

## One Fungus, One Name: Defining the Genus *Fusarium* in a Scientifically Robust Way That Preserves Longstanding Use

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## ABSTRACT

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In this letter, we advocate recognizing the genus *Fusarium* as the sole name for a group that includes virtually all *Fusarium* species of importance in plant pathology, mycotoxicology, medicine, and basic research. This phylogenetically guided circumscription will free scientists from any obligation to use other genus names, including teleomorphs, for species nested within this clade, and preserve the application of the name *Fusarium* in the way it has been used for almost a century. Due to recent changes in the International Code of Nomenclature for algae, fungi, and plants, this is an urgent matter that requires community attention. The alternative is to break the longstanding concept of *Fusarium* into nine or more genera, and remove important taxa such as those in the *F. solani* species complex from the genus, a move we believe is unnecessary. Here we present taxonomic and nomenclatural proposals that will preserve established research connections and facilitate communication within and between research communities, and at the same time support strong scientific principles and good taxonomic practice.

**The importance of the name *Fusarium*.** When we say, “I work on *Fusarium*,” we mean we work on a fungus that causes plant and animal diseases, produces mycotoxins, has six species with complete genome sequences in advanced stages of annotation and many more in progress, has revealed fascinating modes of genetic change with broad evolutionary implications (23) and can be consumed as a processed food (i.e., Quorn). In a recent survey among the international community of plant pathologists, two *Fusarium* species, *F. graminearum* and *F. oxysporum* were ranked fourth and fifth, respectively, on a list of top 10 fungal plant pathogens based on scientific/economic importance (12). When we conduct research on *Fusarium*, we can feel reasonably confident that its prospects will be aided by the recognized significance of the group. When we publish a paper with “*Fusarium*” in the title, the genus’ h-index (19) of 66 since 2002 (Table 1) should give us confidence that it has a huge audience. And perhaps most importantly, there is a large and active research community that identifies strongly with the name and interacts through a *Fusarium* Subcommittee of the International Society of Plant Pathology, a Fusigroup that focuses on genomics and meets in conjunction with the U.S. and European Fungal Genetics Conferences, an International *Fusarium* Workshop that convenes every 5 years, and annual *Fusarium* Laboratory Workshops that have been held every year since 2001. Special journal issues and symposia on *Fusarium* are commonplace in the fields of plant pathology, mycology, and mycotoxicology. In addition to a community of applied and basic researchers focused on a group of organisms represented by the name *Fusarium*, the name is also the primary portal that brings outside researchers and citizens with little or no experience in systematics or mycology, including plant breeders, producers of food and other products, genomicists, farmers, and physicians, into contact with the *Fusarium* community. Thus, the name is an important facilitator of communication, both among members of the *Fusarium* community and in making connections to its stakeholders. As we go about conducting research, writing grant proposals and papers, and attending workshops focused on *Fusarium*, most of us give little if any thought to what *Fusarium* is and what it is not. We are now presented with an urgent need to give this matter some serious thought.

This year witnesses an important and transformational change for *Fusarium* systematics, yet the *Fusarium* community may not realize its far-reaching impact. Fungi that produce asexual and sexual stages (“pleomorphic fungi”) have been allowed under a special provision of the former International Code of Botanical Nomenclature (ICBN, Article 59) to have separate names referring to the sexual (“teleomorph”) and asexual stages (“anamorph”); when referring to the whole fungus (“holomorph”), the

teleomorph name has taken precedence, at least until now. At the 2011 meeting of the Nomenclature Session of the Botanical Congress in Melbourne, it was decided that the former Article 59 will no longer apply as of 1 January 2013 (18). Under this provision [“One Fungus One Name or “1F1N”; (44)], all names, whether they are typified by an anamorph or a teleomorph, will be on equal footing in terms of priority, so the opportunity exists to conserve anamorph names such as *Fusarium* in a way that the scientific community sees fit.

TABLE 1. Reference and internet search results for 15 agriculturally and medically important fungal/oomycete names; names associated with *Fusarium* are in bold

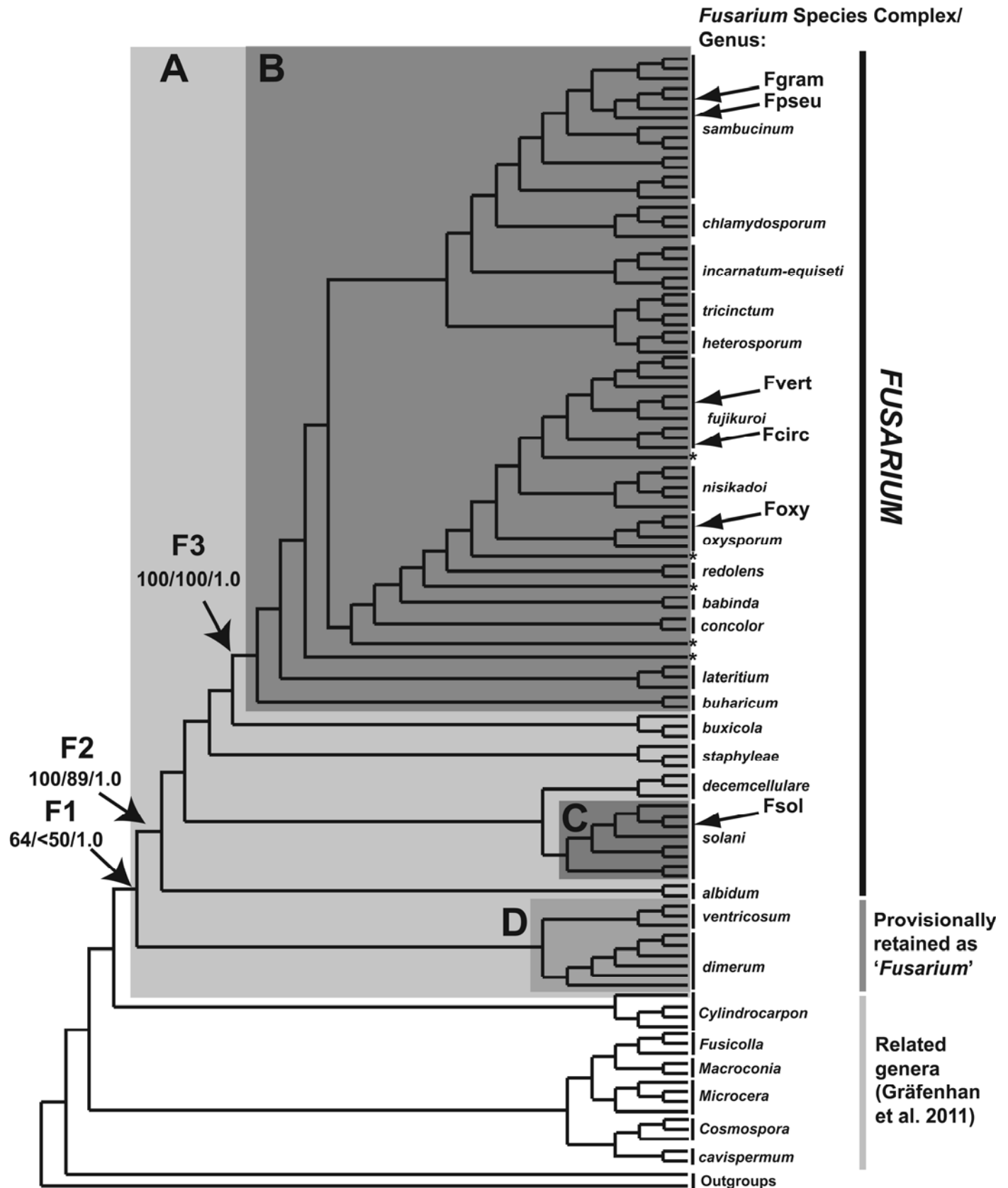
Taxon <sup>a</sup>	References <sup>b</sup>	h-index <sup>c</sup>	Google hits <sup>d</sup>
<i>Saccharomyces</i>	9,917	108	7,620,000
<i>Candida</i>	9,016	100	39,900,000
<i>Aspergillus</i>	7,822	81	6,440,000
<b><i>Fusarium</i></b>	<b>5,397</b>	<b>66</b>	<b>3,810,000</b>
<i>Cryptococcus</i>	1,665	59	395,000
<i>Neurospora</i>	789	51	317,000
<i>Phytophthora</i>	2,656	48	1,920,000
<i>Trichoderma</i>	1,738	45	1,790,000
<i>Penicillium</i>	2,066	35	2,470,000
<i>Magnaporthe</i>	619	37	671,000
<i>Ustilago</i>	368	34	171,000
<i>Colletotrichum</i>	1,032	31	673,000
<b><i>Gibberella</i></b>	<b>277</b>	<b>30</b>	<b>314,000</b>
<i>Verticillium</i>	749	29	282,000
<i>Mycosphaerella</i>	401	28	513,000
<i>Alternaria</i>	965	28	1,230,000
<b><i>Nectria</i></b>	<b>51</b>	<b>11</b>	<b>388,000</b>
<i>Neocosmospora</i>	8	2	62,200
<b><i>Haematonectria</i></b>	<b>2</b>	<b>1</b>	<b>14,900</b>
<i>Cyanonectria</i>	2	2	8,750
<i>Geejayessia</i>	1	1	1,050
<i>Albonectria</i>	1	1	7,260
<b><i>Fusarium solani</i></b>	<b>299</b>	<b>21</b>	<b>433,000</b>
<b><i>Nectria haematococca</i></b>	<b>27</b>	<b>10</b>	<b>207,000</b>
<b><i>Fusarium graminearum</i></b>	<b>568</b>	<b>37</b>	<b>447,000</b>
<b><i>Gibberella zeae</i></b>	<b>152</b>	<b>24</b>	<b>132,000</b>
<b><i>Fusarium verticillioides</i></b>	<b>285</b>	<b>24</b>	<b>133,000</b>
<b><i>Gibberella moniliformis</i></b>	<b>11</b>	<b>6</b>	<b>51,700</b>

<sup>a</sup> Taxon names in bold are associated with the terminal *Fusarium* clade.

<sup>b</sup> References published from 2002 to present were retrieved from ISI Web of Knowledge on 14 May 2012 using the taxon name as a query under “Title.”

<sup>c</sup> h-index is the number of references with at least that number or more citations. For example, of the 5,397 references with *Fusarium* in the title, 66 have been cited at least 66 times.

<sup>d</sup> Hits retrieved using the taxon name as a query in the Google search engine, from Penn State campus on 14 May 2012.



**Fig. 1.** Cladogram presentation of the *RPB1/RPB2* phylogenetic tree presented in O'Donnell et al. (28). The cladogram is based on one of four most parsimonious trees; see O'Donnell et al. (28) for methodological details. Branch lengths are arbitrary. Values associated with labeled nodes indicate the maximum likelihood bootstrap (ML-BS), maximum parsimony bootstrap (MP-BS), and Bayesian posterior probability (B-PP) values. Major clades/species complexes are labeled on the right, with monotypic taxa marked by an asterisk. Arrows on the right indicate species for which complete genome sequences are released and in an advanced state of annotation: *Fgram* = *F. graminearum*, *FPseu* = *F. pseudograminearum*, *Fvert* = *F. verticillioides*, *Fcirc* = *F. circinatum*, *Foxy* = *F. oxysporum*, and *Fsol* = *F. solani* species complex phylogenetic species 11 (8,11,13,23,45). **A**, Our proposed limits for the use of *Fusarium* as a unitary name, delimited by Node F1. **B**, Limitation of *Fusarium* to *Gibberella* Clade, delimited by Node F3. **C**, The *F. solani* species complex. **D**, The *F. ventricosum* and *F. dimerum* species complexes, subjected to provisional status as *Fusarium*, awaiting strongly supported phylogenetic inferences that either support or reject their inclusion.

This means the second-class nomenclatural status of *Fusarium* as an anamorph genus will end, allowing the exclusive use of the name *Fusarium* without additional teleomorph names. *Fusarium* researchers have been moving in this direction in recent years, describing sexual stages without a corresponding teleomorph name (9,36). Historically, taxonomic treatments of *Fusarium* have stressed the anamorph (2,3,14,15,20,21,24,26,32,40–42,46), since teleomorphs are unknown for a large majority of the species, and anamorphs are almost always what plant pathologists and other applied biologists observe in culture. An alternative option would be to let *Fusarium* be subsumed entirely under existing teleomorph names, but virtually everyone would agree that conserving its further use is the most desirable outcome. The question is: to what species and clades should the name apply? The way we resolve this question will significantly impact how we study and publish *Fusarium* for the foreseeable future.

**Our Proposal.** Here we argue that the name *Fusarium* should be applied exclusively to all members of a monophyletic group that best fits the longstanding concept of the genus, protected against all competing teleomorph concepts within that group. Recent phylogenetic hypotheses offer two competing monophyletic groups that are potential targets for exclusive use of the name *Fusarium*, presented as nodes F1 and F2 in Figure 1. Both groups include every *Fusarium* species of major research interest, with F2 excluding the *F. dimerum* and *F. ventricosum* complexes. The clade associated with node F1, recently referred to as “the terminal *Fusarium* clade,” was resolved as monophyletic (16,37), but with weak statistical support. In a more comprehensive analysis, F1 received improved support but only in Bayesian analysis, and F2 was strongly supported using three analytical approaches (28). Here we assign *Fusarium* to node F1, but retain the *F. dimerum* and *F. ventricosum* complexes only provisionally as *Fusarium*, recognizing the need for further study.

**Didn't the taxonomists tell us to use teleomorph genus names forty years ago?** The research communities invested in *Fusarium* now have an opportunity to adopt a simple and rational system where every *Fusarium* species is referred to solely by the name of this well-known anamorph. Scientists likely recall being told to adopt the use of teleomorph names, so a proposal to go back to using *Fusarium* will be met with skepticism. Researchers working on members of the *F. solani* species complex faithfully adopted the teleomorph name *Nectria haematococca* for their organisms of choice in the 1970s (43), only to learn a couple of decades later that the name *Nectria* had been misapplied to this group (34), with no satisfactory teleomorph name replacing it (27). Quite reasonably, some of these workers have chosen to keep using the name *Nectria* in the face of the taxonomic instability, particularly applied to *N. haematococca* mating populations (8). Our intent here is to establish a scientifically robust yet practical and stable usage that will optimally serve all *Fusarium* research in the long run. While *N. haematococca* remains in use, it will become more and more difficult to communicate in the literature and elsewhere without using a standardized nomenclature.

Biological databases such as MycoBank (10) and GenBank will likely have the greatest influence on usage. MycoBank was established as the central depository of fungal names and naturally, GenBank looks to MycoBank and other mycological resources for guidance on fungal taxonomy. Still, the application of *Fusarium* nomenclature in GenBank has been inconsistent. Currently, GenBank accessions from the *F. solani* species complex are deposited under four different genus names (i.e., *Fusarium*, *Nectria*, *Neocosmospora*, and its later synonym *Haematonectria*). In contrast, isolates of *F. graminearum* and *F. verticillioides* are consistently converted to their teleomorph names, *Gibberella zeae* and *G. moniliformis*. Of course, GenBank is not the source of this confusion; it only reflects the confused state of Dual Nomenclature associated with *Fusarium*. MycoBank and GenBank do

not wish to impose a taxonomic view on users; they simply make an effort to communicate a framework as established by taxonomists. We expect that MycoBank and GenBank will adopt the circumscription of *Fusarium* put forward by the research community and accepted by the International Committee on Nomenclature, which means that the community must step forward to voice its needs, or face having the decision made for it. So what is to become of *Fusarium* species such as *N. haematococca*? We argue that it is far more desirable that they appear in GenBank as *Fusarium* species than as *Haematonectria*, *Neocosmospora*, or whatever other genus name might be proposed for them, as long as it is scientifically reasonable to do so.

**Taxonomic changes based on scientifically robust principles are a good thing.** Taxonomic name changes are often necessary and practical (33). We advocate employing a molecular phylogenetic approach to guide such changes so that taxonomy best aligns with evolutionary history and fully realizes its predictive potential. Such changes may be inconvenient, or rearrange long-established taxonomic groups, but where they have a solid scientific foundation they facilitate good scientific practice and guide biological discovery. With the move away from Dual Nomenclature, certainly some radical changes will be necessary in many fungal groups, but these are ultimately in the best interests of scientific progress. Many such practical changes have already occurred in *Fusarium*. In addition to those cited in Rossman and Palm-Hernandez (33), *F. nivale* was moved from *Fusarium* to *Microdochium* based on morphological data (35); because the two genera reside in different subclasses of Ascomycota (*Fusarium* in Hypocreomycetidae, *Microdochium* in Xylariomycetidae), science was poorly served by the previous misplacement of *M. nivale* in *Fusarium*. Using phylogenetics as a guide, Gräfenhan et al. (16) segregated a large number of phylogenetically disjunct species from *Fusarium* into existing, revised, and new genera in the Nectriaceae. Most of these changes, which removed obscure species of little or no known practical importance, represent significant and practical advances in *Fusarium* systematics. However, as we will discuss later, we differ strongly with these authors regarding the eventual circumscription of *Fusarium*.

**Criteria for circumscribing the genus *Fusarium* in a post-Article 59 world.** We promote the following three standards in circumscribing the generic limits of *Fusarium*.

1. **Monophyly:** It should represent an evolutionarily exclusive lineage or monophyletic group that includes the type species (i.e., *Fusarium sambucinum*). Our circumscription of *Fusarium* is presented in Figure 1, and with more detail in Figure 1 of O'Donnell et al. (28).
2. **Tradition:** The monophyletic group should be chosen in the way that conforms best to longstanding taxonomic concepts of the genus as practiced by the broader plant pathological, mycotoxicological, and clinical microbiological research communities. The name should be applied to the most inclusive clade where the name *Fusarium* has been most commonly and sensibly used. In other words, the best solution is that of *primum non nocere*: first do no harm, and avoid unnecessary changes to the practical concept.
3. ***Fusarium* first:** Teleomorph generic concepts are of extremely limited use within *Fusarium*. A large majority of cultures and diseased material that taxonomic end-users work with contain only asexual stages, and most *Fusarium* species, including many key groups such as the *F. oxysporum* complex, have no known sexual stage. Fortunately, with the long awaited changes in the Code, we are now in a position to abandon the use of teleomorph names altogether and simply refer to species by the *Fusarium* name. Furthermore, there is no compelling reason/data to support dividing *Fusarium* according to teleomorph, for the following two reasons: (i) there is a longstanding tradition of

*Fusarium* encompassing multiple teleomorphs (5,39), and (ii) teleomorph evolution, as guided by existing morphological concepts, does not show clear evolutionary patterns. For example, *Neocosmospora* and *Haematonectria* teleomorphs are produced by closely related species within the *F. solani* species complex, rendering the concept of *Haematonectria* nonmonophyletic (27) and *Fusarium* species with *Albonectria* states are polyphyletic (16). In addition, the genus *Fusarium* traces back to Link in 1809 (22), and thus has nomenclatural priority over all associated teleomorph genera. Not surprisingly, Google searches retrieved over five times more records for *Fusarium* than all associated teleomorph names combined (Table 1), so a practical solution also puts *Fusarium* first.

## PROPOSAL

**Unitary use of the name *Fusarium* should be applied to all descendants of the node first defined as the terminal *Fusarium* clade by Gräfenhan et al. (16) and refined by O'Donnell et al. (28).**

**Phylogenetic definition.** Here we apply the rules of PhyloCode (6) to provide a phylogenetic definition of *Fusarium*, which can be amended easily as new data and phylogenetic inferences are obtained.

***Fusarium*** E. Fries 1821: *Systema Mycologicum* 1. XLI (Introductio) [D.M. Geiser & K. O'Donnell, circumscribed herein], converted clade name.

**Definition.** The least inclusive clade containing *Fusarium ventricosum* Appel & Wollenw. 1913, *F. dimerum* Penz. 1882, *F. nematophilum* Nirenberg & G. Hagedorn 2010, *F. decemcellulare* Brick 1908, *F. buxicola* Sacc. 1883, *F. staphyleae* Samuels & Rogerson 1984, *F. solani* (Mart.) Sacc. 1881, and *F. sambucinum* Fuckel 1870. This is a node-based definition in which all of the specifiers are extant and therefore designates a crown clade. Abbreviated definition: *Fusarium ventricosum* Appel & Wollenw. 1913, *F. dimerum* Penz. 1882, *F. nematophilum* Nirenberg & G. Hagedorn 2010, *F. decemcellulare* Brick 1908, *F. buxicola* Sacc. 1883, *F. staphyleae* Samuels & Rogerson 1984, *F. solani* (Mart.) Sacc. 1881, & *F. sambucinum* Fuckel 1870.

**Etymology.** Derived from the Latin *fuscus* (spindle), describing the typical septate conidia produced by most species.

**Reference phylogeny.** Based on largest and second largest RNA polymerase II B subunit (*RPB1* and *RPB2*) gene sequences, labeled as Node F1 in Figure 1 of O'Donnell et al. (28).

**Composition.** Encompasses at least 20 genealogically exclusive lineages: *F. sambucinum*, *F. chlamydosporum*, *F. incarnatum-equiseti*, *F. tricinctum*, *F. heterosporum*, *F. fujikuroi*, *F. nisikadoi*, *F. oxysporum*, *F. redolens*, *F. babinda*, *F. concolor*, *F. lateritium*, *F. buharicum*, *F. buxicola*, *F. staphyleae*, *F. solani*, *F. decemcellulare*, *F. albidum*, *F. dimerum*, and *F. ventricosum* species complexes or clades. See Node F1 in Figure 1 of O'Donnell et al. (28).

**Diagnostic apomorphies.** No true morphological synapomorphies are known for this clade. Asexual spores may include any or all of the following: (i) curved, transversely septate conidia ("macroconidia") produced from sporodochia or pionnotes, (ii) generally smaller conidia of various shapes and septation ("microconidia" and/or "mesoconidia") produced from unbranched or branched mycelial conidiophores, producing conidiogenous cells with one (monophialidic) or more (polyphialidic) openings, and (iii) thick-walled, generally globose thalospores (chlamyospores) produced in or on hyphae or conidia, singly or in chains or bunches. Sexual spores, when observed, produced in flask-shaped fruiting bodies (perithecia) that are usually in shades of red, orange, blue or purple, with little or no stromatal tissue. Asci produced from distinct hymenia, single-walled (unitunicate) containing eight ascospores, which usually possess one or more septa, but can be aseptate.

**Comments.** *Fusarium*, first described by Link (1809: Mag. Ges. Naturf. Freunde, Berlin 3:10), was sanctioned under Fries 1821. Anamorphs within this clade have consistently been described as *Fusarium*, with occasional isolates or species classified in other genera including *Acremonium*, *Cylindrocarpon*, *Pycnofusarium*, *Trichofusarium*, and *Cephalosporium*, particularly when the macroconidial morph is not observed. The inclusion of the *F. dimerum* and *F. ventricosum* species complexes is provisional, due to the weak bootstrap support for the node that includes them in maximum likelihood and maximum parsimony analyses (16,28,37). Bayesian analysis offers strong support (posterior probability [PP] = 100%) for the clade that includes these taxa (Node F1), and the only existing evidence supports their inclusion. Additional phylogenetic and taxonomic work will determine the nomenclatural fate of species in these clades.

**Nomenclature.** The above phylogenetic delimitation of *Fusarium* will require nomenclatural changes to accommodate it in practice. Several generic names, mostly referring to sexual stages, are typified within the terminal *Fusarium* clade, including the name *Gibberella*. In fact, the names *Fusarium* and *Gibberella* are typified in the same member of the terminal *Fusarium* clade, *F. sambucinum* Fuckel and its teleomorph *G. pulicaris* Fr. (Sacc.). To accommodate this phylogenetic delimitation in a logical way, the following combinations are required:

*Fusarium albidum* (Rossman) O'Donnell & Geiser, comb. nov.

MYCOBANK ID: MB 800574

≡ *Albonectria albida* (Rossman) Guu & Y.M. Ju, Bot. Stud. 48(2):189. 2007.

≡ *Nectria albida* Rossman, Mycol. Pap. 150:79. 1983.

*Fusarium albosuccineum* (Pat.) O'Donnell & Geiser, comb. nov.

MYCOBANK ID: MB 800609

≡ *Albonectria albosuccinea* (Pat.) Rossman & Samuels, in Rossman, Samuels, Rogerson & Lowen, Stud. Mycol. 42:107. 1999.

≡ *Calonectria albosuccinea* Pat., Bull. Soc. Mycol. Fr. 8(2):132. 1892.

*Fusarium verrucosum* (Pat.) O'Donnell & Geiser, comb. nov.

MYCOBANK ID: MB 800610

≡ *Calonectria verrucosa* Patouillard, Bull. Soc. mycol. Fr. 11(4):228. 1895.

≡ *Albonectria verrucosa* (Pat.) Rossman & Samuels, in Rossman, Samuels, Rogerson & Lowen, Stud. Mycol. 42:108. 1999.

≡ *Nectria astromata* Rossman, Mycotaxon 8(2):550. 1979.

*Fusarium cicatricum* (Berk.) O'Donnell & Geiser, comb. nov.

MYCOBANK ID: MB 800611

≡ *Geejayessia cicatricum* (Berk.) Schroers, Stud. Mycol. 68(1):124. 2011.

≡ *Sphaeria sanguinea* Bolton var. *cicatricum* Berk., Mag. Zool. Bot. 1:48. 1837.

*Fusarium cyanostomum* (Sacc. & Flageolet) O'Donnell & Geiser, comb. nov.

MYCOBANK ID: MB 800612

≡ *Cyanonectria cyanostoma* (Sacc. & Flageolet) Samuels & Chaverri, Mycol. Progr. 8(1):56. 2009.

≡ *Nectria cyanostoma* Sacc. & Flageolet, Atti del Congr. bot. di Palermo:53. 1902.

*Fusarium plagianthi* (Dingley) O'Donnell & Geiser, comb. nov.

MYCOBANK ID: MB 800613

≡ *Nectria plagianthi* Dingley, Trans. Roy. Soc. N.Z. 79(2):196. 1951.

*Fusarium rusci* (Sacc.) O'Donnell & Geiser, comb. nov.

MYCOBANK ID: MB 800614

≡ *Trichofusarium rusci* (Sacc.) Bubák, Bull. Herb. Boissier, 2 sér. 6:488. 1906.

≡ *Fusarium roseum* Link var. *rusci* Sacc., Michelia 2 (no. 7):294. 1881.

= *Pycnofusarium rusci* D. Hawksw. & Punith., Trans. Br. Mycol. Soc. 61(1):63. 1973.

*Fusarium neocosmosporiellum* O'Donnell & Geiser, nom. nov.

MYCOBANK ID: MB 800615

≡ *Neocosmospora vasinfecta* E.F. Sm., Bull. U.S. Department of Agriculture 17:45. 1899.

(non-*Fusarium vasinfectum* G.F. Atk. 1892).

## DISCUSSION

Defining genera is an inherently subjective endeavor. Scientific principles govern good taxonomy, but taxonomists have choices regarding where to draw generic limits. In instances where monophyly (Criterion 1) and other scientific principles are satisfied, we have considerable latitude in Criteria 2 and 3 to accommodate practical concerns and longstanding use. Criterion 3 above, which gives greater weight to the name *Fusarium*, conflicts with approaches used to define genera of hypocrealean fungi established in Rossman et al. (34), which emphasizes teleomorph differences. Recent work by Schroers et al. (37) cites this approach as a guiding principle for revising the concept of *Cyanonectria* and describing the new genus *Geejayessia*, both of which are nested within the terminal *Fusarium* clade and consist entirely of species with typical *Fusarium* asexual stages. While in principle teleomorph differences may correlate well with genealogically exclusive groups and serve as a perfectly reasonable option for delimiting generic boundaries in many ascomycete groups, we argue that its application here is both impractical and scientifically unnecessary.

**A monophyletic *Fusarium*.** Multiple phylogenetic studies have resolved with varying support a monophyletic group that includes a large majority of species traditionally considered to be *Fusarium* that also includes virtually every species of agricultural, clinical, and research importance. This clade is referred to as the “terminal *Fusarium* clade” in Gräfenhan et al. (16); the type species of *Fusarium*, *F. sambucinum*, is nested within it. In that study this node received weak statistical support [ $<95\%$  Bayesian PP,  $<75\%$  maximum likelihood and parsimony bootstrap (ML and MP BS)], but the analysis was based only on partial sequences of the second largest RNA polymerase II B-subunit (*RPB2*) gene and ATP citrate lyase (*ac11*), with  $\sim 80\%$  of the phylogenetic signal coming from *RPB2*. In an analysis by Schroers et al. (37) based on the same gene regions, the terminal *Fusarium* clade received 76% MP BS support and 100% PP. A neighboring clade (one that excludes two taxa labeled as ‘*Nectria ventricosa*’) received “moderate” support (either  $>75\%$  ML or MP or  $>95\%$  PP) in their study. The terminal *Fusarium* clade received further support in our recent study utilizing sequences from both the largest and second largest ribosomal RNA polymerase II B-subunit genes (*RPB1* and *RPB2* [28]). The two genes in this study provided relatively similar levels of phylogenetic signal, and were analyzed in a much more inclusive set of ingroup taxa ( $n = 93$ ) than those of Gräfenhan et al. ( $n = 26$ ) and Schroers et al. ( $n = 19$ ). These genes resolved a node that is compatible to the terminal *Fusarium* clade (labeled “F1” in that study and in Figure 1), receiving  $>95\%$  PP, but ML and MP bootstrap support remained poor. The *RPB1/RPB2* study also resolved an alternative hypothesis to F1 for the circumscription of *Fusarium* (28). A clade nested within the terminal *Fusarium* clade, “F2”, received much stronger statistical support (100% ML BS, 87% MP BS, and 100% PP) and includes all of F1 except for the *F. dimerum* and *F. ventricosum* species complexes. Because of the inconsistent phylogenetic support for the inclusion of *F. dimerum* and *F. ventricosum* species complexes in the terminal *Fusarium* clade, their retention in *Fusarium* is given a provisional status in our proposal (Fig. 1D). While both of these groups have a long tradition of inclusion in *Fusarium*, and members of the *F. dimerum* species complex are occasional human pathogens and commonly encountered sapro-

phytes (38), their removal from *Fusarium* will not have a great impact on common usage. Still, the only evidence available supports, less than convincingly, their retention in a monophyletic *Fusarium*, and at this time no compelling alternate nomenclatural options exist for them. Most importantly, both competing hypotheses for the circumscription of *Fusarium* strongly retain the economically important *F. solani* species complex in the genus.

**Excluded taxa.** A number of lineages basal to the terminal *Fusarium* clade that produce *Fusarium*-like anamorphs were recently moved to new, revised, or existing genera based on morphological and phylogenetic considerations (*Microcera*, *Macroconia*, *Fusicolla*, and *Stylonectria* [16]). Most of the *Fusarium*-like species in these basal lineages occur as saprophytes in soil, on trees and other fungi, and in aquatic habitats, but some are putative parasites of insects or endophytes. While these taxa traditionally have been included in treatments of *Fusarium*, they have not been reported to cause diseases of plants and humans and other vertebrates and none are known to produce mycotoxins, so they are largely ignored by applied biologists. Therefore, we support their removal from *Fusarium* with the caveat that it needs to be more fully assessed by additional data and analyses.

**Comments on a somewhat conflicting viewpoint.** Gräfenhan et al. (16) and Schroers et al. (37) also in effect argue for a phylogenetically based, unitary application of the name *Fusarium*, but they focus on a single clade nested within the terminal *Fusarium* clade where a large majority of the known sexual stages fit the morphological concept of *Gibberella* (Node F3, Clade B in Fig. 1). This strongly supported “*Gibberella* clade” has been resolved consistently since the first molecular phylogenetic studies of *Fusarium* (17). Many economically important *Fusarium* species are nested within the *Gibberella* clade, including the type species of *Fusarium* (*F. sambucinum*), but it excludes many other agriculturally and medically important species, particularly those in the *F. solani* species complex, which are responsible for approximately two-thirds of all fusarial infections of humans and other animals (30).

The Gräfenhan et al. (16) and Schroers et al. (37) viewpoint is consistent with a tradition that emphasizes the teleomorph in recognizing generic boundaries. While this approach has been productive in delimiting genera in the Hypocreales (34), we argue that our “*Fusarium* First” approach is necessary because of the huge longstanding investment that has already been made in the name *Fusarium*, applied almost always to a group approximated by the terminal *Fusarium* clade. Generalizing beyond *Fusarium* to other genera of major importance, we offer a morph-neutral view regarding the precedence of teleomorph names. Once genealogically exclusive groups are identified, we advocate that a given genus name should be assigned to the most inclusive clade where the name has been most commonly and sensibly established, with no automatic preference given to genera typified as teleomorphs versus anamorphs. Unfortunately, many economically important genera are likely to be nonmonophyletic, necessitating radical changes.

**The impact of limiting *Fusarium* to the *Gibberella* clade.** The *F. solani* clade is represented in Figure 1C; Gräfenhan et al. (16) labeled taxa within this clade as “*Haematonectria*” or “*Neocosmospora*” but species in this group are mostly known as ‘*F. solani*’ or formae speciales of *F. solani* (e.g., *F. solani* f. sp. *pisi*). This group encompasses at least 60 phylogenetically diagnosable species, including many species of importance in agriculture, medicine and biological research, and as such, it has a long tradition of inclusion within the genus *Fusarium* (25). Members of this clade include a number of important pathogens of a variety of crops, including several species that cause sudden death syndrome of soybean (1). Members of the *F. solani* complex are the most common *Fusarium* species isolated from human infec-

tions (30) and they accounted for the majority of the pathogens in the 2005–06 outbreaks of contact lens-associated corneal infections (7). Because of its status as a model system in plant pathology, and it is interesting metabolic capabilities, a member of '*N. haematococca* MP VI' ('NhMPVI' or *F. solani* species complex phylogenetic species [11]) was targeted as one of the first *Fusarium* species for complete genome sequencing (8). Through comparisons of the NhMPVI genome with those of three species within in the *Gibberella* clade, some fascinating insights about the genomic nature of adaptation were revealed (8). Genomic characteristics of NhMPVI include an expanded genome due to the existence of small, conditionally dispensable chromosomes and large contiguous portions of chromosomes containing genes of unknown origin. Surprisingly, these are features it shares with *F. oxysporum*, a member of the *Gibberella* clade (23). In fact, *F. solani* (excluded from *Fusarium* if it is limited to the *Gibberella* clade) and *F. oxysporum* share a great deal of ecological and morphological similarities, and they are often presented together when individuals are trained to identify them morphologically. Based on the fact that some members of the *F. solani* species complex cause infections of plants and humans, a strong connection has been established among the medical and phytopathological communities that work on these *Fusarium* species and the broader *Fusarium* research communities. While the *F. solani* and *F. oxysporum* species complexes are clearly quite distinct phylogenetically, together they form part of a larger, strongly supported monophyletic group, so there is no compelling reason to overrule a century of established use and segregate the *solani* complex into a new genus.

The name *F. solani* in current usage has been applied to many of the 60 diagnosable phylogenetic species in the complex, reflecting the limitations of morphological species recognition within this species-rich complex. An alphanumerical system of nomenclature for phylogenetic species in the *F. solani* species complex provides that (29), but it is an incomplete substitute for an actual binomial. Providing such names must be a priority in parallel with the transition to INIF usage.

A number of other fungi with a clear connection to *Fusarium* would be removed if the name were restricted to the *Gibberella* clade, including *F. buxicola* and *F. decemcellulare*, not to mention the *F. dimerum* species complex. While most of these fungi are of unknown economic importance, a large majority of them produce a classic *Fusarium* anamorph (37,38). We argue that recognizing the limits of the genus as the node corresponding to F1 in Figure 1, or a nearby node revealed through more thorough phylogenetic analyses, will avoid the unnecessary splitting of this cohesive group. At the same time, we strongly concur with the goal of Gräfenhan et al. (16), to "provide a functional single-name system that respects the principles of the ICBN and refrain from attempting to perpetuate a dual nomenclatural system where it is unlikely to be used by most scientists working on the practical aspects of these fungi," and offer this alternative proposal in the same spirit.

**Summary and further considerations.** In accordance with changes in the International Code of Nomenclature for algae, fungi, and plants, we propose the sole use of the name *Fusarium* to the clade representing the terminal *Fusarium* clade (16,28,37) (Node F1 in Fig. 1), with the *F. dimerum* and *F. ventricosum* species complexes retained in a provisional status, effective 1 January 2013. An obvious advantage is that our proposal will circumvent a need to use at least eight generic names in that lineage. We also voice our strong opposition to any proposal to name any other subclade at the rank of genus within this clade, including the phylogenetically and morphologically diverse lineages within the *Gibberella* clade. Assuming that the proposal for unitary use of the name *Fusarium* is accepted and applied, further research is needed to refine the generic boundary, and most importantly, to accurately assign species names within the

genus. *Fusarium* remains littered with names in use that are typified ambiguously, or lack types entirely; the work of Gräfenhan et al. (16) is an excellent start in this endeavor. A first effort to solve this problem involves making a list of names in use within the genus that can then be scrutinized one by one. In addition to existing names, scores of unnamed phylogenetic species are being recognized, and we need a robust system for reconciling existing taxonomic schemes with our rapidly expanding knowledge of *Fusarium* phylogeny. Additional phylogenetic research, likely based on much larger, genome-level data sets, will eventually be employed to reconstruct a more detailed evolutionary history of *Fusarium* and allow us to further assess its monophyly (16,28). And most importantly, our rapidly expanding knowledge of *Fusarium* diversity must be communicated effectively to the user community—this will require a well-coordinated community effort and support mechanisms for digitally cataloging and sharing relevant data and cultures.

Despite these challenges, the future of *Fusarium* systematics should be viewed with tremendous optimism. A great degree of clarity has emerged in recent decades with regard to *Fusarium* species boundaries, subgeneric groups, and generic limits. A deluge of genomic data, which is on the way, will enable us to reevaluate *Fusarium* phylogeny and examine mechanisms underlying their evolution at the genome scale. Improved bioinformatic tools (31), in combination with the global connectivity enabled by the Internet, will provide researchers with rapid access to the information whenever and wherever they need it.

The concept of *Fusarium* has evolved to represent a very large and diverse set of taxa over the last century. While this size and diversity can present challenges, and arguments have abounded about species concepts in the genus, none of the previous major taxonomic treatments of *Fusarium* elected to break it up in a significant way. Along with the generic concept, an equally large and diverse community of researchers has evolved, leading to a long list of seminal discoveries in both practical and basic science that have had major impacts in plant pathology, medical mycology and fungal biology. Overall, we argue that the size and diversity of this genus is one of its most positive attributes, not a flaw in need of correction. As Booth said (4), "Taxonomists... must always be aware of the service element to other scientists. Taxonomy is a basic science fundamental to many branches of research...and if we cannot give an indication of the true genealogical relationships that exist between the species we are failing in our profession." As did Gräfenhan et al. (16) and Schroers et al. (37), we offer this circumscription of *Fusarium* in that very spirit. However, the service element does not end with genealogical relationships. Once that criterion is satisfied, we must do everything we can to facilitate effective communication and research, and the simplest rule for doing that is not to make unnecessary changes.

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