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Letter to the Editor

e-Xtra*

Phylogenomic Analysis of a 55.1-kb 19-Gene Dataset Resolves a Monophyletic *Fusarium* that Includes the *Fusarium solani* Species Complex

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ABSTRACT

Scientific communication is facilitated by a data-driven, scientifically sound taxonomy that considers the end-user's needs and established successful practice. In 2013, the *Fusarium* community voiced near unanimous support for a concept of *Fusarium* that represented a clade comprising all agriculturally and clinically important *Fusarium* species, including the *F. solani* species complex (FSSC). Subsequently, this concept was challenged in 2015 by one research group who proposed dividing the genus *Fusarium* into seven genera, including the FSSC described as members of the genus *Neocosmospora*, with subsequent justification in 2018 based on claims that the 2013 concept of *Fusarium* is polyphyletic. Here, we test this claim and provide a phylogeny based on exonic nucleotide sequences of 19 orthologous protein-coding genes that strongly support the monophyly of *Fusarium* including the FSSC. We reassert the practical and scientific argument in support of a genus *Fusarium* that includes the FSSC and several other basal lineages, consistent with the longstanding use of this name among plant pathologists, medical mycologists, quarantine officials, regulatory agencies, students, and researchers with a stake in its taxonomy. In recognition of this monophyly, 40 species described as genus *Neocosmospora* were recombined in genus *Fusarium*, and nine others were renamed *Fusarium*. Here the global *Fusarium* community voices strong support for the inclusion of the FSSC in *Fusarium*, as it remains the best scientific, nomenclatural, and practical taxonomic option available.

Keywords: evolution, fungal pathogens

Scientific advances and new fungal nomenclatural rules have forced necessary changes in fungal names in recent years, many of which are inconvenient. Unlike other fungal genera in which phylogenetics and nomenclatural conflicts forced very difficult taxonomic decisions (e.g., *Magnaporthe/Pyricularia*; Zhang et al. 2016), there is a clear path to define genus *Fusarium* phylogenetically, eliminate confusing dual nomenclature/taxonomy, and maintain a generic circumscription that has been widely used for over a century (Bilai 1955; Booth 1971; Gams and Nirenberg 1989; Gerlach and Nirenberg 1982; Joffe 1974; Leslie and Summerell 2006a; Matuo 1972; Nelson et al. 1983; Raillo 1950; Snyder and Hansen 1941; Summerell 2019; Wollenweber 1913; Wollenweber and Reinking 1935). The highest impact taxonomic outcome at stake is the segregation of *F. solani* and the *F. solani* species complex (FSSC) out of genus *Fusarium* into the relatively obscure taxon *Neocosmospora*, the type of which represents a morphologically aberrant lineage within the FSSC. Here we argue that this move is scientifically unnecessary and impractical, and we refute phylogenetic arguments that have been presented to support it (Sandoval-Denis and Crous 2018).

The scientific argument for a monophyletic *Fusarium* in Geiser et al. (2013) was strongly supported by 66 authors from 17 countries representing the *Fusarium* community. The goal was to promote a generic concept of *Fusarium* that is scientifically (i.e., monophyletic) and nomenclaturally sound and at the same time minimizes disruption by protecting scientifically valid, longstanding use. *Fusarium* is one of the most commonly used ascomycete generic names in the scientific literature (Geiser et al. 2013), so this practical consideration is essential because of the negative impact of disconnecting past, current, and future uses of the name.

The Geiser et al. (2013) phylogenetic circumscription of genus *Fusarium* precisely corresponds to a monophyletic group that encompassed all economically important *Fusarium* species, originally termed the terminal *Fusarium* clade (herein abbreviated TFC; Gräfenhan et al. 2011). Members of this clade almost always produce spores and colonies with a recognizable *Fusarium* morphology. The TFC included the type species of *Fusarium*, *F. sambucinum*, the same species in which the competing teleomorph genus *Gibberella* is typified: *G. pulicaris*. This overlap made it straightforward to propose unitary use of the name *Fusarium* over *Gibberella* (Rossman et al. 2013). That proposal, however, did not address the many *Fusarium* species within the TFC with connections to teleomorph genera other than *Gibberella*, comprising the FSSC and all other species complexes in Figure 1 that resolve basally with respect to the *F. buharicum* species complex.

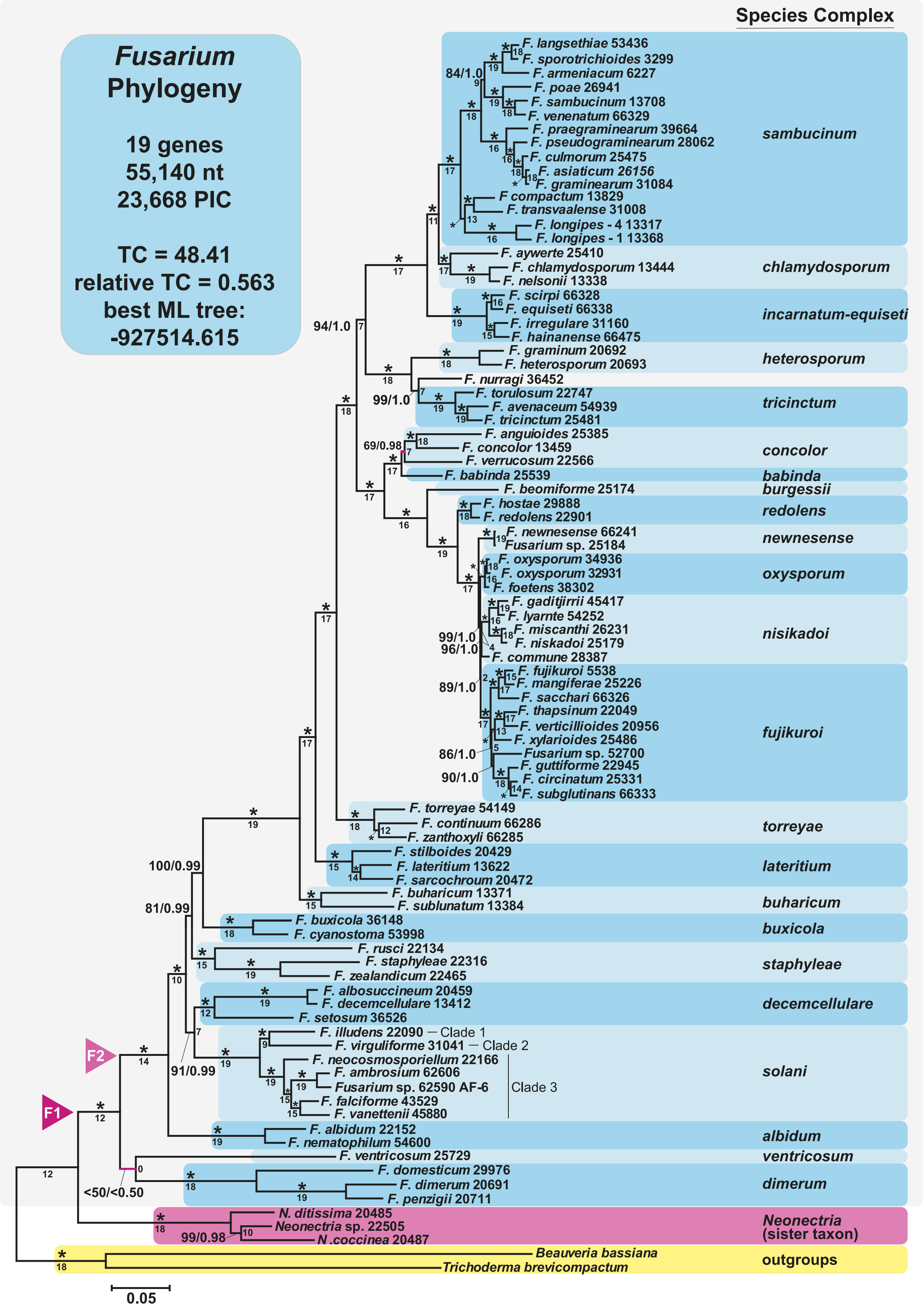

Fig. 1. Partitioned maximum likelihood bootstrapped (ML-BS) phylogram of the genus *Fusarium*, based on full-length exonic nucleotide sequences of 19 protein-coding genes (Table 1), inferred using IQ-TREE (Nguyen et al. 2015). Nodes supported by 100% ML bootstrap (5,000 replicates; BS) and 1.0 Bayesian posterior probability (BPP), including F1 and F2, are indicated with asterisks; ML-BS/BPP values are shown for nodes receiving <100%/1.0 support. Two branches highlighted in magenta received BS < 70 and BPP < 0.99. Two shades of blue highlight 23 species complexes within the genus *Fusarium*. Numerals situated adjacent to nodes represent gene concordance factors calculated by IQ-TREE 2 for that node, expressed as the number of loci that resolve it out of 19. PIC = parsimony informative character and TC = tree credibility.

Geiser et al. (2013) proposed that all members of the TFC be included in the genus *Fusarium*, not just those associated with genus *Gibberella*, and synonymized competing genera in the TFC under that name. Based on portions of two loci (the second-largest RNA polymerase II B-subunit [*rpb2*] and larger ATP citrate lyase [*acl1*] genes), the Gräfenhan et al. (2011) phylogenetic analysis provided only weak statistical support for the node associated with the TFC. The proposal in Geiser et al. (2013) was based on a phylogenetic analysis of a much larger set of species in the TFC that utilized more informative loci (*rpb2*, as well as the largest RNA polymerase II B-subunit gene *rpb1*; O'Donnell et al. 2013). This analysis also resolved the TFC as monophyletic ("node F1"), with improved but still weak statistical support (<70% maximum parsimony bootstrapping [MP-BS] and maximum likelihood bootstrapping [ML-BS]; 1.0 Bayesian posterior probability [BPP]). Recognizing this uncertainty, a second node ("F2"), which received much stronger statistical support (87% MP-BS; 100% ML-BS; 1.0 BPP), was offered as an alternative to F1, should more rigorous analyses reject the monophyly of F1. F2 comprises all of F1 except its two basal-most clades (the *F. ventricosum* and *F. dimerum* species complexes; FVSC and FDSC, respectively). Notably, both the F1 and the F2 hypotheses include the FSSC within the genus *Fusarium*.

Based on a phylogenetic analysis of nine concatenated loci and a rich sampling of nectriaceous taxa, Lombard et al. (2015) also resolved the same TFC node, but again with weak statistical support. Although the aforementioned studies all resolved the same node, with different levels of support, Sandoval-Denis and Crous (2018) claimed with no new phylogenetic evidence that the concept of *Fusarium* proposed by Geiser et al. (2013) is polyphyletic. However, as carefully accounted for in Geiser et al. (2013) and O'Donnell et al. (2013), statistical support for that node based on analyses of *RPB1* and *RPB2* was in need of a more rigorously tested phylogeny using additional genes. In this article, we address this with a phylogenetic inference based on complete exonic nucleotide sequences of 19 protein-coding genes, derived from whole-genome sequences of 89 taxa, 47 of which were generated in the present study (Supplementary Table S1). The resulting analysis provides 100% ML-BS/1.0 BPP for the monophyly of *Fusarium* as delimited by Geiser et al. (2013) (i.e., the F1 node in Fig. 1), reaffirming the taxonomic hypothesis that *Fusarium* has nomenclatural priority over all names typified in that clade, including *Neocosmospora*.

We also present a phylogeny of 77 FSSC species based on three loci: portions of *rpb2* and translation elongation factor 1-α (*tef1*) and rDNA (a contiguous portion of the nuclear ribosomal RNA gene repeat comprising the internal transcribed spacer and the D1 to D2 regions of the nuclear large subunit). Sandoval-Denis and Crous (2018) and Sandoval-Denis et al. (2019) typified and named many of the previously unnamed species within the FSSC. This is an extremely important advance in the taxonomy of this group, an effort that will greatly facilitate scientific communication about these fungi. However, we disagree with their placement in genus *Neocosmospora*, for reasons we outline here and in O'Donnell et al. (2020). Accordingly, we list the combinations of these taxa in genus *Fusarium* (Aoki et al. 2020), along with other FSSC species typified or previously combined in genus *Neocosmospora*.

MATERIALS AND METHODS

Selection and extraction of marker loci. Exonic nucleotide sequences of the 19 housekeeping genes (Table 1) used to infer the *Fusarium* phylogeny in this study were selected based on (i) their use in previous studies for inferring phylogenetic relationships within this genus and across the kingdom Fungi (Floudas et al. 2012; O'Donnell et al. 2013; Sarver et al. 2011; Villani et al. 2019; Watanabe et al. 2011), (ii) their utility in previous studies of the distribution and evolution of secondary metabolite genes/gene clusters in the genus *Fusarium* (Brown and Proctor 2016; Brown et al. 2020; Busman et al. 2012; Kim et al. 2020; Proctor et al. 2009, 2010, 2013, 2018), and (iii) their relative lengths. Full-length exonic sequences of each gene were obtained from whole-genome sequences of 89 taxa, generated in house at the U.S. Department of Agriculture Agricultural Research Service National Center for Agricultural

TABLE 1. Phylogenetic data summary of 19 genes analyzed in this study

Locus[a]	Protein encoded	Identifier[b]	Chromosome[c]	Nucleotide sites (*n*)	Amino acids (*n*)[d]	PICs (*n*)[e]	PICs/site	Total PICs (%)	Model[f]
acl1	ATP citrate lyase large subunit	FFUJ_13230	4	1,473	490	505	0.34	2.13	TN+F+I+G4
*act1**	Actin	FFUJ_00687	1	1,425	474	641	0.45	2.71	TIM2+F+I+G4
*cal1**	Calmodulin	FFUJ_12207	8	450	149	117	0.26	0.49	TNe+I+G4
cpr1	Cytochrome P450 reductase	FFUJ_04716	2	2,085	694	949	0.46	4.01	TIM2+F+I+G4
dpa1	DNA polymerase alpha subunit	FFUJ_08551	7	4,491	1,498	2,233	0.50	9.43	GTR+F+I+G4
*dpe1**	DNA polymerase epsilon subunit	FFUJ_13258	4	6,699	2,232	3,005	0.45	12.70	GTR+F+I+G4
fas1	Fatty acid synthase alpha subunit	FFUJ_04562	2	5,622	1,880	2,191	0.39	9.26	TIM2+F+I+G4
fas2	Fatty acid synthase beta subunit	FFUJ_04563	2	6,330	2,109	2,608	0.41	11.02	TN+F+I+G4
*ku70**	ATP-dependent DNA helicase II	FFUJ_04557	2	1,959	652	1,020	0.52	4.31	SYM+I+G4
lcb2	Sphinganine palmitoyl transferase subunit	FFUJ_09546	9	2,121	706	910	0.42	3.84	TIM2+F+I+G4
mcm7	DNA replication licensing factor	FFUJ_02741	3	2,526	841	1,211	0.48	5.12	GTR+F+I+G4
*pgk1**	Phosphoglycerate kinase	FFUJ_09403	9	1,257	418	447	0.36	1.89	TIM2+F+I+G4
rpb1	RNA polymerase largest subunit	FFUJ_00736	1	5,382	1,793	2,348	0.44	9.92	TIM2+F+I+G4
rpb2	RNA polymerase second largest subunit	FFUJ_07996	5	3,882	1,293	1,667	0.43	7.04	TIM2e+F+I+G4
*tef1**	Translation elongation factor 1-alpha	FFUJ_05795	6	1,383	460	299	0.22	1.26	GTR+F+I+G4
top1	Topoisomerase	FFUJ_02999	3	2,859	952	1,505	0.53	6.36	TIM2+F+I+G4
tsr1	Ribosomal biogenesis protein	FFUJ_09872	9	2,493	830	1,261	0.51	5.33	GTR+F+I+G4
tub1	Tubulin alpha subunit	FFUJ_00614	1	1,350	449	383	0.28	1.62	TIM+F+I+G4
*tub2**	Tubulin beta subunit	FFUJ_04397	2	1,353	450	368	0.27	1.55	TN+F+I+G4
Total				55,140	18,370	23,668		100.00	

[a] Asterisks indicate that the individual gene tree does not resolve F1.

[b] Gene identifier in the *Fusarium fujikuroi* genome (Wiemann et al. 2013).

[c] Chromosomal location as mapped to the *F. fujikuroi* genome (Wiemann et al. 2013).

[d] Amino acid count, which does not account for in-frame insertions/deletions.

[e] Parsimony-informative characters (PICs) in the nucleotide alignment.

[f] Best evolutionary model as determined by Bayesian information criterion estimated in IQ-TREE.

Utilization Research ($n = 65$) or by the Beijing Genome Institute ($n = 4$) or downloaded from the National Center for Biotechnology Information GenBank database ($n = 20$; Supplementary Table S1).

Genomic DNA for sequencing was extracted from mycelia grown in liquid glucose-yeast-peptone medium (2% glucose, 0.3% yeast extract, and 1% peptone) for 2 to 3 days, harvested by filtration, lyophilized, and ground to a powder. Genomic DNA was then extracted using a ZR Fungal/Bacterial DNA MiniPrep kit (Zymo Research, Irvine, CA), the Qiagen Genomic-Tip 20/G protocol, or a previously described chloroform-phenol-based method (Raeder and Broda 1985). For data generated in house, sequence reads were generated using the MiSeq systems (Illumina) and processed using CLC Genomics Workbench (CLC) versions 8 to 20 (Qiagen) as previously described (Laraba et al. 2020a, b; Proctor et al. 2018). Sequence reads were imported into CLC and then screened against genome sequences of 84 bacterial species to remove contaminating DNA introduced during library preparation and/or the sequencing process. Reads were trimmed to remove low-quality data and assembled using the following parameter settings in CLC: word size, 20; bubble size, 50; minimum contig length, 500; auto-detect paired distances, checked; and perform scaffolding, checked.

Protein coding genes were predicted with the AUGUSTUS program (Stanke et al. 2006) using *F. graminearum* genes as a reference and the fgenesh algorithm (Solovyev et al. 2006) implemented online in Softberry (http://www.softberry.com). Gene sequences were retrieved from coding region databases of each strain using the BLASTn function in CLC and query sequences from *F. fujikuroi*, *F. graminearum*, and *F. vanettenii* (formerly reported as *Nectria haematococca* mating population MPVI; Coleman et al. 2009). Sequences of each gene were aligned with the query sequences using MUSCLE (Edgar 2004) as implemented in MEGA7 (Kumar et al. 2016), and the resulting alignments were examined for differences between predicted coding regions and the query sequences. When necessary, genes were manually annotated using genome sequence data to correct errors introduced by the automated annotation, particularly with respect to predicted intron-splicing sites. The three loci utilized for phylogenetic analysis of the FSSC were those utilized in previous studies (O'Donnell et al. 2008; Sandoval-Denis and Crous 2018).

Molecular phylogenetics. Two multilocus datasets were assembled and analyzed using partitioned ML-BS (5,000 replicates) with IQ-TREE 1.6.12 for MacOS (Nguyen et al. 2015; http://www.iqtree.org/) and Bayesian inference with MrBayes v.3.2.7 (Ronquist et al. 2012). A partitioned 19-gene 55.1-kb dataset was assembled to assess *Fusarium* monophyly (Table 1). It contained complete exonic nucleotide sequences for 84 fusaria, a putative sister group comprising three *Neonectria* species, and sequences of two non-nectriaceous hypocrealean taxa, *Beauveria bassiana* (Cordycipitaceae) and *Trichoderma brevicompactum* (Hypocreaceae), which were used to root the phylogeny. A partitioned three-locus 3.2-kb dataset was constructed to infer evolutionary relationships among 77 species within the FSSC, derived from previous studies (O'Donnell et al. 2008; Sandoval-Denis et al. 2019). Sequences were aligned with MUSCLE and then manually edited using TextPad 8 (//www.textpad.com/home) to improve the alignment. ModelFinder (Kalyaanamoorthy et al. 2017) was used to identify the best-fit model of molecular evolution for each partition based on the Bayesian information criterion scores (Chernomor et al. 2016). Bayesian inference was conducted using 1,000,000 generations in four chains (three cold, and one hot, with 25% burn-in), using the $GTR+\Gamma+I$ evolutionary model. To assess compatibility of individual loci in the phylogenetic inference, gene compatibility factors (gCFs) were calculated using IQ-TREE v.2.1.2 (Minh et al. 2020a, b); gCF values, representing the proportion of gene partitions that resolve a particular node, were translated into numerals representing the number of supporting loci out of 19. In addition, internode certainty (IC), IC-all (ICA), tree certainty (TC), and relative TC values (Salichos and Rokas 2013; Salichos et al. 2014) were calculated for the IQ-TREE partitioned ML tree in RAxML v.8.2.12 (Kobert et al. 2016; Stamatakis 2014). Aligned 19- and three-locus datasets and best ML trees in NEXUS format, with genes partitioned as charsets, are included in Supplementary Figures S1, S2, and S3 and also deposited in TreeBASE (study S27101).

RESULTS

***Fusarium* phylogenetics.** The 19-gene nucleotide alignment of full-length exons totaled 55,140 sites, 23,668 of which were parsimony informative (Table 1). Individual genes provided a range of 0.5% (*cal1*) to 12.7% (*dpe1*) of the total parsimony informative sites in the concatenated character set. In the best ML phylogeny (Fig. 1), 72 of 86 inferred nodes were supported at the 100% level by ML- BS as well as 1.0 BPP, with only two nodes receiving <80% BS/<0.99 BPP support (highlighted in Fig. 1). The F1/TFC node, upon which the Geiser et al. (2013) circumscription was based (O'Donnell et al. 2013), received 100% BS/1.0 BPP, as did the previously proposed alternate node F2. The ML and Bayesian trees (Supplementary Fig. S1) were topologically identical except for placement of *F. ventricosum* within node F1 (see discussion below), which neither method resolved with statistical confidence (BS < 50%; 0.88 BPP for an alternative topology; see Fig. 1 and Supplementary Fig. S1).

Based on gCF values, 53 of 86 internodes in the ML tree were supported by at least 16 of 19 loci in the dataset, whereas 71 of 86 were supported by at least half (Supplementary Fig. S3). Nodes F1 and F2 were supported by 12 and 14 individual loci. The most poorly supported node in the ML tree (unresolved in the majority-rule bootstrap consensus tree and by Bayesian analysis) placed *F. ventricosum* as a sister to the FDSC, within the F1 node. In 7 of 19 individual gene trees (*act1*, *cal1*, *dpe1*, *ku70*, *pgk1*, *tef1*, and *tub2*; Supplementary Fig. S2), ingroup taxa (usually *F. ventricosum*) resolved among outgroup taxa. These genes tend to be shorter and have lower parsimony informative character (PIC)/base pair values than those that resolve F1 (Table 1). However, the F1/TFC, inclusive of *F. ventricosum*, was supported in each of the remaining 12 individual gene trees, with bootstrap values between 78 and 100%. Three loci (*fas1*, *fas2*, and *ku70*) representing 24.6% of the PICs in the matrix are colocated within approximately 30 kb on the same contig (FFUJ_scaffold03) of the *F. fujikuroi* genome sequence. Removal of these linked loci and reanalysis using IQ-TREE resolved the F1/TFC node with 100% ML bootstrap support (*results not shown*). The IC and ICA values for the F1 node were 0.19 and 0.33, respectively (Supplementary Fig. S3), indicating that roughly 70% of the genes support the bipartition (see Fig. 2 in Salichos et al. 2014). This value is similar to the proportion of 12 of 19 (approximately 63%) indicated by gCF, and evident by visual inspection of individual gene trees (Supplementary Figs. S2 and S3). TC, representing the sum of IC values across trees, was 48.41, and relative TC, representing TC normalized to the maximum TC for the phylogeny, was 0.563.

Three additional species complexes recognized within genus *Fusarium* since the publication of the *rpb1* + *rpb2* phylogeny (O'Donnell et al. 2013) are represented in the dataset: the *F. torreyae* species complex (Zhou et al. 2018), the *F. newnesense* species complex (Laurence et al. 2016), and the *F. burgessii* species complex (here represented by *F. beomiforme*; Laraba et al. 2018; Laurence et al. 2011; Nelson et al. 1987), bringing the total to 23 species complexes recognized within the genus. Each of these species complexes received at least 95% ML-BS, except for the *F. concolor* species complex (FconSC), which received 69% ML-BS/0.98 BPP support. This lack of resolution appears to be attributable to FconSC's sister taxon, the *F. babinda* species complex, being represented by a single taxon in the dataset. When *F. babinda* was removed, FconSC received 100% BS support (*results not shown*). Similarly, the FVSC is represented by a single taxon on a long branch, which likely explains the failure to resolve its placement

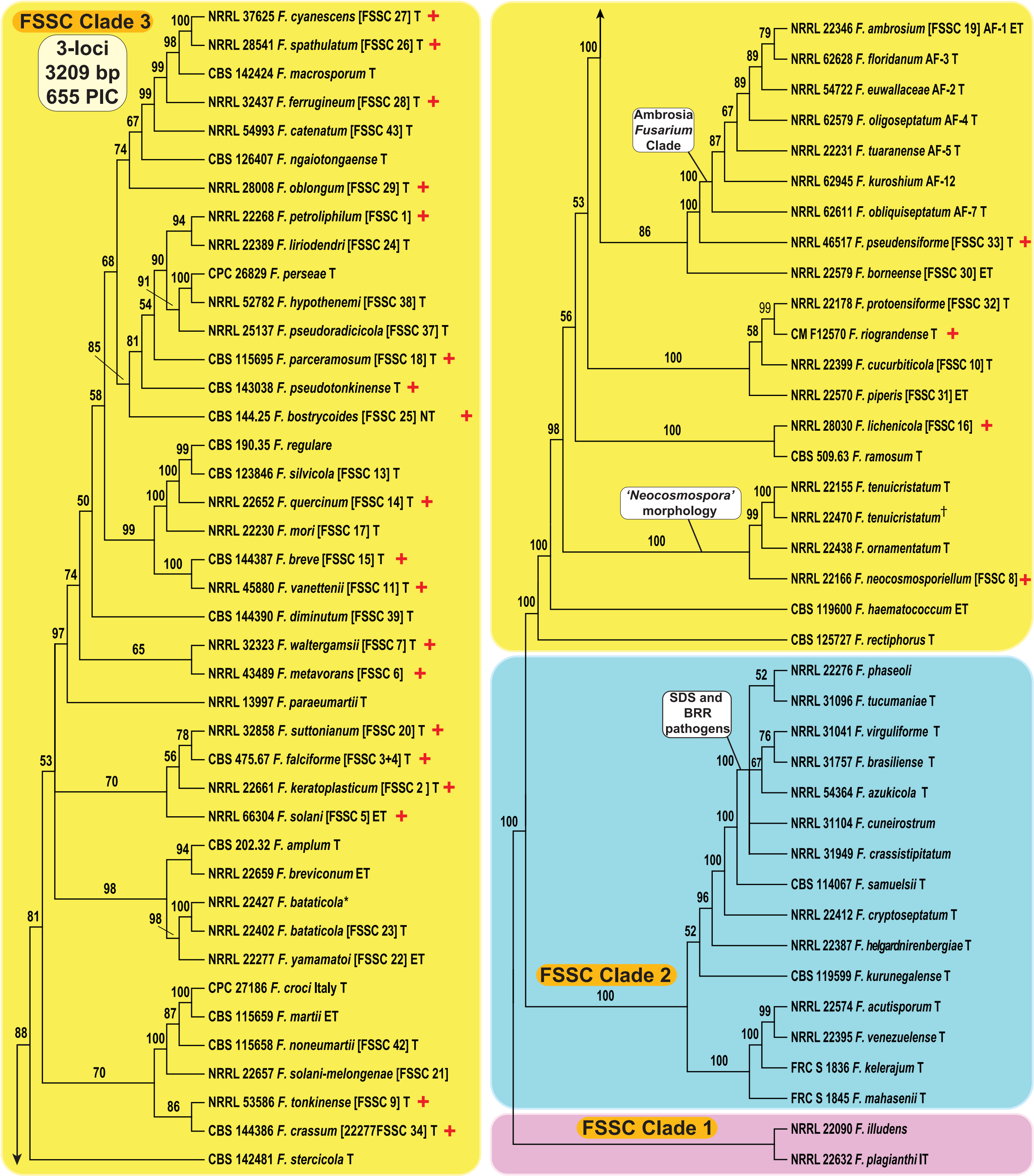

Fig. 2. Partitioned maximum likelihood bootstrapped (ML-BS) cladogram of the *Fusarium solani* species complex (FSSC) based on *tef1*, *rpb2*, and rDNA, inferred using IQ-TREE (Nguyen et al. 2015). Clades 1, 2, and 3 represent designations proposed in O'Donnell (2000). Numerical designations corresponding to an informal ad hoc nomenclature for phylogenetic species in the FSSC (e.g., FSSC 1) are provided in brackets. The ambrosia *Fusarium* clade (Kasson et al. 2013), the clade that encompasses species with typical *Neocosmospora* morphology, and the clade consisting of soybean sudden death syndrome (SDS) and bean root rot (BRR) pathogens, are indicated. ML-BS values, based on 5,000 replicates, are shown for each node. Plus signs indicate medically important species. Asterisk indicates the type of *N. striata*, combined under *F. bataticola*. Daggers indicate the type of *N. boninensis*, combined under *F. tenuicristatum* (Appendix). PIC = parsimony informative character, T = type isolate, ET = epitype isolate, and IT = isotype isolate.

(Felsenstein 1978). However, it does resolve within the FTC/F1 node with 100% ML-BS and 1.0 BPP support, as it did with weaker support in previous studies (Gräfenhan et al. 2011; Lombard et al. 2015; O'Donnell et al. 2013).

FSSC phylogenetics. The three-locus DNA alignment for the FSSC comprised 3,209 sites (665 for *TEF1*, 956 for rDNA, and 1,588 for *RPB2*), 655 of which were parsimony-informative (164 for *TEF1*, 131 for rDNA, and 360 for *RPB2*). In the best ML cladogram, the previously identified major clades 1, 2, and 3 (O'Donnell 2000) were resolved with 100% bootstrap support. Three clades with unique morphologies and host associations were also resolved within the FSSC: (i) the subclade within clade 3 that is morphologically associated with *Neocosmospora*'s type (Smith 1899), (ii) the ambrosia *Fusarium* clade (AFC; Kasson et al. 2013; O'Donnell et al. 2015), and (iii) the soybean sudden death syndrome (SDS) and bean root rot (BRR) pathogen clade nested in clade 2 (Aoki et al. 2012).

Taxonomy. Recognizing that *Neocosmospora* sensu Lombard et al. (2015), Sandoval-Denis and Crous (2018), and Sandoval-Denis et al. (2018, 2019) represents a later synonym of *Fusarium* under this taxonomic hypothesis, species combinations (Aoki et al. 2020) are listed in the Appendix.

Importantly, we retained as distinct species the important SDS and BRR pathogens in the FSSC, *F. phaseoli*, *F. tucumaniae*, *F. virguliforme*, *F. brasiliense*, *F. cuneirostrum*, *F. crassistipitatum*, and *F. azukicola*, which were synonymized under *F. phaseoli* by Sandoval-Denis et al. (2019). The latter authors performed a split graph analysis and interpreted reticulate patterns as evidence that these groups are conspecific. This is in contrast to previous work providing evidence that they were genealogically exclusive (Aoki et al. 2005, 2012). However, the split graph analysis was based on *tef1*, *rpb2*, and *rDNA*, with only 12 parsimony informative sites among these taxa, and they did not analyze the more phylogenetically informative loci that indicated genealogical exclusivity among these species (Aoki et al. 2012). Although the levels of sequence divergence among these species were very small, and scrutiny of the species boundaries based on information-rich phylogenomic datasets is encouraged, the reticulate pattern illustrating homoplasy could be attributable to processes other than intraspecific genetic exchange, including incomplete lineage sorting and convergence. The synonymization by Sandoval-Denis et al. (2019) also does not account for the morphological differences among these species, nor reported distinctions in their symptomology and host range (Aoki et al. 2005, 2012).

DISCUSSION

The rationale for a phylogenetic delimitation of genus *Fusarium* outlined by Geiser et al. (2013), reaffirmed here, can be considered on its own merit. However, we emphasize that the 166 scientists from 30 countries (i.e., core global *Fusarium* community) who coauthored the present publication enthusiastically support it as the best scientifically and nomenclaturally valid taxonomic option. We argue that the alternative posed by Lombard et al. (2015) is based on a taxonomic viewpoint that binds the concept of *Fusarium* to a teleomorph name, *Gibberella*. This approach was first hinted at (Gräfenhan et al. 2011; Schroers et al. 2011), and later manifested in a proposal (Lombard et al. 2015) to split genus *Fusarium* into seven genera within the TFC: *Fusarium* (*Gibberella*'s de facto replacement), *Albonectria*, *Bisifusarium*, *Cyanonectria*, *Geejayessia*, *Neocosmospora*, and *Rectifusarium*. Although the generic concepts proposed by Lombard et al. (2015) are monophyletic and nomenclaturally valid, they fail on the practicality criterion because they exclude species with a longstanding place in genus *Fusarium*. We see no benefit in splitting genus *Fusarium* in favor of competing names that are largely tied to rarely observed sexual stages.

The most important exclusion by Lombard et al. (2015) is that of the FSSC, which was moved to the genus *Neocosmospora* in their taxonomic proposal. The type species, *Neocosmospora vasinfecta*, which was recombined in *Fusarium* as *F. neocosmosporiellum* (Geiser et al. 2013), represents an atypical morphological lineage derived within the FSSC (Figs. 1 and 2). *F. neocosmosporiellum* and related species produce an asexual stage that, unlike most FSSC species, lacks the fusiform sporodochial macroconidia that are the hallmark of genus *Fusarium*, and a homothallic sexual stage consisting of smooth, thin-walled perithecia and ascospores that are mostly single celled (Smith 1899; Wollenweber and Reinking 1935). However, *F. neocosmosporiellum* produces microconidiophores typical of the FSSC (Domsch et al. 1980). Viewed within a robust phylogenetic framework, *F. neocosmosporiellum* clearly represents a morphologically aberrant FSSC lineage whose species have lost the ability to produce the iconic multiseptate macroconidia and only occasionally produce two-celled ascospores (O'Donnell 2000; O'Donnell et al. 2013). Similarly, most of the 19 species in the AFC are morphologically unique within the FSSC in that they produce club-shaped macroconidia that are hypothesized to be adaptive to roles associated with the ambrosia beetle symbiosis (Kasson et al. 2013).

While *Neocosmospora* works nomenclaturally as an available genus name typified within the FSSC, it would be unfortunate if its aberrant morphology were to replace *Fusarium*, which represents the dominant morphology of the group. Because *Neocosmospora* is the oldest teleomorph name associated with the FSSC, this awkward nomenclatural option seemed reasonable when it was applied under dual nomenclature (e.g., Nalim et al. 2011). However, the demise of dual nomenclature as of 1 January 2013 opened the door to a much more practical and attractive option: *Fusarium*, an older name, and the dominant longstanding generic concept associated with the FSSC. Highlighting that status, "*Fusarium solani*" generated >100 times more Google hits than "*Neocosmospora*" (3,000,000 to 27,600; search conducted on 9 July 2020). In summary, we argue that the practical and most scientifically attractive option is to combine *Neocosmospora* species under genus *Fusarium* (Geiser et al. 2013), not the other way around.

We refute the argument that inclusion of the FSSC in genus *Fusarium* "implies a denial of the current phenotypic … evidence" (Sandoval-Denis et al. 2019) and, to the contrary, argue that the name "*Neocosmospora*" is an atypical phenotypic fit for the FSSC. Sandoval-Denis et al. (2019) do not apply a rigorous test or accounting of phenotypic synapomorphies that invalidate the Geiser et al. (2013) circumscription. Iconic *Fusarium* multiseptate macroconidia are observed in a majority of FSSC species, as they are in members of every other *Fusarium* species complex. In addition to the aforementioned *F. neocosmosporiellum*, occasional isolates within multiple FSSC species appear to lack macroconidium production (Gams 1971; O'Donnell 2000; Short et al. 2013; Summerbell and Schroers 2002). However, the vast majority of isolates in the FSSC do produce these spores, and a lack of macroconidia is occasionally observed in *Fusarium* sensu Lombard et al. (2015) as well (e.g., *F. xyrophilum*; Laraba et al. 2020a). Although the FSSC is morphologically distinguishable from other *Fusarium* species complexes, we do not accept that these differences are sufficiently significant to require recognition as a separate genus. To wit, the concept of *Fusarium* in existence for over a century has consistently accommodated this level of phenotypic diversity in the recognition of taxonomic subgroups within the genus (Wollenweber 1913; Wollenweber and Reinking 1935).

While there are indeed morphological and ecological trends associated with the phylogenetic structure within our circumscription of the genus *Fusarium*, there are no convincing nomenclatural, scientific, or practical criteria that obligate splitting it into multiple genera. Illustrating similarities between the FSSC and other *Fusarium* clades, FSSC species share many morphological, ecological, and genomic characteristics with the *F. oxysporum* species complex

(FOSC), which Lombard et al. (2015) retain in genus *Fusarium*. FSSC and FOSC often are coisolated from the same soil and plant samples; while they can be resolved morphologically, misidentification of one as the other is common. FSSC and FOSC are cosmopolitan residents of soil and the rhizosphere, and of decaying and living plant material, where they may act as parasites and/or endophytes. Interestingly, their ecological similarities are reflected in their genomes, with both having significantly expanded accessory genomes that include supernumerary, conditionally dispensable chromosomes that harbor niche adaptive genes (Coleman et al. 2009; Ma et al. 2010; Waalwijk et al. 2018). Although these two groups occupy different clades within genus *Fusarium* and placing them in separate genera is a discretionary option, plant pathologists and medical mycologists have treated them as congeneric for the past century. International *Fusarium* Laboratory Workshops, which have been held regularly since the 1970s (Leslie and Summerell 2006b), present FSSC and FOSC, which is retained in genus *Fusarium* by Lombard et al. (2015), together in lectures and the laboratory, reflecting the shared ecological, morphological, and genomic characteristics that are relevant to clinicians and researchers. In short, we argue that the individual lineages that comprise the monophyletic *Fusarium* sensu Geiser et al. (2013) share more in common than not.

In support of splitting the genus *Fusarium* into seven genera and promoting the FSSC as *Neocosmospora*, additional claims were made about the status of the TFC as a monophyletic group (Sandoval-Denis and Crous 2018), including (i) the Geiser et al. (2013) concept of *Fusarium* is "polyphyletic" and (ii) moving it to *Neocosmospora* represents a "more natural classification." To correct the record, there are no published phylogenies known to the authors of this article with appropriate taxon sampling and resolving power showing the TFC to be anything but monophyletic, including the Lombard et al. (2015) phylogeny. Comparisons of the phylogeny in Lombard et al. (2015) with those in Geiser et al. (2013), O'Donnell et al. (2013), and Gräfenhan et al. (2011) reveal that a monophyletic TFC is resolved in all of them. Certainly, as has been shown in many publications, there is phylogenetic structure within the genus *Fusarium*, but phylogenetic structure is not synonymous with polyphyly (i.e., having multiple distinct evolutionary origins; Farris 1990); a strongly supported monophyletic genus can encompass strongly supported monophyletic subgroups. Nor would it be reasonable to argue that a genus can accommodate only a certain degree of phylogenetic structure, particularly when its well-studied taxonomy has unanimously accommodated substructure, in the form of sections (Wollenweber 1913) and now phylogenetic lineages referred to as species complexes (O'Donnell et al. 2013).

We also reject the assertion that splitting the FSSC off as *Neocosmospora* represents a "more natural classification." Given that *Neocosmospora* sensu Sandoval-Denis et al. (2019) and the circumscription of *Fusarium* in Geiser et al. (2013) are both monophyletic, the two concepts are of equal status regarding scientific support. In fact, Geiser et al. (2013) openly critiqued the phylogenetic evidence underlying their taxonomic hypothesis and presented an alternative circumscription of *Fusarium* in case additional data did not support this hypothesis. Although the concept proposed by Geiser et al. (2013) is based on phylogenetics, it is rooted in the first taxonomic synthesis of *Fusarium* (Wollenweber and Reinking 1935), and subsequent modifications based on modern morphological (e.g., moving '*F. nivale*' into *Microdochium*; Samuels and Hallett 1983) and phylogenetic (Gräfenhan et al. 2011; O'Donnell et al. 2013) information. It retains all agriculturally, medically, and economically important species in genus *Fusarium*. In contrast to the claim that *Neocosmospora* is the more natural classification for the FSSC, we find its transfer to *Neocosmospora* unnatural in light of this historical and practical context. It is a morphologically counterintuitive, unnecessarily disruptive solution to a taxonomic problem that does not exist.

Our phylogenetic circumscription of *Fusarium* mirrors that of genus *Aspergillus* in several ways (Samson et al. 2014). *Aspergillus* is also one of the most commonly used generic names in kingdom Fungi, and it corresponds to a strongly supported clade (Kocsubé et al. 2016; Steenwyk et al. 2019). Both genera harbor great species diversity, with new species being discovered at high rates. However, the *Aspergillus* clade encompasses much greater morphological diversity than *Fusarium*, including sexual stages varying from asci enclosed within wefts of hyphal elements (*Neosartorya*, associated with *A. fumigatus*) to cleistothecia enclosed in sclerotial ascostromata (*Petromyces*, associated with *A. flavus*). While the familiar *Aspergillus* conidiophore morphology dominates, the clade also includes aberrant anamorph forms such as *Phialosimplex*. In the case of genus *Aspergillus*, it was decided that the broader circumscription was the most reasonable solution among nomenclaturally and scientifically valid options (Samson et al. 2014), and all competing generic concepts have been subsumed under *Aspergillus*. While molecular phylogenetic studies over the past three decades have revealed that genera *Aspergillus* and *Fusarium* are much larger than documented using morphology alone, it is important to note that both are monophyletic as presently circumscribed.

The strong statistical support presented in the 19-locus phylogeny solidifies the taxonomic hypothesis assigning the name *Fusarium* to all descendants of node F1 in Geiser et al. (2013) and O'Donnell et al. (2013), and the TFC sensu Gräfenhan et al. (2011). This finding further negates the unsupported claim that *Fusarium* sensu Geiser et al. (2013) is polyphyletic, and it eliminates any remaining doubt regarding the robustness of the TFC/F1 node. As a result, all competing generic names typified in this clade, including *Albonectria*, *Bisifusarium*, *Cyanonectria*, *Geejayessia*, *Gibberella*, *Neocosmospora*, and *Rectifusarium*, are recognized as *Fusarium*. With taxon discovery and phylogenomic datasets rapidly accumulating, we will continue to scrutinize and refine our taxonomic hypothesis and promote a scientifically robust and practical, user-friendly generic concept. As shown here, consideration of additional data has significantly strengthened the inference that the present circumscription of *Fusarium* is monophyletic (Geiser et al. 2013).

Taxonomy's purpose is to foster clear scientific communication, and the job of taxonomists is to refine it with that in mind. In doing so, taxonomists must not only recommend improved communication going forward but also weigh the costs of altering longstanding, effective communication (Booth 1978; Wingfield et al. 2012). This communication underlies international trade and agricultural biosecurity, pesticide and crop cultivar registration, and accurate identification and reporting of etiological agents essential for plant, animal, and human disease management. In some cases, scientific evidence and practical merit require inconvenient disruptions of and changes in taxonomic usage to accommodate nomenclatural rules and scientific rigor. As spelled out here and in Geiser et al. (2013), we assert that inclusion of the FSSC in genus *Neocosmospora* rather than *Fusarium* is not such a case. In this age, when molecular phylogenetics is informing a vastly improved taxonomy, the *Fusarium* community is fortunate that the genus-level taxonomy is supported by a phylogenetically rigorous, nomenclaturally sound, and user-friendly solution allowing undisrupted unitary use of the name *Fusarium*. In the interest of a robust taxonomy that facilitates communication, we welcome cogent, data-driven alternative taxonomic hypotheses that fully consider the scientific, nomenclatural, and practical ramifications.

APPENDIX

A list of taxonomic changes follows (Aoki et al. 2020):

Fusarium acutisporum (Sand.-Den. & Crous) O'Donnell, Geiser, Kasson & T. Aoki, Index Fungorum 440: 1. 2020. [IF 557667]

≡ *Neocosmospora acutispora* Sand.-Den. & Crous, Persoonia 43:108. 2019. [MB 831170]

Fusarium ambrosium (Gadd & Loos) Agnihothr. & Nirenberg, Stud. Mycol. 32:98. 1990. [MB 130225]

≡ *Monacrosporium ambrosium* Gadd & Loos, Trans. Br. Mycol. Soc. 31:17. 1947. [MB 288427]
≡ *Neocosmospora ambrosia* (Gadd & Loos) L. Lombard & Crous, Stud. Mycol. 80:227. 2015. [MB 810957]
Note: Also known as FSSC 19.

Fusarium amplum (Sand.-Den. & Crous) O'Donnell, Geiser, Kasson & T. Aoki, Index Fungorum 440:1. 2020. [IF 557668]

≡ *Neocosmospora ampla* Sand.-Den. & Crous, Persoonia 43:110. 2019. [MB 831171]

Fusarium bataticola (Sand.-Den. & Crous) O'Donnell, Geiser, Kasson & T. Aoki, Index Fungorum 440:1. 2020. [IF 557670]

≡ *Neocosmospora bataticola* Sand.-Den. & Crous, Persoonia 43:112. 2019. [MB 831172]
Note: Also known as FSSC 23.
= *Neocosmospora striata* Udagawa & Y. Horie, Trans. Mycol. Soc. Japan 16:340. 1975. [MB 318599] (non-*Fusarium striatum* Sherb. 1915 [MB 240201])
= *Neocosmospora parva* Mahoney, Mycologia 68:1111. 1976. [MB 318598]
= *Fusarium solani* f. *batatas* T.T. McClure, Phytopathology 41:75. 1951. [MB 537090] (non-*Fusarium batatas* Wollenw. 1914. [MB 175963])
Note: Also known as *Nectria haematococca* mating population II (NhMPII).

Fusarium bomiense (Z.Q. Zeng & W.Y. Zhuang) O'Donnell, Geiser, Kasson & T. Aoki, Index Fungorum 440:1. 2020. [IF 557671]

≡ *Neocosmospora bomiensis* Z.Q. Zeng & W.Y. Zhuang, Phytotaxa 319(2):177. 2017. [MB 570412]

Fusarium borneense (Petr.) O'Donnell, Geiser, Kasson & T. Aoki, Index Fungorum 440:1. 2020. [IF 557672]

≡ *Neocosmospora borneensis* (Petr.) Sand.-Den. & Crous, Persoonia 43:115. 2019. [MB 831173]
≡ *Nectria borneensis* Petr., Sydowia 8:20. 1954. [MB 301755]
Note: Also known as FSSC 30.

Fusarium bostrycoides Wollenw. & Reinking, Phytopathology 15(3):166. 1925. [MB 258714]

≡ *Neocosmospora bostrycoides* (Wollenw. & Reinking) Sand.-Den., L. Lombard & Crous, Persoonia 43:115. 2019. [MB 831174]
Note: Also known as FSSC 25.

Fusarium breve (Sand.-Den. & Crous) O'Donnell, Geiser, Kasson & T. Aoki, Index Fungorum 440:1. 2020. [IF 557673]

≡ *Neocosmospora brevis* Sand.-Den. & Crous, Persoonia 43:119. 2019. [MB 831176]
Note: Also known as FSSC 15.

Fusarium breviconum (Wollenw.) O'Donnell, Geiser, Kasson & T. Aoki, Index Fungorum 440:1. 2020. [IF 557674]

≡ *Hypomyces haematococcus* var. *breviconus* Wollenw., Fusaria autographice delineata 3:828. 1930. [MB 373029]
≡ *Neocosmospora brevicona* (Wollenw.) Sand.-Den. & Crous, Persoonia 43:117. 2019. [MB 831175]
≡ *Nectria haematococca* var. *brevicona* (Wollenw.) Gerlach, *Fusarium*: Diseases, Biology, and Taxonomy (State College), p. 422. 1981. [MB 117167]
= *Fusarium solani* var. *minus* Wollenw., Die Fusarien, ihre Beschreibung, Schadwirkung und Bekämpfung (Berlin). p. 134. 1935. [MB 185066]

Fusarium catenatum (Sand.-Den. & Crous) O'Donnell, Geiser & T. Aoki, Index Fungorum 440:1. 2020. [IF 557675]

≡ *Neocosmospora catenata* Sand.-Den. & Crous, Persoonia 41:115. 2018. [MB 822898]
Note: Also known as FSSC 43.

Fusarium crassum (Sand.-Den. & Crous) O'Donnell, Geiser, Kasson & T. Aoki, Index Fungorum 440:1. 2020. [IF 557676]

≡ *Neocosmospora crassa* Sand.-Den. & Crous, Persoonia 43:122. 2019. [MB 831177])
Note: Also known as FSSC 34.

Fusarium croci (Guarnaccia, Sand.-Den. & Crous) O'Donnell, Geiser & T. Aoki, Index Fungorum 440:1. 2020. [IF 557677]

≡ *Neocosmospora croci* Guarnaccia, Sand.-Den. & Crous, Persoonia 40:17. 2017. [MB 820251]

Fusarium cryptoseptatum (Sand.-Den. & Crous) O'Donnell, Geiser, Kasson & T. Aoki, Index Fungorum 440:1. 2020. [IF 557678]

≡ *Neocosmospora cryptoseptata* Sand.-Den. & Crous, Persoonia 43:122. 2019. [MB 831178]

Fusarium cucurbiticola O'Donnell, Geiser, Kasson & T. Aoki, Index Fungorum 440:2. 2020. [IF 557679]

≡ *Neocosmospora cucurbitae* Sand.-Den., L. Lombard & Crous, Persoonia 43:125. 2019. [MB 831179] (non-*Fusarium cucurbitae* Taubenh. 1920 [MB 509348])
= *Fusarium solani* f. *cucurbitae* W.C. Snyder & H.N. Hansen, Amer. J. Bot. 28:740. 1941. [MB 346145]
= *Fusarium solani* f. sp. *cucurbitae* W.C. Snyder & H.N. Hansen, Root rots caused by Phycomycetes 28:740. 1941. [MB 434083]
= *Hypomyces solani* f. *cucurbitae* W.C. Snyder & H.N. Hansen, Amer. J. Bot. 28:741. 1941. [MB 346179]
≡ *Nectria haematococca* var. *cucurbitae* (W.C. Snyder & H.N. Hansen) Dingley, New Zealand J. Agric. Res. 4:337. 1961. [MB 349909]
≡ *Nectria solani* f. *cucurbitae* (W.C. Snyder & H.N. Hansen) G.R.W. Arnold, Z. Pilzk. 37:193. 1972. [MB 348526]
Note: Also known as *Nectria haematococca* mating population I (NhMPI) and FSSC 10.

Fusarium cyanescens (G.A. de Vries, de Hoog & Bruyn) O'Donnell, Geiser & T. Aoki, Index Fungorum 440:2. 2020. [IF 557680]

≡ *Phialophora cyanescens* G.A. de Vries, de Hoog & Bruyn, Antonie van Leeuwenhoek 50(2):150. 1984. [MB 107121]
≡ *Neocosmospora cyanescens* (G.A. de Vries, de Hoog & Bruyn) Summerbell, Schroers & Scott, Biology of Microfungi (Cham) 183. 2016. [MB 813864]
≡ *Cylindrocarpon cyanescens* (G.A. de Vries, de Hoog & Bruyn) Sigler, J. Clin. Microbiol. 29:1858. 1991. [MB 499349]
Note: Also known as FSSC 27.

Fusarium diminutum (Sand.-Den. & Crous) O'Donnell, Geiser, Kasson & T. Aoki, Index Fungorum 440:2. 2020. [IF 557681]

≡ *Neocosmospora diminuta* Sand.-Den. & Crous, Persoonia 43:127. 2019. [MB 831180]
Note: Also known as FSSC 39.

Fusarium euwallaceae S. Freeman, Z. Mendel, T. Aoki & O'Donnell, Mycologia 105(6):1599. 2013. [MB 803293]

≡ *Neocosmospora euwallaceae* (S. Freeman, Z. Mendel, T. Aoki & O'Donnell) Sand.-Den., L. Lombard & Crous, Persoonia 43:129. 2019. [MB 831181]

Fusarium falciforme (Carrión) Summerb. & Schroers, J. Clin. Microbiol. 40(8):2872. 2002. [MB 483950]

≡ *Cephalosporium falciforme* Carrión, Mycologia 43: 523. 1951. [MB 294124]

≡ *Acremonium falciforme* (Carrión) W. Gams, Cephalosporium-artige Schimmelpilze (Stuttgart):139. 1971. [MB 308145]
≡ *Neocosmospora falciformis* (Carrión) L. Lombard & Crous, Stud. Mycol. 80:227. 2015. [MB 810958]
Note: Also known as FSSC 3 + 4.

Fusarium ferrugineum (Sand.-Den. & Crous) O'Donnell, Geiser, Kasson & T. Aoki, Index Fungorum 440:2. 2020. [IF 557682]

≡ *Neocosmospora ferruginea* Sand.-Den. & Crous, Persoonia 43:130. 2019. [MB 831182]

Fusarium haematococcum Nalim, Samuels & Geiser, Mycologia 103(6):1322. 2011. [MB 519837]

= *Nectria haematococca* Berk. & Broome var. *haematococca*, J. Linn. Soc. Bot. 14:116. 1875. [MB 417425]
≡ *Neocosmospora haematococca* (Berk. & Broome) Nalim, Samuels & Geiser, Mycologia 103(6):1322. 2011. [MB 519835]
Note: Also known as FSSC 28.

Fusarium helgardnirenbergiae O'Donnell, Geiser, Kasson & T. Aoki, Index Fungorum 440:2. 2020. [IF 557683]

≡ *Neocosmospora nirenbergiana* Sand.-Den. & Crous, Persoonia 43:145. 2019. [MB 831189] (non-*Fusarium nirenbergiae* L. Lombard & Crous 2018. [MB 826845])
Etymology: In honor of Dr. Helgard Nirenberg.

Fusarium hengyangense (Z.Q. Zeng & W.Y. Zhuang) O'Donnell, Geiser, Kasson & T. Aoki, Index Fungorum 440:2. 2020. [IF 557684]

≡ *Neocosmospora hengyangensis* Z.Q. Zeng & W.Y. Zhuang, Phytotaxa 319: 179. 2017. [MB 570411]

Fusarium hypothenemi (Sand.-Den. & Crous) O'Donnell, Geiser, Kasson & T. Aoki, Index Fungorum 440:2. 2020. [IF 557685]

≡ *Neocosmospora hypothenemi* Sand.-Den. & Crous, Persoonia 43:132. 2019. [MB 831183]
Note: Also known as FSSC 38.

Fusarium illudens C. Booth, The genus *Fusarium*: 54. 1971. [MB 314215]

= *Neocosmospora illudens* (Berk.) L. Lombard & Crous, Stud. Mycol. 80:227. 2015. [MB 810959]
≡ *Nectria illudens* Berk., The botany of the Antarctic Voyage II, Flora Novae-Zealandiae 2:203. 1855. [MB 170632]

Fusarium kelerajum Samuels, Nalim & Geiser, Mycologia 103(6):1326. 2011. [MB 519856]

= *Neocosmospora keleraja* Samuels, Nalim & Geiser, Mycologia 103(6):1326. 2011. [MB 519854]

Fusarium keratoplasticum Geiser, O'Donnell, Short & Ning Zhang, Fungal Genetics Biol. 53:68. 2013. [MB 802390]

≡ *Neocosmospora keratoplastica* (Geiser, O'Donnell, Short & Ning Zhang) Sand.-Den. & Crous, Persoonia 41: 120. 2017. [MB 822900]
Note: Also known as FSSC 2.

Fusarium kuroshium (F. Na, J.D. Carrillo & A. Eskalen ex Sand.-Denis & Crous) O'Donnell, Geiser, Kasson & T. Aoki, Index Fungorum 440:2. 2020. [IF 557669]

≡ *Neocosmospora kuroshio* F. Na, J.D. Carrillo & A. Eskalen ex Sand.-Den. & Crous, Persoonia 43:137. 2019. [MB 831184]
≡ (*Fusarium kuroshium* F. Na, J.D. Carrillo & A. Eskalen, Plant Dis. 102:1159. 2018. Nom. inval., Art. 40.7 [MB 821907])

Fusarium kurunegalense Samuels, Nalim & Geiser, Mycologia 103(6):1323. 2011. [MB 519848]

= *Neocosmospora kurunegalensis* Samuels, Nalim & Geiser, Mycologia 103(6):1324. 2011. [MB 519847]

Fusarium lichenicola C. Massal., Annales Mycologici 1(3):223. 1903. [MB 200576]

≡ *Neocosmospora lichenicola* (C. Massal.) Sand.-Den. & Crous, Persoonia 41:120. 2018. [MB 822901]
≡ *Bactridium lichenicola* (C. Massal.) Wollenw. [as '*lichenicolum*'], Fusaria autographica delineata 1: no. 456 (1916). [MB 101879]
≡ *Cylindrocarpon lichenicola* (C. Massal.) D. Hawksw., Bull. Br. Mus. Nat. Hist., Bot. 6(3):273. 1979. [MB 312456]
Note: Also known as FSSC 16.

Fusarium liriodendri (Sand.-Den. & Crous) O'Donnell, Geiser, Kasson & T. Aoki, Index Fungorum 440:2. 2020. [IF 557686]

≡ *Neocosmospora liriodendri* Sand.-Den. & Crous, Persoonia 43:139. 2019. [MB 831185]
Note: Also known as FSSC 24.

Fusarium macrosporum (Sand.-Den., Guarnaccia & Polizzi) O'Donnell, Geiser & T. Aoki, Index Fungorum 440:2. 2020. [IF 557687]

≡ *Neocosmospora macrospora* Sand.-Den., Guarnaccia & Polizzi, Persoonia 40:21. 2017. [MB 820253]

Fusarium mahasenii Samuels, Nalim & Geiser, Mycologia 103(6):1325. 2011. [MB 519853]

= *Neocosmospora mahasenii* Samuels, Nalim & Geiser, Mycologia 103(6):1325. 2011. [MB 519852]

Fusarium martii Appel & Wollenw., Arbeiten Kaiserl. Biol. Anst. Land- u. Forstw. 8:83. 1910. [MB 249096]

≡ *Neocosmospora martii* (Appel & Wollenw.) Sand.-Den. & Crous, Persoonia 43:142. 2019. [MB 831187]

Fusarium metavorans Al-Hatmi, S.A. Ahmed & de Hoog, Med. Mycol. 56:S147. 2018. [MB 821742]

≡ *Neocosmospora metavorans* (Al-Hatmi, S.A. Ahmed & de Hoog) Sand.-Den. & Crous, Persoonia 41:121. 2018. [MB 823687]
Note: Also known as FSSC 6.

Fusarium mori (Sand.-Den. & Crous) O'Donnell, Geiser, Kasson & T. Aoki, Index Fungorum 440:2. 2020. [IF 557688]

≡ *Neocosmospora mori* Sand.-Den. & Crous, Persoonia 43:143. 2019. [MB 831188]
(*Fusarium solani* f. *mori* Sawada, Special Publication College of Agriculture, National Taiwan University 8:222. 1959. Nom. inval., Art. 39.1 [MB 353476])
(*Hypomyces solani* f. *mori* Y. Sakurai & Matuo, Ann. Phytophathol. Soc. Japan 24:222. 1959. Nom. inval., Art. 39.1 [MB 353542])
Note: Also known as *Nectria haematococca* mating population III (NhMPIII) and FSSC 17.

Fusarium neocosmosporiellum O'Donnell & Geiser, Phytopathology 103(5):405. 2013. [MB 800615]

≡ *Neocosmospora vasinfecta* E.F. Sm., Bulletin Div. Veg. Phsyiol. Pathol. U.S. Dept. Agric. 17:45. 1899. [MB 241907] (non-*Fusarium vasinfectum* G.F. Atk. 1892. [MB 225413])
Typification (for *Neocosmospora vasinfecta*): Lectotype: USA: Pl. V, Figures 1 and 2 as collected on 8 October 1895 (Smith, Bull. U.S. Dept Agric. 17, 1899; Sandoval-Denis et al. 2019) [MBT 387252]; Neotype: USA, SOUTH CAROLINA: Cameron, a dried specimen on cotton (*Gossypium hirsutum*), collected on October 1902, *William A. Orton* (BPI 630336, Cannon & Hawksworth 1984) [IF 596775]; Epitype: USA, ILLINOIS: southern area, isolated from a cyst of *Heterodera*

glycines in a soil sample from soybean field, 6 April 1983, *Lori M. Carris*, CARRIS E-8-8 (BPI 910920, a dried culture of NRRL 22166, Aoki et al. 2020 [IF 557666]; Carris and Glawe 1989). Ex-epitype culture NRRL 22166 = ATCC 62199.

= *Neocosmospora vasinfecta* E.F. Sm. var. *africana* (Arx) P.F. Cannon & D. Hawksw., Trans. Br. Mycol. Soc. 82(4):676. 1984. [MB 116939]

≡ *Neocosmospora africana* Arx, Antonie van Leeuwenhoek 21(2):161. 1955. [MB 301806]

Note: Also known as FSSC 8.

Fusarium ngaiotongaense O'Donnell, Geiser, Kasson & T. Aoki, Index Fungorum 440:3. 2020. [IF 557689]

≡ *Neocosmospora longissima* Sand.-Den. & Crous, Persoonia 43:141. 2019. [MB 831186] (non-*Fusarium longissimum* Sacc. & P. Syd. 1899 [MB 229470])

Etymology: *Ngaiotonga* + *-ensis* from the name of its type locality.

Fusarium noneumartii (Sand.-Den. & Crous) O'Donnell, Geiser, Kasson & T. Aoki, Index Fungorum 440:3. 2020. [IF 557690]

≡ *Neocosmospora noneumartii* Sand.-Den. & Crous, Persoonia 43:145. 2019. [MB 831190]

Note: Also known as FSSC 42.

Fusarium oblongum (Sand.-Den. & Crous) O'Donnell, Geiser, Kasson & T. Aoki, Index Fungorum 440:3. 2020. [IF 557691]

≡ *Neocosmospora oblonga* Sand.-Den. & Crous, Persoonia 43:148. 2019. [MB 831191]

Note: Also known as FSSC 29.

Fusarium oligoseptatum T. Aoki, Kasson, S. Freeman, Geiser & O'Donnell, Fungal Syst. Evol. 1:29. 2018. [MB 822305]

≡ *Neocosmospora oligoseptata* (T. Aoki et al.) Sand.-Den. & Crous, Persoonia 43:149. 2019. [MB 831192]

Fusarium ornamentatum (M.A.F. Barbosa) O'Donnell, Geiser & T. Aoki, Index Fungorum 440:3. 2020. [IF 557692]

≡ *Neocosmospora ornamentata* M.A.F. Barbosa, Garcia de Orta, Revista da Junta de Investigações do Ultramar (Ministério de Ultramar, Lisboa), sér. Est. agron. 13(1):17. 1965. [MB 335130]

Fusarium paraeumartii (Sand.-Den. & Crous) O'Donnell, Geiser, Kasson & T. Aoki, Index Fungorum 440:3. 2020. [IF 557693]

≡ *Neocosmospora paraeumartii* Sand.-Den. & Crous, Persoonia 43:149. 2019. [MB 831193]

Fusarium parceramosum (Sand.-Den. & Crous) O'Donnell, Geiser, Kasson & T. Aoki, Index Fungorum 440:3. 2020. [IF 557694]

≡ *Neocosmospora parceramosa* Sand.-Den. & Crous, Persoonia 43:151. 2019. [MB 831194]

Note: Also known as FSSC 18.

Fusarium perseae (Sand.-Den. & Guarnaccia) O'Donnell, Geiser & T. Aoki, Index Fungorum 440:3. 2020. [IF 557695]

≡ *Neocosmospora perseae* Sand.-Den. & Guarnaccia, Fungal Syst. Evol. 1:136. 2018. [MB 824587]

Fusarium petroliphilum (Q.T. Chen & X.H. Fu) Geiser, O'Donnell, D.P.G. Short & N. Zhang, Fungal Genet. Biol. 53:69. 2013. [MB 802539]

≡ *Fusarium solani* var. *petroliphilum* Q.T. Chen & X.H. Fu, Acta Mycol. Sinica, Suppl.: 330. 1987. [MB 127720]

≡ *Neocosmospora petroliphila* (Q.T. Chen & X.H. Fu) Sand.-Den. & Crous, Persoonia 41:121. 2018. [MB 822902]

Note: Also known as *Nectria haematococca* mating population V (NhMPV) and FSSC 1.

Fusarium phaseoli (Burkh.) T. Aoki & O'Donnell, Mycologia 95(4):671. 2003. [MB 488914]

≡ *Fusarium martii* f. *phaseoli* Burkh., Mem. Cornell U. Agr. Exp. Station 26:1007. 1919. [MB 489076]

≡ *Neocosmospora phaseoli* (Burkh.) L. Lombard & Crous, Stud. Mycol. 80:227. 2015. [MB 810962]

Also, we recognize the following six valid existing species as distinct from *F. phaseoli*:

Fusarium tucumaniae T. Aoki, O'Donnell, Yosh. Homma & Lattanzi, Mycologia 95(4):664. 2003. [MB 489463]

≡ *Neocosmospora tucumaniae* (T. Aoki et al.) L. Lombard & Crous, Stud. Mycol. 80:228. 2015. [MB 810966]

Fusarium virguliforme O'Donnell & T. Aoki, Mycologia 95:667. 2003. [MB 489315]

≡ *Neocosmospora virguliformis* (O'Donnell & T. Aoki) L. Lombard & Crous, Stud. Mycol. 80:228. 2015. [MB 810967]

Fusarium brasiliense T. Aoki & O'Donnell, Mycoscience 46:166. 2005. [MB 338753]

Fusarium cuneirostrum O'Donnell & T. Aoki, Mycoscience 46:170. 2005. [MB 341392]

Fusarium crassistipitatum Scandiani, T. Aoki & O'Donnell, Mycoscience 53:171. 2011. [MB 561257]

Fusarium azukicola T. Aoki, H. Suga, F. Tanaka, Scandiani & O'Donnell, Mycologia 104:1075. 2012. [MB 563147]

Fusarium piperis (F.C. Albuq.) O'Donnell, Geiser, Kasson & T. Aoki, Index Fungorum 440:3. 2020. [IF 557696]

≡ *Neocosmospora piperis* (F.C. Albuq.) Sand.-Den. & Crous, Persoonia 43: 152. 2019. [MB 831195]

≡ *Fusarium solani* f. *piperis* F.C. Albuq., Circular do Instituto Agronómico do Norte 5:19. 1961. [MB 349447]

Note: Also known as FSSC 31.

Fusarium plagianthi (Dingley) O'Donnell & Geiser, Phytopathology 103(5):404. 2013. [MB 800613]

≡ *Nectria plagianthi* Dingley, Trans. Proc. Royal Soc. New Zealand 79: 196. 1951. [MB 301780]

≡ *Neocosmospora plagianthi* (Dingley) L. Lombard & Crous, Stud. Mycol. 80:227. 2015. [MB 810963]

Fusarium protoensiforme (Sand.-Den. & Crous) O'Donnell, Geiser, Kasson & T. Aoki, Index Fungorum 440:3. 2020. [IF 557697]

≡ *Neocosmospora protoensiformis* Sand.-Den. & Crous, Persoonia 43:156. 2019. [MB 831197]

Note: Also known as FSSC 32.

Fusarium pseudensiforme Samuels, Nalim & Geiser, Mycologia 103(6):1323. 2011. [MB 519839]

= *Neocosmospora pseudensiformis* Samuels, Nalim & Geiser, Mycologia 103(6):1323. 2011. [MB 519838]

Note: Also known as FSSC 33.

Fusarium pseudoradicicola (Sand.-Den. & Crous) O'Donnell, Geiser, Kasson & T. Aoki, Index Fungorum 440:3. 2020. [IF 557698]

≡ *Neocosmospora pseudoradicicola* Sand.-Den. & Crous, Persoonia 43:157. 2019. [MB 831198]

Note: Also known as FSSC 37.

Fusarium pseudotonkinense (Sand.-Den. & Crous) O'Donnell, Geiser, Kasson & T. Aoki, Index Fungorum 440:3. 2020. [IF 557699]

≡ *Neocosmospora pseudotonkinensis* Sand.-Den. & Crous, Persoonia 43:159. 2019. [MB 831199]

Fusarium quercinum O'Donnell, Geiser, Kasson & T. Aoki, Index Fungorum 440:4. 2020. [IF 557700]

≡ *Neocosmospora quercicola* Sand.-Den. & Crous, Persoonia 43:159. 2019. [MB 831200] (non-*Fusarium quercicola* Oudem. 1902 [MB 204737])

Etymology: *quercinus* (of oak), from the name of the original host plant, *Quercus cerris*.

Note: Also known as FSSC 14.

Fusarium ramosum (Batista & H. Maia) O'Donnell, Geiser & T. Aoki, Index Fungorum 440:4. 2020. [IF 557701]

≡ *Hyaloflorea ramosa* Batista & H. Maia, Anais Soc. Biol. Pernambuco 13(1):155. 1955. [MB 298527]

≡ *Neocosmospora ramosa* (Batista & H. Maia) L. Lombard & Crous, Stud. Mycol. 80:227. 2015. [MB 810242]

Fusarium rectiphorus Samuels, Nalim & Geiser, Mycologia 103(6):1324. 2011. [MB 519851]

= *Neocosmospora rectiphora* Samuels, Nalim & Geiser, Mycologia 103(6):1324. 2011. [MB 519850]

= *Neocosmospora bomiensis* Z.Q. Zeng & W.Y. Zhuang, Phytotaxa 319:177. 2017. [MB 570412]

Fusarium regulare (Sand.-Den. & Crous) O'Donnell, Geiser, Kasson & T. Aoki, Index Fungorum 440:4. 2020. [IF 557702]

≡ *Neocosmospora regularis* Sand.-Den. & Crous, Persoonia 43:162. 2019. [MB 831201]

Fusarium rhizophorae (Dayarathne) O'Donnell, Geiser, Kasson & T. Aoki, Index Fungorum 440:4. 2020. [IF 557703]

≡ *Neocosmospora rhizophorae* Dayarathne, in Dayarathne, Jones, Maharachchikumbura, Devadatha, Sarma, Khongphinitbunjong, Chomnunti & Hyde, Mycosphere 11(1): 112. 2020. [MB 556595]

Fusarium riograndense Dallé Rosa, Ramirez-Castrillón, P. Valente, Fuent., van Diepen. & Goldani, J. Mycol. Med. 28:33. [MB 814515]

≡ *Neocosmospora riograndensis* (Dallé Rosa et al.) Sand.-Den. & Crous, Persoonia 43:165. 2019. [MB 831202]

Fusarium samuelsii (Sand.-Den. & Crous) O'Donnell, Geiser, Kasson & T. Aoki, Index Fungorum 440:4. 2020. [IF 557704]

≡ *Neocosmospora samuelsii* Sand.-Den. & Crous, Persoonia 43:165. 2019. [MB 831204]

Fusarium silvicola (Sand.-Den. & Crous) O'Donnell, Geiser, Kasson & T. Aoki, Index Fungorum 440:4. 2020. [IF 557705]

≡ *Neocosmospora silvicola* Sand.-Den. & Crous, Persoonia 43:167. 2019. [MB 831205]

= *Fusarium solani* f. *robiniae* Matuo & Y. Sakurai, Ann. Phytopathol. Soc. Japan 30:35. 1965. [MB 348448] (non-*Fusarium robiniae* Pass. 1891. [MB 203747])

= *Hypomyces solani* f. *robiniae* Matuo & Y. Sakurai, Ann. Phytophathol. Soc. Japan 30:35. 1965. [MB 349586]

Note: Also known as FSSC 13.

≡ *Nectria solani* f. *robiniae* (Matuo & Y. Sakurai) G.R.W. Arnold, Z. Pilzk. 37(1-4):193. 1972. [MB 348527]

Note: Also known as *Nectria haematococca* mating population VII (NhMPVII).

Fusarium solani (Mart.) Sacc., Michelia 2(7):296. 1881. [MB 190352]

≡ *Fusisporium solani* Mart., Die Kartoffel-Epidemie der letzten Jahre oder die Stockfäule und Räude der Kartoffeln: 20. 1842. [MB 194746]

≡ *Neocosmospora solani* (Mart.) L. Lombard & Crous, Stud. Mycol. 80:228. 2015. [MB 810964]

= *Neocosmospora rubicola* L. Lombard & Crous, Stud. Mycol. 80:227. 2015. [MB 810243]

Note: Also known as FSSC 5.

Fusarium solani-melongenae O'Donnell, Geiser, Kasson & T. Aoki, Index Fungorum 440:4. 2020. [IF 557706]

≡ *Neocosmospora ipomoeae* (Halst.) L. Lombard & Crous, Stud. Mycol. 80:227. 2015. [MB 810960]

≡ *Nectria ipomoeae* Halst., Rep. N. J. State Agric. Exp. Stat. 12: 281 (1891) [MB 210931] (non-*Fusarium ipomoeae* M.M. Wang, Qian Chen & L. Cai 2019 [MB 829538], non-*Fusarium batatas* Wollenw. 1914 [MB 175963])

≡ *Hypomyces ipomoeae* (Halst.) Wollenw., Phytopathology 3(1):34. 1913. [MB 212639]

≡ *Haematonectria ipomoeae* (Halst.) Samuels & Nirenberg, in Rossman, Samuels, Rogerson & Lowen, Stud. Mycol. 42:136. 1999. [MB 460446]

Etymology: From the correct name of its original plant host, *Solanum melongena* (Halstead 2015), represented by its holotype, BPI 552416 (Sandoval-Denis et al. 2019).

Fusarium spathulatum (Sand.-Den. & Crous) O'Donnell, Geiser, Kasson & T. Aoki, Index Fungorum 440:4. 2020. [IF 557707]

≡ *Neocosmospora spathulata* Sand.-Den. & Crous, Persoonia 43:171. 2019. [MB 831206]

Note: Also known as FSSC 26.

Fusarium sphaerosporum Q.T. Chen & X.H. Fu, Acta Mycol. Sin., Suppl. 1:331. 1987 [MB 127721]

≡ *Neocosmospora sphaerospora* (Q.T. Chen & X.H. Fu) Sand.-Den. & Crous, Persoonia 43:173. 2019. [MB 832096]

Fusarium spinulosum (Pfenning) O'Donnell, Geiser, Kasson & T. Aoki, Index Fungorum 440:4. 2020. [IF 557708]

≡ *Neocosmospora spinulosa* Pfenning, Sydowia 47:66. 1995. [MB 413567]

Fusarium stercicola Šišić, Al-Hatmi, Baćanović-Šišić, S.A. Ahmed & Finckh, Antonie van Leeuwenhoek 111:1793. 2018. [MB 823581]

≡ *Neocosmospora stercicola* (Šišić et al.) Sand.-Den. & Crous, Persoonia 43:173. 2019. [MB 831207]

= *Fusarium witzenhausenense* Šišić et al., Antonie van Leeuwenhoek 111:1795. 2018. [MB 823582]

Fusarium suttonianum (Sand.-Den. & Crous) O'Donnell, Geiser & T. Aoki, Index Fungorum 440:4. 2020. [IF 557709]

≡ *Neocosmospora suttoniana* Sand.-Den. & Crous, Persoonia 41:123. 2018. [MB 822903]

Note: Also known as FSSC 20.

Fusarium tenuicristatum (S. Ueda & Udagawa) O'Donnell, Geiser & T. Aoki, Index Fungorum 440:4. 2020. [IF 557710]

≡ *Neocosmospora tenuicristata* S. Ueda & Udagawa, Mycotaxon 16(2):387. 1983. [MB 109113]

= *Neocosmospora boninensis* Udagawa, Y. Horie & P.F. Cannon, Sydowia 41:350. 1989. [MB 125987]

Fusarium theobromae Appel & Strunk, Centralbl. Bakteriol. Parasitenk., 1. Abt. 13:685. 1904. [MB 235605]

≡ *Neocosmospora theobromae* (Appel & Strunk) Sand.-Den. & Crous, Persoonia 43:174. 2019. [MB 831208]

Fusarium tonkinense (Bugnic.) O'Donnell, Geiser & T. Aoki, Index Fungorum 440:4. 2020. [IF 557711]

≡ *Cylindrocarpon tonkinense* Bugnic., Encyclopédie Mycologique 11:181. 1939. [MB 255134]

≡ *Neocosmospora tonkinensis* (Bugnic.) Sand.-Den. & Crous, Persoonia 41:126. 2018. [MB 822904]

≡ *Fusarium ershadii* Papizadeh, van Diepeningen & Zamanizadeh, Eur. J. Plant Pathol. 151:693. 2018. (nom. illegit. as a superfluous name, Art 52.1). [MB 817602]

Note: Also known as FSSC 9.

Fusarium vanettenii O'Donnell, Geiser, Kasson & T. Aoki, Index Fungorum 440:5. 2020. [IF 557712]

≡ *Neocosmospora pisi* (F.R. Jones) Sand.-Den. & Crous, Persoonia 43:154. 2019. [MB 831196]

≡ *Fusarium martii* var. *pisi* F.R. Jones, J. Agric. Res. 26:459. 1923. [MB 270614]

≡ *Fusarium solani* f. *pisi* (F.R. Jones) W.C. Snyder & H.N. Hansen, Am. J. Bot. 28:740. 1941. [MB 351714]

(*Fusarium pisi* (F.R. Jones) A. Šišić et al. Sci. Rep. 8:2. 2018. Nom. inval., Art. 42.1 [MB 824719])

Note: Also known as *Nectria haematococca* mating population VI (NhMPVI) and FSSC 11.

Etymology: In honor of the late Hans D. Van Etten, whose laboratory conducted extensive studies on this species, making the first connection between plant pathogenicity and the fungal accessory genome.

Fusarium venezuelense O'Donnell, Geiser, Kasson & T. Aoki, Index Fungorum 440:5. 2020. [IF 557713]

≡ *Neocosmospora robusta* Sand.-Den. & Crous, Persoonia 43:165. 2019. [MB 831203] (non-*Fusarium robustum* Gerlach 1977 [MB 314220])

Etymology: *Venezuela* + *-ensis* from the name of its type locality.

Fusarium waltergamsii O'Donnell, Geiser & T. Aoki, Index Fungorum 440:5. 2020. [IF 557714]

≡ *Neocosmospora gamsii* Sand.-Den. & Crous, Persoonia 41:116. 2018. [MB 822899] (non-*Fusarium gamsii* Torbati, Arzanlou, Sand.-Den. 2019 [MB 825228])

Etymology: In honor of the late Dr. Walter Gams.

Note: Also known as FSSC 7.

Fusarium yamamotoi O'Donnell, Geiser, Kasson & T. Aoki, Index Fungorum 440:5. 2020. [IF 557715]

≡ *Nectria elegans* W. Yamam. & Maeda, Sci. Rep. Hyogo Univ. Agric. 3:15. 1957. [MB 301759] (non-*Fusarium elegans* Appel & Wollenw. 1910 [MB 451612])

≡ *Neocosmospora elegans* (W. Yamam. & Maeda) Sand.-Den. & Crous, Persoonia 43:127. 2019. [MB 831226]

(*Fusarium elegans* W. Yamamoto & Maeda, Trans. Mycol. Soc. Japan 3:115. 1962. Nom. illegit., Art 53.1 [MB 330986])

(*Fusarium solani* f. *xanthoxyli* Y. Sakurai & Matuo, Ann. Phytopathol. Soc. Japan 26:117. 1961. Nom. inval., Art. 39.1 [MB 350973])

(*Hypomyces solani* f. *xanthoxyli* Y. Sakurai & Matuo, Ann. Phytopathol. Soc. Japan 26:117. 1961. Nom. inval., Art. 39.1 [MB 350974])

Note: Also known as *Nectria haematococca* mating population IV (NhMPIV) and FSSC 22.

Etymology: in honor of the late Dr. Wataro Yamamoto who originally found *Nectria elegans* and studied trunk blight of *Zanthoyxlum piperitum*.

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