycotoxicological properties of *Fusarium* species in the GFC with respect to their phylogeny as indicated in Fig. 1. Morphological characters that define each species were reported by Booth (1971), Gerlach and Nirenberg (1982), Nelson *et al*. (1983), Nirenberg and O'Donnell (1998), Aoki *et al*. (2001) and Leslie and Summerell (2006). The presence of macroconidia typical of the GFC (*i.e*. slender, thin walled and almost straight with parallel dorsal and ventral surfaces) are indicated with "+" (Leslie and Summerell, 2006). Taxa that have not yet been formally described are indicated in parenthesis with "ND". For the major secondary metabolites, "++" represents the production of significant level of the specific compound, "+" and "-" indicate trace and not detected amounts, respectively, while "?" signifies that the trait has not been examined in a specific species. References for the production of a specific mycotoxin by a certain species are as follows: 1. Marasas *et al*. (1984); 2. Marasas *et al*. (1986); 3. Bacon *et al*. (1996); 4. Shephard *et al*. (1999); 5. Leslie *et al*. (2004a); 6. Desjardins (2006); 7. Moretti *et al*. (2007); 8. Fotso *et al*. (2002); 9. Leslie *et al*. (2005b); 10. Marasas *et al*. (1991); 11. Nelson *et al*. (1992); 12. Thiel *et al*. (1991); 13. Logrieco *et al*. (1998); 14. Leslie and Summerell (2006); 15. Leslie *et al*. (1996); 16. Booth (1971); 17. Sydenham *et al*. 1997; 18. Desjardins *et al*. (2000a).

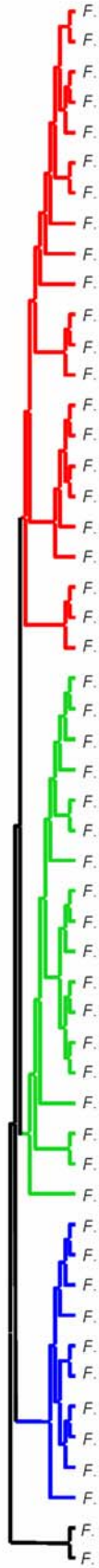
species, they are distinguishable using BSR (Klittich and Leslie, 1992), mycotoxin production (Fig. 2), host preference (Fig. 3) and DNA-based information (Xu *et al*., 1995; O'Donnell and Cigelnik, 1997) amongst other methods (Klittich *et al*., 1997). *Fusarium thapsinum* is a causal agent of stalk rot and kernel mould in sorghum, but it also has been associated with banana, maize, peanut (Klittich *et al*., 1997) and native grasses in the USA (Leslie *et al*., 2004a). Unlike *F. verticillioides*, it produces high levels of moniliformin and low levels of fumonisins (Klittich *et al*., 1997; Leslie *et al*., 2004a). *Fusarium verticillioides* and *F. thapsinum* are morphologically similar to *F. andiyazi*, but the production of unique pseudochlamydospores by the latter species distinguishes it from any other taxon (Marasas *et al*., 2001). *Fusarium andiyazi*, a sorghum pathogen, produces fumonisins in trace levels,

and otherwise little is known about its mycotoxin production capabilities (Rheeder *et al*., 2002). Despite substantial similarity in their morphology, *F. verticillioides* and *F. thapsinum* are not phylogenetically very closely related (Fig. 1), while the phylogenetic affinity of *F. andiyazi* remains to be determined.

The "African Clade" includes most of the GFC chlamydospore-formers, specifically *F. dlamini*, *F. napiforme*, *F. nygamai*, *F. acutatum*, *F. pseudoanthophilum*, *F. udum* and *F. xylarioides* (O'Donnell *et al*., 1998, 2000b; Geiser *et al*., 2005). *Fusarium dlamini* can easily be misidentified as *F. napiforme* or the "American Clade" taxon *F. anthophilum* (see below; Fig. 2). This is due to the production of napiform microconidia by both species. However, *F. anthophilum* does not produce chlamydospores (Marasas *et al*., 1985) while *F. napiforme* produces microconidia in chains (Marasas *et al*., 1987). *Fusarium dlamini* is associated with plant debris in the soils of Southern Africa and it is characterised by allantoid to fusiform and napiform microconidia produced in false heads on monophialides (Marasas *et al*., 1985). *Fusarium napiforme* was initially identified from millet and sorghum grains in Southern Africa (Marasas *et al*., 1987; Onyike *et al*., 1991, 1992) and more recently, it has been identified as a human pathogen (Melcher *et al*., 1993). *Fusarium dlamini* and *F. napiforme* are both known to produce fumonisins (Nelson *et al*., 1992) and moniliformin (Marasas *et al*., 1991), while they respectively also produce beauvericin (Logrieco *et al*., 1998; Moretti *et al*., 2007) and fusaric acid (Bacon *et al*., 1996) (Fig. 2).

Based on morphology, *F. nygamai* shares traits with *F. pseudonygamai*, *F. verticillioides*, *F. napiforme* and *F. thapsinum* (Fig. 2). *Fusarium nygamai* is, however, most similar to *F. pseudonygamai*, although the latter species produces swollen hyphal cells rather than chlamydospores (Nirenberg and O'Donnell, 1998). These two fungi are also associated with different plant hosts (Fig. 3), with *F. pseudonygamai* isolated from pearl millet, and *F. nygamai* associated with many hosts such as sorghum, millet, maize and broad bean to name just a few (Leslie and Summerell, 2006). *Fusarium nygamai* can be distinguished from *F. napiforme* by the production of polyphialides in the former species (Leslie and Summerell, 2006), although this character is difficult to detect and considered an unreliable morphological trait (Burgess and Trimboli, 1986). Chlamydospore production and microconidial arrangement in shorter chains distinguishes *F. nygamai* from *F. verticillioides* and *F. thapsinum* (Leslie and Summerell, 2006). *Fusarium nygamai* produces fumonisins (Thiel *et al*., 1991; Nelson *et al*., 1992; Leslie *et al*., 2005b), beauvericin (Logrieco *et al*., 1998; Moretti *et al*., 2007), moniliformin (Leslie *et al*., 2005b) and fusaric acid (Desjardins, 2006) (Fig. 2). Although Marasas *et al*. (1991) reported that *F. nygamai* produces moniliformin, Leslie and Summerell (2006) suggest that the specific isolates probably represented *F. pseudonymgamai*, which is known to produce moniliformin and fusaproliferin (Fotso *et al*., 2002; Leslie *et al*., 2005b).

Besides both being chlamydospore-formers, *F. xylarioides* and *F. udum* also cause serious vascular wilt diseases of coffee and pigeonpea, respectively (Booth, 1971). Booth (1971) reported *F. xylarioides* with "sex-linked morphological characters" and termed these "male and female" strains. His view was that "male" isolates produced curved, cylindrical, and 5–7-septate macroconidia, while "female" isolates produced small, highly curved, 0–3-septate macroconidia. Using the PSR, Geiser *et al*. (2005) concluded that "male" strains belong to the *Lateritium* clade or section, while "female" strains represent authentic *F. xylarioides* isolates that form part of the GFC (Fig. 1). *Fusarium udum* is characterised by strongly curved, 1–3-septate (occasionally 5-septate) macroconidia and ovoid-fusoid or curved single-celled microconidia (Booth, 1971). Morphologically, *F. udum* is most similar to *F. acutatum* that is also associated with pigeonpea disease, but the macroconidial acute apical cell of *F. acutatum* differentiates it from *F. udum* (Nirenberg and O'Donnell, 1998). Together, *F. xylarioides*, *F. udum* and *F. acutatum* appear to form a closely related group that also includes *F. phyllophilum* (Fig. 1). The latter species is a leaf pathogen of



| | PLANT HOST | | | OTHER SUBSTRATE | REFERENCES |
|---|---|---|---|---|---|
| | LATIN NAME | FAMILY | GEOGRAPHIC ORIGIN | | |
| *F. verticillioides* (A) | *Zea mays* | Poaceae | Central America | soil - Israel | Gerlach and Nirenberg, 1982; Joffe and Palti, 1977 |
| *F.* sp. NRRL 25615 | *Oryza sativa* | Poaceae | Southeast Asia | | O'Donnell *et al.*, 2000 |
| *F. brevicatenulatum* | *Striga asiatica* | Scrophulariaceae | Africa[1] | | Nirenberg *et al.*, 1998 |
| *F. pseudoanthophilum* | *Zea mays* | Poaceae | Central America | | Nirenberg *et al.*, 1998 |
| *F. pseudonygamai* | *Pennisetum typhoides* | Poaceae | Northern Africa | | Nirenberg & O'Donnell, 1998 |
| *F. napiforme* (B) | *Sorghum bicolor* | Poaceae | Northern Africa | soil - Africa | Marasas *et al.*, 1987; Jeschke *et al.*, 1990 |
| *F. ramigenum* | *Ficus carica* | Moraceae | Middle East[2] | | Nirenberg and O'Donnell, 1998 |
| *F.* sp. NRRL 26793 | *Striga hermonthica* | Scrophulariaceae | Africa[1] | | O'Donnell *et al.*, 1998 |
| *F. lactis* | *Ficus carica* | Moraceae | Middle East[2] | | Nirenberg and O'Donnell, 1998 |
| *F. nygamai* (C) | *Sorghum bicolor* | Poaceae | Northern Africa | soil - South Africa | Burgess and Trimboli, 1986 |
| *F. thapsinum* (D) | *Sorghum bicolor* | Poaceae | Northern Africa | | Klittich *et al.*, 1997 |
| *F. denticulatum* | *Ipomoea batatas* | Convolvulaceae | Central America | | Nirenberg and O'Donnell, 1998 |
| *F. pseudocircinatum* (E) | *Solanum* species | Solanaceae | South America | *Heteropsylla incise* (Homoptera: Psyllidae) | Nirenberg and O'Donnell, 1998 |
| *F. udum* | *Cajanus cajan* | Fabaceae | Asia or Eastern Africa[3] | | Booth, 1971 |
| *F.* sp. NRRL 26064 | *Sorghum bicolor* | Poaceae | Northern Africa | | O'Donnell *et al.*, 2000 |
| *F. phyllophilum* (F) | *Gasteria* species | Asphodelaceae | South Africa[4] | | Nirenberg and O'Donnell, 1998 |
| *F. xylarioides* | *Coffea* species | Rubiaceae | East Africa | | Booth, 1971; Geiser *et al.*, 2005 |
| *F. acutatum* | *Cajanus cajan* | Fabaceae | Asia or Eastern Africa[3] | wheat aphids | Nirenberg and O'Donnell, 1998 |
| *F.* sp. NRRL 25221 | *Zea mays* | Poaceae | Central America | | O'Donnell *et al.*, 1998 |
| *F.* sp. NRRL 26061 | *Striga hermonthica* | Scrophulariaceae | Africa[1] | | O'Donnell *et al.*, 2000 |
| *F.* sp. NRRL 26152 | *Striga hermonthica* | Scrophulariaceae | Africa[1] | | O'Donnell *et al.*, 2000 |
| *F. dlamini* | n/a | n/a | n/a | soil - South Africa | Marasas *et al.*, 1985 |
| *F. bactridioides* (G) | n/a | n/a | n/a | | Wollenweber, 1934 |
| *F. succisae* | *Succisa pratensis* | Dipsacaeae | Europe, Africa[5] | | Gerlach and Nirenberg, 1982 |
| *F. anthophilum* (H) | *Zizania palustris* | Poaceae | North America | soil - Australia | Nyvall *et al.*, 1999; Sangalang *et al.*, 1995 |
| *F. bulbicola* (I) | *Nerine bowdenii* | Amaryllidaceae | South Africa[6] | | Nirenberg and O'Donnell, 1998 |
| *F. circinatum* | *Pinus* species | Pinaceae | Northern Hemisphere | | Nirenberg and O'Donnell, 1998 |
| *F.* sp. NRRL 29124 | *Bidens pilosa* | Asteraceae | South America[7] | | O'Donnell *et al.*, 2000 |
| *F. subglutinans* (J) | *Zea mays* | Poaceae | Central America | | Nelson *et al.*, 1983 |
| *F.* sp. NRRL 26757 | ornamental reed | n/a | South Africa | | O'Donnell *et al.*, 2000 |
| *F.* sp. NRRL 26756 | ornamental grass | n/a | South Africa | | O'Donnell *et al.*, 2000 |
| *F.* sp. NRRL 25346 | *Ipomoea batatas* | Convolvulaceae | Central America | | O'Donnell *et al.*, 1998 |
| *F. sterilihyphosum* | *Mangifera indica* | Anacardiaceae | Southeast Asia | | Britz *et al.*, 2002 |
| *F.* sp. NRRL 25195 | n/a | n/a | n/a | | O'Donnell *et al.*, 1998 |
| *F.* sp. NRRL 25807 | n/a | n/a | n/a | soil - Australia | O'Donnell *et al.*, 1998 |
| *F. konzum* | *Andropogon gerardii* | Poaceae | North America | | Zeller *et al.*, 2003 |
| *F.* sp. NRRL 25622 | *Zea mays* | Poaceae | Central America | | O'Donnell *et al.*, 2000 |
| *F. begoniae* | *Begonia* hybrid | Begoniaceae | South America | | Nirenberg and O'Donnell, 1998 |
| *F.* sp. NRRL 25204 | palm | n/a | n/a | | O'Donnell *et al.*, 1998 |
| *F. guttiforme* | *Ananas comosus* | Bromeliaceae | South America | | Nirenberg and O'Donnell, 1998 |
| *F. globosum* (K) | *Zea mays* | Poaceae | Central America | | Rheeder *et al.*, 1996 |
| *F. proliferatum* (L) | *Asparagus officinalis* | Asparagaceae | Europe, Asia, Africa | | Elmer, 2001 |
| *F. fujikuroi* | *Oryza sativa* | Poaceae | Southern Asia | | Gerlach and Nirenberg, 1982 |
| *F. fractiflexum* | *Cymbidium* species | Orchidaceae | Asia[8] | | Aoki *et al.*, 2001 |
| *F. mangiferae* | *Mangifera indica* | Anacardiaceae | Southeast Asia | | Britz *et al.*, 2002 |
| *F.* sp. NRRL 26427 | n/a | n/a | n/a | soil - Papua New Guinea | O'Donnell *et al.*, 2000 |
| *F. concentricum* | *Musa sapientum* | Musaceae | South Asia | aphid | Nirenberg and O'Donnell, 1998 |
| *F.* sp. NRRL 25303 | *Oryza sativa* | Poaceae | Southern Asia | | O'Donnell *et al.*, 1998 |
| *F.* sp. NRRL 25309 | *Triticum* species | Poaceae | Middle East | | O'Donnell *et al.*, 1998 |
| *F. sacchari* (M) | *Saccharum officinarum* | Poaceae | South Asia | | Leslie *et al.*, 2005 |
| *F. oxysporum* | | | | | |
| *F. inflexum* | | | | | |

**Fig. 3**. Comparison of the host associations of *Fusarium* species in the GFC with respect to their phylogeny as indicated in Fig. 1. The geographic region where the specific plants presumably evolved or where they have been domesticated is indicated according to Sauer (1993) or as follows: 1. Mohamed *et al*. (2001); 2. Kislev *et al*. (2006); 3. van der Maesen (1990); 4. Smith and van Wyk (1991); 5. Adams (1995); 6. Vorster and Spreeth (1996); 7. Holm *et al*. (1977); 8. Du Puy and Cribb (1988). Where specific fungal strains were isolated from substrates other than plant tissue, the geographic region in which the samples were collected is indicated. For specific species/lineages that are associated with more than one host or substrate, alternative hosts/substrates are indicted in parentheses with A-M as follows: A: Isolated from teosinte (*Zea* sp., Poaceae, Central America) (Desjardins *et al*., 2000b), native prairie grasses in USA (Leslie *et al*., 2004a), millet (*Pennisetum typhoides*, Poaceae, Northern Africa) and sorghum (*Sorghum bicolor*, Poaceae, Northern Africa) (Leslie *et al*., 2005b); B: Found on millet by Marasas *et al*. (1987), as well as in Australian soil by Burgess and Summerell (1992) and Sangalang *et al*. (1995); C: Also described from bean roots (*Phaseolus vulgaris*, Fabaceae, Central and South America) and soils from Australia, Thailand and Puerto Rico (Burgess and Trimboli, 1986); D: Also associated with banana (*Musa sapientum*, Musaceae, South Asia), maize (*Zea mays*, Poaceae, Central America), peanuts (*Arachis hypogaea*, Fabaceae, South America) (Klittich *et al*., 1997) and native grasses in USA prairie (Leslie *et al*., 2004a); E: Reported also from *Pinus kesiya* (Pinaceae, Northeast Asia), textile and dead leaves (Nirenberg and O'Donnell, 1998); F: Also described from *Dracaena* and *Sansevieria* spp. [Dracaenaceae, Africa and Asia (Mwachala and Mbugua, 2007)]; G: Discovered parasitising *Cronartium conigenum*, a cone blister rust of *Pinus leiophylla* (Pinaceae, North and Central America) (Wollenweber, 1934); H: Also associated with *Lolium* sp. (Poaceae, Europe, Asia and Africa) (Engels and Kramer, 1996); I: Also described from *Vallota* and *Haemanthus* spp. (Nirenberg and O'Donnell, 1998) both belonging to South African Amaryllidaceae (Vorster and Spreeth, 1996); J: Also found on banana (Jiménez *et al*., 1993), wild rice (*Zizania palustris*, Poaceae, North America) (Nyvall *et al*., 1999), millet (Onyike *et al*., 1992), sorghum (Onyike *et al*.,1991), teosinte (Desjardins *et al*., 2000b) and native prairie grasses (Leslie *et al*., 2004a); K: Also described from wheat (*Triticum* sp., Poaceae, Middle East) (Aoki and Nirenberg, 1999); L: Colonises banana (Jimenez *et al*., 1993), sorghum (Leslie *et al*., 1990), maize (Logrieco *et al*., 1995), rice (Desjardins *et al*., 2000a), mango (*Mangifera indica*, Anacardiaceae, South Asia) (Marasas *et al*., 2006) and native grasses in USA (Leslie *et al*., 2004a); M: Also isolated from sorghum (Leslie *et al*., 2005b).

plants in the families Asphodelaceae and Dracaenaceae and it produces clavate conidia in false heads and chains from mono- and polyphialides (Gerlach and Nirenberg, 1982; *acutatum* produces trace or low levels of beauvericin, enniatins and fumonisins, while *F. phyllophilum* produces high levels of moniliformin, significant levels of beauvericin and low levels of fumonisins (Fotso *et al*., 2002; Desjardins, 2006; Moretti *et al*., 2007). *Fusarium xylarioides* has not yet been tested for mycotoxin production.

Based on phylogeny, the chlamydospore-former *F. pseudoanthophilum* is most closely related to *F. brevicatenulatum* (Fig. 1). *Fusarium pseudoanthophilum* is associated with maize cultivated in Zimbabwe, whereas *F. brevicatenulatum* was initially isolated from a parasitic weed of cereals in Madagascar (Nirenberg *et al*., 1998). Both species are characterised by long-oval to obovoid microconidia produced in false heads and short chains on monophialides and less occasionally also polyphialides (Fig. 2) and the only morphological feature separating them are the chlamydospores and pyriform microconidia produced by *F. pseudoanthophilum* (Nirenberg *et al*., 1998). It is these pyriform microconidia that makes the species morphologically similar Nirenberg and O'Donnell, 1998; Figs. 2 and 3). In terms of mycotoxins, *F. udum* produces fusaric acid (Booth, 1971) and low levels of fusaproliferin (Moretti *et al*., 2007), *F.* to *F. anthophilum* ("American Clade"; see below), but the production of very short chains and chlamydospores by the former differentiates them (Nirenberg *et al*., 1998). Strains of *F. pseudoanthophilum* are known to produce beauvericin, while *F. brevicatenulatum* strains produce fumonisins (Fotso *et al*., 2002).

*Fusarium ramigenum* is most closely related to *F. napiforme* based on phylogenetic data (Fig. 1), although it does not resemble this species morphologically (Fig. 2). *Fusarium ramigenum* is, however, similar to *F. lactis* (Nirenberg and O'Donnell, 1998; O'Donnell *et al*., 1998, 2000b), which differs from *F. ramigenum* by its production of microconidia in geniculate chains (Nirenberg and O'Donnell, 1998). Both *F. ramigenum* and *F. lactis* have been isolated from figs in the USA (Nirenberg and O'Donnell, 1998), but only *F. lactis* has been proven to cause endosepsis (Michailides *et al*., 1994, 1996). The mycotoxicology of these two species is also very similar, as both have been recognised as producers of moniliformin (Fotso *et al*., 2002), whilst Moretti *et al*. (2007) reported that a strain of *F.*

*lactis* also produced beauvericin.

The results of phylogenetic analyses group the remaining two "African Clade" species *F. denticulatum* and *F. pseudocircinatum* with the microconidial chain-former *F. thapsinum* (Fig. 1). *Fusarium denticulatum* is a leaf pathogen of sweet potato that was previously misidentified as *F. lateritium* (Clark *et al*., 1995; Nelson *et al*., 1995). Nirenberg and O'Donnell (1998) described it as a new species, which is uniquely characterised by denticulate polyphialidic conidiogeneous openings. *Fusarium pseudocircinatum*, isolated from various substrates in pantropical regions, displays morphological characters typical of *F. subglutinans* in the "American Clade" (see below; Fig. 2), although they are distinguishable based on the production of coiled sterile hyphae in *F. pseudocircinatum* (Nirenberg and O'Donnell, 1998). This trait is, however, also observed in the "American Clade" species *F. circinatum* and *F. sterilihyphosum* (see below; Fig. 2), from which *F. pseudocircinatum* can be distinguished by its short microconidial chains (Nirenberg and O'Donnell, 1998) and the different numbers of cells in the macroconidia (Britz *et al*., 2002b), respectively. Mycotoxigenically, *F. denticulatum* has been shown to produce enniatins and *F. pseudocircinatum* fusaproliferin and fumonisins, while both species are known to produce beauvericin and moniliformin (Fotso *et al*., 2002; Desjardins, 2006; Moretti *et al*., 2007).

***The "American Clade"***

The so-called "American Clade" contains 18 phylogenetic lineages, of which ten have been described using morphology (Wollenweber, 1934; Gerlach and Nirenberg, 1982; Nelson *et al*., 1983; Nirenberg and O'Donnell, 1998; Britz *et al*., 1999, 2002b). The species *F. subglutinans*, *F. circinatum* and *F. konzum* can also be diagnosed using BSR. Their respective teleomorphs are *G. subglutinans* (MP E), *G. circinata* (MP H) and *G. konza* (MP I) (Britz *et al*., 1999; Samuels *et al*., 2001; Zeller *et al*., 2003). The majority of the described species in this clade display morphological traits typical of those described for *F. subglutinans* by Nelson *et al*. (1983) (Fig. 2). Application of PSR has, however, facilitated the resolution of this taxon, which is now known to include the "American Clade" species *F. subglutinans sensu stricto*, *F. circinatum*, *F. begoniae*, *F. bulbicola*, *F. sterilihyphosum* and *F. guttiforme*, the "African Clade" species *F. pseudocircinatum* discussed above and the "Asian Clade" species (see below) *F. sacchari*, *F. concentricum* and *F. mangiferae* (O'Donnell and Cigelnik, 1997; Nirenberg and O'Donnell, 1998; O'Donnell *et al*., 1998; Britz *et al*., 2002b; Leslie *et al*., 2005a).

The morphological characters that define *F. subglutinans sensu stricto* are single-celled oval microconidia produced only in false heads from mono- and polyphialides (Nelson *et al*., 1983). This fungus is morphologically very similar to *F. anthophilum* and *F. succisae* (Fig. 2), although they can be distinguished by pyriform microconidia in *F. anthophilum* (Nelson *et al*., 1983) and "U"-shaped macroconidia in *F. succisae* (Gerlach and Nirenberg, 1982; Nelson *et al*., 1983). *Fusarium subglutinans* is a globally distributed pathogen of *Zea* species and it has also been associated with plants such as banana, millet, sorghum and many others (Leslie and Summerell, 2006), as well as with human infections (Summerell, 2003). *Fusarium succisae* causes flower rot of *Succisa pratensis* (Gerlach and Nirenberg, 1982; Nirenberg and O'Donnell, 1998) while *F. anthophilum* is associated with *Lolium* species and *Zizania palustris* (wild rice) but has never been shown to be a pathogen (Engels and Kramer, 1996; Nyvall *et al*., 1999). *Fusarium subglutinans* and *F. anthophilum* both appear to include a number of cryptic lineages (Steenkamp *et al*., 2002; Zeller *et al*., 2003). Mycotoxigenically, *F. subglutinans* has been shown to produce trace levels of fumonisins (Nelson *et al*., 1992), moniliformin, fusaric acid (Marasas *et al*., 1984), beauvericin (Logrieco *et al*., 1998) and fusaproliferin (Moretti *et al*., 2007). *Fusarium anthophilum* produces moniliformin (Marasas *et al*., 1986), fumonisins (Nelson *et al*., 1992) and together with *F. succisae* it is also known to produce beauvericin and fusaproliferin (Moretti *et al*., 2007).

*Fusarium circinatum* is the causal agent of pitch canker and had been known for many years as *F. subglutinans* forma specialis *pini*

due to its host specificity to *Pinus* species (Correll *et al*., 1991). Its current name refers to the coiled sterile hyphae, a character it shares with *F. sterilihyphosum* and the "African Clade" species *F. pseudocircinatum* (Nirenberg and O'Donnell, 1998; Britz *et al*., 2002b). Morphologically, *F. circinatum* is differentiated from *F. pseudocircinatum* by the production of erect conidiophores and arrangement of microconidia only in false heads (Nirenberg and O'Donnell, 1998). *Fusarium sterilihyphosum* is associated with mango malformation in South Africa and it is differentiated from these two species by the morphology of its macroconidia (Britz *et al*., 2002b). *Fusarium circinatum* has been reported to produce beauvericin and fusaproliferin (Fotso *et al*., 2002; Desjardins, 2006; Moretti *et al*., 2007), while the mycotoxicology of *F. sterilihyphosum* is unknown.

Another species in the *F. subglutinans sensu lato* group is *F. guttiforme* associated with rotten pineapple fruits (Nirenberg and O'Donnell, 1998). Aerial conidia of *F. guttiforme* are very similar to those produced by *F. circinatum* (Fig. 2), although *F. guttiforme* is most likely to be confused with *F. subglutinans sensu stricto* and the "Asian Clade" species *F. sacchari* (Nirenberg and O'Donnell, 1998; see below). *Fusarium guttiforme* can be differentiated from *F. sacchari* by the oval to allantoid/ fusoid microconidia in the former species and from *F. circinatum* by the production of its sterile coiled hyphae. Furthermore, *F. subglutinans* can be distinguished from *F. guttiforme* by the latter's production of obovoid microconidia and more conidogeneous openings (Britz *et al*., 2002b; Leslie and Summerell, 2006). *Fusarium guttiforme* has been reported to produce beauvericin and fusaproliferin (Fotso *et al*., 2002; Desjardins, 2006; Moretti *et al*., 2007).

Morphologically, *F. begoniae* and *F. bulbicola* are difficult to differentiate from each other and/or from other species in the *F. subglutinans sensu lato* group. These two species are, however, not closely related (Fig. 1). *Fusarium begoniae* is a pathogen of *Begonia* hybrids, while *F. bulbicola* is associated with bulb rot in various horticulturally important plants (Nirenberg and O'Donnell, 1998). Conidiophores of *F. begoniae* are prostrate and seldom branched, while the conidiophores of *F. bulbicola* are erect and regularly branched. *Fusarium begoniae* has been reported to produce moniliformin, fumonisins (Fotso *et al*., 2002) and fusaproliferin (Moretti *et al*., 2007), while *F. bulbicola* produces fusaproliferin and beauvericin (Moretti *et al*., 2007).

*Fusarium konzum* was isolated from native prairie grasses in the USA (Zeller *et al*., 2003). This species is characterised by oval, pyriform and napiform to globose microconidia that are borne on mono- and polyphialides and arranged singly or in small false heads in the aerial mycelium. *Fusarium konzum* is morphologically most similar to *F. antho-philum* due its pyriform microconidia, but the longer monophialides and more swollen polyphialides found in *F. konzum* distinguish them (Zeller *et al*., 2003). In terms of phylo-geny, *F. konzum* is closely related to *F. sterili-hyphosum* (Fig. 1) that produces coiled sterile hyphae. *Fusarium konzum* produces fumo-nisins, fusaproliferin and beauvericin (Leslie *et al*., 2004a), while one strain has also been reported to produce gibberllin (Malonek *et al*., 2005).

*Fusarium bactridioides* is the only species in the so-called "American Clade" that has been reported to produce chlamydospores (O'Donnell *et al*., 1998). However, this trait needs to be verified, as the ex holotype of this species does not produce chlamydospores (Nirenberg and O'Donnell, 1998). This fungus was isolated as a pathogen of the rust fungus *Cronartium conigenum* (Wollenweber, 1934). Due to its stout, slightly curved and thick-walled macroconidia, it was previously classified in Section *Discolor* by Wollenweber (1934) and Gerlach and Nirenberg (1976). Very little is known regarding its biology, pathology or mycotoxicology.

***The "Asian Clade"***

With its ten known phylogenetic lineages, the so-called "Asian Clade" is the smallest of the three GFC clades (Fig. 1). Only three of these lineages await characterisation and seven have been formally described using the MSR (Nelson *et al*., 1983; Rheeder *et al*., 1996; Aoki *et al*., 2001; Britz *et al*., 2002b; Leslie *et al*., 2005a). Three of these morpho-species are known to produce sexual stages and

are recognisable using the BSR. *Gibberella sacchari*, *G. fujikuroi* and *G. intermedia* are the teleomorphs of *F. sacchari*, *F. fujikuroi* and *F. proliferatum*, which correspond to MP B, C and D, respectively (Kuhlman, 1982; Leslie, 1991, 1995; Samuels *et al*., 2001; Leslie *et al*., 2005a).

In terms of morphology and biology *F. fujikuroi* and *F. proliferatum* are very similar (Leslie *et al*., 2007), and the PSR seems to be the least time-consuming and most effective method of separating them. Both species produce their microconidia from false heads and in chains from poly- and monophialides (Gerlach and Nirenberg, 1982). However, they are associated with different hosts (Fig. 3) as *F. fujikuroi* causes bakane disease of rice and *F. proliferatum* is associated with a vast number of agricultural hosts (Leslie and Summerell, 2006). They can also be distinguished using the BSR (Kuhlman, 1982; Leslie, 1991, 1995; Samuels *et al*., 2001), although the biological separation between the species is apparently incomplete as some isolates of both species are inter-fertile and able to produce hybrid progeny (Desjardins *et al*., 1997; Leslie *et al*., 2004b, 2007). The two species also differ mycotoxicologically, with *F. proliferatum* known to produce higher levels of fumonisins than *F. fujikuroi* (Rheeder *et al*., 2002; Fandohan *et al*., 2003; Desjardins, 2006). Certain strains of *F. proliferatum* are able to produce even higher levels of fumonisins than some strains of *F. verticillioides* (Rheeder *et al*., 2002; Leslie *et al*., 2004a), which is a great health concern as *F. proliferatum* is associated with many agricultural crops. *Fusarium proliferatum* also produces enniatins, fusaproliferin and fusarins (Fig. 2; Marasas *et al*., 1986; Desjardins, 2006; Moretti *et al*., 2007). Except for a single strain of *F. konzum*, *F. fujikuroi* is the only species in the GFC recognised to produce gibberellins (Sun and Snyder, 1981; Malonek *et al*., 2005). Both *F. proliferatum* and *F. fujikuroi* have been reported as producers of beauvericin, fusaric acid and moniliformin (Marasas *et al*., 1986; Bacon *et al*., 1996; Logrieco *et al*., 1998; Desjardins, 2006; Moretti *et al*., 2007).

Based on phylogeny (Fig. 1), the four species *F. fujikuroi*, *F. proliferatum*, *F. globosum* and *F. fractiflexum* form a well-supported group. Within this group, *F. proliferatum* is most closely related to *F. globosum* that occurs in maize, while *F. fractiflexum* that is associated with a leaf disease of *Cymbidium* species in Japan (Aoki *et al*., 2001) represents the basal taxon. Morphologically, *F. globosum* is quite similar to *F. proliferatum* and *F. fujikuroi*, but globose microconidia produced singly or in clusters distinguishes it from them (Rheeder *et al*., 1996). *Fusarium fractiflexum* also shares morphological characters with *F. proliferatum* and *F. fujikuroi*, but the fact that it produces microconidia in geniculate chains on the aerial mycelium distinguishes it from them (Leslie and Summerell, 2006). Although the latter trait resembles that of *F. lactis*, the two species can be differentiated based on colony colour, conidial length and host preference (Aoki *et al*., 2001). From a mycotoxicological point of view, *F. globosum* also resembles *F. proliferatum* and *F. fujikuroi*, although it does not produce fusaric acid and moniliformin. There is no information available regarding the mycotoxicology of *F. fractiflexum*.

The "Asian" *F. subglutinans sensu lato* species *F. sacchari*, *F. concentricum* and *F. mangiferae* are all associated with different plant hosts. *Fusarium sacchari* is well known as a causal agent of the pokkah boeng disease of sugar cane (Gerlach and Nirenberg, 1982). *Fusarium concentricum* has been associated with banana in Guatemala and Costa Rica and insects in South Korea (Nirenberg and O'Donnell, 1998). *Fusarium mangiferae* is a causal agent of mango inflorescence malformation (Freeman *et al*., 1999; Steenkamp *et al*., 2000a; Britz *et al*., 2002b). Based on morphology, *F. concentricum* is most similar to the "American Clade" species *F. circinatum* and *F. guttiforme*, but *F. circinatum* produces coiled hyphae, while *F. guttiforme* produces greater numbers of polyphialides that are more strongly branched (Nirenberg and O'Donnell, 1998). Morphologically, *F. sacchari*, *F. mangiferae* and *F. subglutinans sensu stricto* are extremely difficult to distinguish from each other and their unambiguous separation requires information on host associations and application of the BSR and PSR (Kuhlman, 1982; Leslie, 1995; Steenkamp *et al*., 2000a; Britz *et al*., 2002b). Very little is known concerning the mycotoxicology of *F. sacchari* and *F. mangiferae* because they were all

treated as *F. subglutinans* for many years. *Fusarium concentricum* has been reported to produce beauvericin, enniatins, fusaproliferin and moniliformin (Fotso *et al*., 2002; Desjardins 2006; Moretti *et al*., 2007).

**Evolution of the GFC**

According to the biogeographic hypothesis of O'Donnell *et al*. (1998), all of the species and lineages in the so-called "African", "American" and "Asian" clades should be associated with hosts that have evolved or that have centres of origin on the African, American and Asian continents, respectively. For the most part, this seems to be true as specific *Fusarium* species appear to have emerged with their host plants on the respective continents (Fig. 3). However, there are a number of exceptions where the species composition of the clades does not fit this hypothesis (Fig. 3). For example, *F. verticillioides* is a member of the "African Clade", although its maize and teosinte hosts are now widely accepted to have a Mexican or Central American origin (e.g. Sauer, 1993). Other "African Clade" species with non-African origins include *F. pseudoanthophilum* and *F. denticulatum* (Nirenberg and O'Donnell, 1998; Nirenberg *et al*., 1998; Sauer, 1993). In the "American Clade", species such as *F. succisae*, *F. bulbicola* and *F. sterilihyphosum* are all associated with non-American host plants (Gerlach and Nirenberg, 1982; Nirenberg and O'Donnell, 1998; Britz *et al*., 2002b; Sauer, 1993; Adams, 1995; Vorster and Spreeth, 1996). In the so-called "Asian Clade", the most notable exception is *F. globosum* that was originally isolated in South Africa (Rheeder et al., 1996) and subsequently reported to be associated with wheat in Japan (Aoki and Nirenberg, 1999). These exceptions were attributed to anthropological dispersal of economically important plants and host jumps by the fungi (O'Donnell *et al*., 1998). For example, it was postulated that following the introduction of American hosts such as *Z. mays* and *Ipomoea batatas* into Africa, species such as *F. verticillioides* and *F. pseudoanthophilum* established their associations with maize and *F. denticulatum* with sweet potato. Trans-oceanic dispersal without the influence of humans was also invoked to explain the occurrence of an "American Clade" fungus (*Fusarium* sp. NRRL 25807; Fig. 3) in Australian forest soil (O'Donnell *et al*., 1998). Therefore, despite the fact that the general species compositions of the GFC clades apparently support the vicariant biogeographic hypothesis, much additional research, especially in indigenous regions where human interference in biodiversity is limited, is required to completely explain the existence of these clades.

At first glance, the morphological traits applied in the taxonomy of the GFC appear not be phylogentically informative (Fig. 2) because shared traits among different species does not seem to reflect ancestry (e.g. Steenkamp *et al*., 1999, 2000a). This is particularly true for the ability of some species to produce sterile coiled hyphae, e.g. the "American Clade" species *F. circinatum* and *F. sterilihyphosum* and the "African Clade" species *F. pseudocircinatum* (Fig. 2). The production of microconidia with distinctive shapes and from specific forms of conidiophores also does not reflect the evolutionary history of this complex (Fig. 2). However, the aerial arrangement of microconidia seems to be an informative character, as all the examined "American Clade" species produce their microconidia in false heads only and never in chains, while most of the "Asian Clade" species produce their microconidia in false heads and long chains. Among the "African Clade" species, all bear their microconidia in false heads, although the majority also produce mostly short micro-conidial chains (Fig. 2). Also, the "African Clade" includes all but one the chlamydospore-formers (Fig. 2). If the "African Clade" indeed represents the ancestral GFC clade because of its speciose and phylogenetically diverse nature (O'Donnell *et al*., 1998), the first members of the complex probably represented fungi able to produce chlamydospores and to form their microconidia in false heads and chains. Later, the ability to produce chlamydospores were lost in most lineages (Fig. 2). The ability to produce microconidia in chains also appears to have been lost early during the evolution of the "American Clade" as this trait has not been detected among any of the examined species that all primarily display a *F. subglutinans*-like morphology (Fig. 2).

Analysis of the distribution of mycotoxin production capabilities relative to the phylogeny of the GFC suggests that the ability to produce a specific mycotoxin is not phylogenetically informative (Fig. 2). However, it does appear that the "African Clade" includes the largest number of mycotoxigenic species and that they produce the greatest diversity of secondary metabolites. Although these trends may be due to taxonomic sampling bias, they would also be consistent with the idea of an ancestral "African Clade" for the GFC. Nevertheless, very little information regarding the evolution of the genes and pathways involved in mycotoxin production is available for the GFC. So far only the fumonisin and gibberellin biosynthetic pathways, both encoded by large gene clusters (reviewed by Proctor et al. 2004; Malonek *et al*., 2005) have been analysed from an evolutionary point of view. Proctor *et al*. (2004) showed that the sporadic distribution of fumonisin biosynthetic genes across the GFC potentially explains the discontinuous distribution of the production of this mycotoxin (Fig. 2) by the members of the complex. With respect to gibberellins, non-production by specific GFC species was largely attributed to non-functional genes (Malonek and Tudzynski, 2003), because most of the examined GFC species have at least one gene or the entire gibberellin biosynthetic cluster (Malonek *et al*., 2005). As these gene clusters act as "selfish" genetic elements, horizontal gene transfer is thought to play an important role in their evolution and distribution (e.g. Rosewich and Kistler, 2000; Walton, 2000). Indeed, it has been suggested that the evolution of the fumonisin and gibberellin production capabilities in the GFC is determined by the effects of both horizontal gene transfer and/or differential inheritance from a common ancestor (Proctor *et al*., 2004; Malonek *et al*., 2005; Seifert and Lévesque, 2004). Whether this would also be the case for the various other mycotoxins produced by species in the GFC, remains to be determined.

**Future perspectives**

The concurrent application of MSR, BSR and PSR has contributed significantly to resolving taxonomic confusion in the GFC and it has facilitated the recognition and description of all the species in this complex. Generally, species definitions based on such an integrative approach are extremely robust and have stood the test of time (Leslie and Summerell, 2006).

In our opinion, the only noteworthy limitation associated with the current GFC taxonomy is the description of some species (e.g. *F. begoniae*, *F. bactridioides*, *F. phyllophilum*, *F. pseudonygamai*, *F. ramigenum F. brevicatenu-latum*, *F. pseudoanthophilum* and *F. fracti-flexum*) (Nirenberg and O'Donnell, 1998; Nirenberg *et al*., 1998; Aoki *et al*., 2001) based on very small numbers of strains. Although these species probably represent valid taxa, their polyphasic re-evaluation and definition using populations of isolates that more accurately represent them in nature (Leslie *et al*., 2001) will substantially improve our perception of their biological relevance. This is also true for the various phylogenetic species or lineages of the GFC (O'Donnell *et al*., 1998; 2000b) that still await formal description.

Full appreciation of the evolution of important GFC characters such as mycotoxin production and phytopathogenicity will depend to a large extent on our ability to resolve the true phylogenetic history of this complex and its species. This in turn would be dependent on the reconstruction of a well-resolved phylogeny for the GFC, which will require inclusion of additional and previously unexploited genomic regions for phylogenetic analysis and suitably representative *Fusarium* isolates. Even though many species are already known in this complex, its current composition is strongly biased towards species that are of agricultural, medical or veterinary importance. Hardly any information is available regarding the diversity of GFC species in unique niches and indigenous ecosystems. The exploration of such areas will certainly reveal numerous additional members of this complex and their inclusion in analyses will substantially enhance the phylogenetic resolution of the GFC. Combined with determining the possible ages of the GFC clades, such studies will allow modification or unequivocal acceptance of the vicariant biogeographic hypothesis (O'Donnell *et al*., 1998) and help to clarify the role of the host in the evolution of these fungi. As the exploitation of

full genome sequences becomes more feasible, comparative and phylogenomic approaches will facilitate elucidation of the evolution of various morphological, reproductive and other biological properties such as mycotoxin biosynthesis in the *Fusarium* species of the GFC.

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