History of *Fusarium* Systematics

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In 1935, Wollenweber and Reinking published their monumental work on *Fusarium* taxonomy (30) that has become the standard reference on this subject, and all systems of *Fusarium* taxonomy published since 1935 are based on this publication. Wollenweber and Reinking began with approximately 1,000 named species of *Fusarium* and organized these into 16 sections:

Eupionnotes	*Arthrosporiella*
Macroconia	*Gibbosum*
Spicarioides	*Discolor*
Submicrocera	*Lateritium*
Pseudomicrocera	*Liseola*
Arachnites	*Elegans*
Sporotrichiella	*Martiella*
Roseum	*Ventricosum*

These sections contained 65 species, 55 varieties, and 22 forms. One can begin to appreciate the magnitude of this task by noting that Wollenweber and Reinking list 77 synonyms for *F. avenaceaum* alone, and 133 synonyms for *F. lateritium* and its teleomorph (30).

The characters used by Wollenweber and Reinking to separate sections were: the presence or absence of microconidia, the shape of microconidia, the presence or absence of chlamydospores, the location of chlamydospores–intercalary or terminal, the shape of macroconidia, and the shape of basal foot cells on the macroconidia. Sections were divided into species, varieties, and forms on the basis of the color of the stroma, the presence or absence of sclerotia, the number of septations in macroconidia, and the length and width of macroconidia. In section *Elegans,* great emphasis was placed on measurements of length and width of macroconidia; species, varieties, and forms were separated on the basis of a few micrometers of difference in length or width and of the number of septations in macroconidia. Each isolate studied was grown on beerwort agar, carrot decoction agar, oatmeal agar, rice mash, alfalfa stems, barley heads, and, in some cases, potato-dextrose agar and potato pieces. Observation of cultures grown on these media tended to emphasize differences rather than similarities and to exaggerate minor differences, such as length and width of macroconidia, that result in finer and finer separations at the species, variety, and form levels, as illustrated by the characters used to separate subsections in section *Elegans* (Table 1). This produced a system so complex that it is difficult or impossible to use it to construct a satisfactory practical key. Many of the characters used by Wollenweber and Reinking to separate species, varieties, and forms are not stable and can be altered readily by growing cultures on various media and under varying environmental conditions.

Two other problems also may be responsible in part for the complexity of this system. Cultural variation or mutation in *Fusarium* may not have been recognized by Wollenweber and Reinking (30), and since their cultures were not started from single conidia, a few of their species and many of their varieties and forms may be cultural mutants of *Fusarium* species. Examples may be *F. sublunatum* and *F. s.* var. *elongatum, F. trichothecioides, F. merismoides* var. *crassum, F. dimerum* var. *nectriodes,* and *F. d.* var. *violaceum.* In addition, some species may have been named on the basis of only one or two cultures. One must examine a large number of representative cultures of the organism to determine the range of variation that may occur within that organism. An examination of only one culture of a fungus cannot reveal the range of variation that may occur; it can, however, produce considerable confusion and difficulty for others attempting to identify these species.

Figure 1 shows the relationship of several other taxonomic systems to that of Wollenweber and Reinking (30) and to each other. *Fusarium* taxonomists often are divided into "lumpers" and "splitters." These terms explain the philosophy employed by taxonomists in determining *Fusarium* species but are not necessarily a reflection of the number of species recognized. In Figure 1 Wollenweber and Gerlach are "splitters" with additional "splitters" on the left and "lumpers" on the right. Gordon (9), Booth (3), and Nelson, Toussoun, and Marasas (22) are listed

TABLE 1. Characters used by Wollenweber and Reinking (30) to separate three subsections in section *Elegans*[a]

Subsection *Orthocera* (five species, six varieties, one form)
Sporodochia absent
Macroconidia 3 to 5 septate
Macroconidia 3–4 × 27–50 μm
Subsection *Constrictum* (one species, five varieties)
Sporodochia present
Macroconidia 3 to 5 septate
Macroconidia 3–3.7 × 30–55.5 μm
Subsection *Oxysporum* (four species, seven varieties, 11 forms)
Sporodochia present
Macroconidia 3 to 5 septate
Macroconidia 3.7–5 × 32–47 μm

Note that the major differences are in measurements of conidia, but there is overlap in the measurements between all sections.

in the middle because they have followed a more moderate philosophy or have combined the results of others with their own research to produce a taxonomic system.

Gerlach (6,7) worked in Wollenweber's laboratory at the Biologische Bundesanstalt, West Berlin, until he retired. Both his philosophy and techniques used in studying *Fusarium* and establishing new species placed him with the "splitters." This is evident from the 78 species that appear in his atlas recently published with Nirenberg (7), a well-illustrated work that uses excellent photographs and line drawings to supplement Wollenweber's original drawings included in part. Gerlach and Nirenberg grew cultures on the eight different media used by Wollenweber and Reinking and under conditions that accentuate differences. They concentrated on these differences rather than on similarities, with the result that a slight cultural difference may have been the basis for a new species or variety. New species were established based on a single culture and, in some cases, on a single mutant culture. This philosophy led to a complex taxonomic system that is difficult to use for the same reasons that Wollenweber and Reinking's system is difficult to use.

The systems of Raillo (23,24) and Bilai (1,2) are not as well understood as other systems (Fig. 1). Raillo studied morphological characters useful in taxonomy and concluded: the form of the apical cell was the guiding character in species determination; the incurvature of conidia, length of the apical cell, number of septa, and width of conidia were the characters used in separating subspecies and varieties; and cultural characters such as pigment, presence of sclerotia, and mode of spore formation were useful in separating forms only. She also studied variability in *Fusarium* by initiating cultures from single conidia and found that the form of the apical cell and the incurvature of conidia remained constant in cultures developed from single conidia; the number of septa was constant in isolates within a single-conidial culture; the length and width of conidia varied considerably in separate isolates within a single-conidial culture; the number of sclerotia varied greatly in separate isolates within a single-conidial culture; and the mode of spore formation (pionnotes, pseudo-pionnotes, and sporodochia) varied in separate isolates within a single-conidial culture.

Bilai (1,2), a Russian researcher, recognized the importance of cultural variation or mutation in *Fusarium* taxonomy. She did a critical analysis of several characters used in *Fusarium* taxonomy by studying experimental variability of individual isolates and establishing the range of variation for some species. In addition, she studied experimental morphogenesis in single-conidial isolates in culture, paying particular attention to the effects of temperature, moisture, length of growth period, and composition of the medium, as well as the method of germination and aging of conidia. Her results showed that the range of variability was greater than that accepted in the diagnosis of many species and often included the features of the whole section. On the basis of these results, she revised the taxonomy of the genus to include only nine sections, 26 species, and 29 varieties. Some of her changes, such as combining section *Liseola* with section *Elegans* and combining section *Gibbosum* with section *Discolor,* are difficult to understand. This system may have been used in Russia, although it has not been accepted and used in other parts of the world.

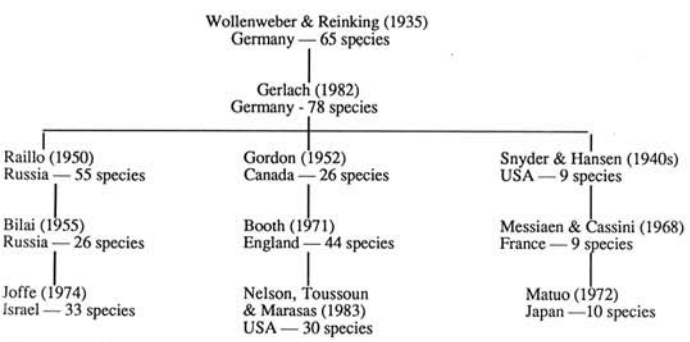

Fig. 1. Principal taxonomic systems for *Fusarium* species showing the relationship of several taxonomic systems to that of Wollenweber and Reinking.

Joffe (16) began working on *Fusarium* in the late 1940s in Russia and later emigrated to Israel and continued his work. He examined a large number of isolates of *Fusarium* from soil, wilting or decaying plants, and seed. These isolates were collected in the warm, semiarid climate of Israel and the cold climate of the U.S.S.R. Other isolates were received from research institutes in several countries. His philosophy and approach to *Fusarium* taxonomy is similar to that of Wollenweber and Reinking (30) and Gerlach (6,7). In fact, his so-called "modern system" appears to be simply a restatement of Wollenweber and Reinking's sections and species with the addition of some names by Gerlach. He included 13 sections, 33 species, and 14 varieties.

Gordon worked in Canada from the 1930s to the 1960s (8–15) with *Fusarium* species isolated from cereal seed, various host plants, and soil from both temperate and tropical geographic areas. His system of taxonomy is closer to that of Wollenweber and Reinking (30) than to that of Snyder and Hansen (25–27). Certain sections of the genus, particularly *Lateritium, Liseola, Elegans,* and *Martiella,* were modified by the revisions proposed by Snyder and Hansen (25–27). His taxonomic system was a compromise between that of Wollenweber and Reinking and Snyder and Hansen.

Booth (3) modified Gordon's system, added information based on his studies, and expanded the information on perfect states (4). A major contribution was information on conidiophores and conidiogenous cells useful in the taxonomy of *Fusarium* species. He showed the value of the presence of polyphialides versus monophialides in separating sections and species. The length and shape of the microconidiophores also was shown to be a reliable character in separating *F. oxysporum, F. solani,* and *F. moniliforme.* Booth made a real effort to bridge the gap between the taxonomic mycologists and plant pathologists and other groups that work with these organisms.

Nelson, Toussoun, and Marasas (22) selected what they considered the best parts of several systems and combined them with results of their own research to develop a compromise system in which utility for practical identification was emphasized. They used *F. oxysporum* and *F. solani,* as described by Snyder and Hansen (25–27), and information on conidiophores, especially that on microconidiophores, as described by Booth (3). The sections of Wollenweber and Reinking (30) containing toxigenic species as well as some other sections were retained. However, the number of species was reduced and varieties and forms combined with the appropriate species. In their opinion this was justified because many of the varieties and forms may have been cultural variants or mutants. The publication of Nelson, Toussoun, and Marasas (22) is illustrated with photographs of macroconidia, microconidia, conidiophores, and chlamydospores produced on carnation leaf agar (5). *Fusarium* species grow well on this medium, produce sporodochia readily, and produce uniform conidia of typical morphology suitable for observation and identification of *Fusarium* species. The book is cross-referenced to the taxonomic systems of Wollenweber and Reinking (30), Gerlach and Nirenberg (7), Booth (3), Joffe (16), Snyder and Hansen (25–27), and Messiaen and Cassini (20), and the index lists all known species names from these systems. If the species name is not known, synoptic keys are provided for identification of sections and species.

Snyder and Hansen (25-27) are considered to be the ultimate "lumpers." In the 1930s W. C. Snyder went to Berlin and spent a year working with Wollenweber in his laboratory. When he returned to Berkeley, he began an extensive research program on the biology and taxonomy of *Fusarium* species in cooperation with H. N. Hansen, who pioneered the use of single-conidial cultures. In the 1940s they published their ideas on the taxonomy of *Fusarium* species in three papers (25–27). In essence this system made nine species out of Wollenweber and Reinking's 16 sections (Table 2). Snyder and Hansen's system is based primarily on the morphology of the macroconidia and an extensive study of the general nature and variability of *Fusarium* species. The basis

for their work was an extensive single-conidial analysis of cultures of *Fusarium* species under identical conditions of substrate and other environmental conditions. These studies revealed a great range of variability in spore length, width, and septation, in kinds and intensities of pigments produced, and in the presence or absence of sporodochia and sclerotia among the subcultures of the same original single-conidial culture. Working with section *Elegans,* they found that progeny of a single parent may be placed in different species and even in different subsections. This is an indication that the characters used for speciation by Wollenweber and Reinking were too narrow.

Snyder and Hansen's work with *F. oxysporum* (section *Elegans*) is the basis for their system (25). This work illustrated the importance of cultural variation in taxonomy and is generally accepted in *Fusarium* taxonomy. Their work with *F. solani,* which is also generally accepted, showed that the variations are inheritable (26). The remaining work, including the lumping of several sections into one species, is not generally accepted (27). The lumping of Wollenweber and Reinking's sections *Arthrosporiella, Discolor, Gibbosum,* and *Roseum* into *F. roseum* has caused a great deal of confusion and controversy. The greater reduction of species eliminated the convenience of naming certain fungi that had been known previously as species. The members of these sections that were pathogenic on cereals were further distinguished by the forma specialis name *cerealis.* Later Snyder and his colleagues proposed the adoption of the nonbotanical name, cultivar, for certain infraspecies populations differing in conidial morphology (28). They stated, "The cultivar provides a means of informally naming plants. It has nothing to do with taxonomy or classification, and therefore is entirely independent of the botanical variety which implies relationship and position in a scheme of plant classification. These two systems of naming serve different purposes and may supplement one another, but neither takes the place of the other." Following these proposals, if one had a pathogenic strain of *F. graminearum,* it would be written *F. roseum* f. sp. *cerealis* 'Graminearum'. If the strain was not pathogenic, the name would be *F. roseum.*

There is a fundamental flaw in the cultivar concept because Snyder, et al (28) considered it an informal device and consequently proposed only a few cultivars that they did not describe and thus left no formal guidelines for future workers. Later, Nash and Snyder (21) named additional cultivars without descriptions. In short, the concept of cultivars was never completely explained or finalized.

On the basis of continued study and usage, it has been concluded that the concept of a single species, *F. roseum* as proposed by Snyder and Hansen (27), cannot be justified and should be abandoned. The reasons for this conclusion are as follows: 1) The reduction of all species in sections *Roseum, Arthrosporiella, Gibbosum,* and *Discolor* was an oversimplification based on insufficient cultural studies, and largely an extrapolation from earlier work on sections *Elegans, Martiella,* and *Ventricosum* (25–27). 2) There are no substantial morphological characters common to all populations included in *F. roseum* by Snyder and Hansen. A few characteristics are common to most populations but taxonomically are of secondary importance. Most populations are reported to form chlamydospores but their formation is erratic in culture. Within populations the formation of microconidia and chlamydospores can be highly variable even under standard conditions. Thus, there is no sound biological reason for placing these populations within a single species based on morphological characteristics even if *F. roseum* is considered to be a complex or super-species (22). 3) The species in *Fusarium* sections *Roseum, Arthrosporiella, Gibbosum,* and *Discolor* are distinct and can be recognized and separated (22,30). 4) The designation f. sp. *cerealis* to denote pathogenicity to cereals is not valid as shown by Tammen (29) and his suggestion to use f. sp. *cerealis* simply to designate pathogenesis is confusing and unnecessary. 5) The use of trinomials and quadrinomials as names is unnecessary, cumbersome, and confusing. 6) The use of the name *F. roseum* f. sp. *cerealis* and cultivar names has caused confusion and misunderstanding in regard to the correct identification of fungi in these sections and has reduced the value of publications in which the name *F. roseum* is used for mycologists, plant pathologists, mycotoxicologists, and others working with these species (17).

TABLE 2. The relationship of the 16 sections of Wollenweber and Reinking (30) to the nine species of Snyder and Hansen (25–27)

Sections of Wollenweber and Reinking	Species of Snyder and Hansen
Eupionnotes	*episphaeria*
Macroconia	*episphaeria*
Spicarioides	*rigidiuscula*
Submicrocera	none
Pseudomicrocera	none
Arachnites	*nivale*
Sporotrichiella	*tricinctum*
Roseum	*roseum*
Arthrosporiella	*roseum*
Gibbosum	*roseum*
Discolor	*roseum*
Lateritium	*lateritium*
Liseola	*moniliforme*
Elegans	*oxysporum*
Martiella	*solani*
Ventricosum	*solani*

Messiaen and Cassini (20) followed Snyder and Hansen's system, but they used botanical varieties instead of cultivars at the subspecies level in *F. roseum.* They provided descriptions for each variety, and a key was provided for the entire system.

Matuo (18) also followed the Snyder and Hansen system and provided a key to the entire system. Matuo and Kobayashi (19) reported that *Hypocrea splendens* produced a conidial state that they named *F. splendens.* However, further work showed that this was most likely a *Nectria* hyperparasite. Matuo was also in favor of lumping *F. lateritium* and *F. roseum,* but this concept has received very little support.

This paper discusses the two extremes in the taxonomy of *Fusarium* species since the turn of the century. The "splitters" are represented by Wollenweber and his colleagues and the "lumpers" by Snyder and Hansen and their colleagues. Neither group produced a practical identification system for *Fusarium* species; Wollenweber's system is too complex and Snyder and Hansen's is too simple. If we use the information in the taxonomic systems discussed in this paper and additional information from current research, a practical system for the identification of *Fusarium* species can be compiled. "New" or "modern" systems for the taxonomy of *Fusarium* species that ignore the collective wisdom and errors of past research are likely to be counterproductive to the development of a better practical taxonomic treatment of the genus.

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