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Perithecial species of *Gibberella*

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INTRODUCTION

In the last decade, the ability to characterize long stretches of the nuclear ribosomal DNA molecule has demonstrated conclusively that asexual fungi can often be phylogenetically incorporated among the Ascomycetes (e.g. Lobuglio *et al.*, 1993; Kuhls *et al.*, 1997). Guadet *et al.* (1989) clearly showed this to be true for *Fusarium.* These authors confirmed what was already known from classical work: that while *Fusarium* is restricted to the Hypocreales, it is polyphyletic because species of the anamorph genus are anamorphs of different teleomorph genera of that order (see review in O'Donnell, 1996). Because the type species of *Fusarium*, *F. sambucinum* Fuckel, is the anamorph of *Gibberella pulicaris* (Fr.) Sacc., *Fusarium* s. str. is the anamorphic or mitotic state of *Gibberella*. Furthermore, DNA sequence analyses have shown that asexual species such as *F. oxysporum* are actually asexual *Gibberella* species (Guadet *et al.*, 1989; O'Donnell *et al.*, 1998).

Booth (1981) listed most of the known connections between fusaria and their teleomorphs. Since that time, some of these teleomorphs have been shown not to belong to the Hypocreales, and their so-called *Fusarium* anamorphs have been removed to other anamorph genera (Table 1). Moreover, within the Hypocreales, *Fusarium* anamorphs are linked to four phylogenetically distinct lineages (Table 1). Whether *Fusarium* anamorphs of *Nectria rigidiuscula* (*Fusarium* sect. *Spicarioides* Wollenw.), *N. haematococca* Berk. & Br. s. lat. (*Fusarium* sect. *Martiella*) or *Nectria* subg. *Dialonectria* (= *Cosmospora, Fusarium* sect. *Eupionnotes,* and probably also *Macroconia, Pseudomicrocera* (Petch) Wollenw., and *Submicrocera* Wollenw.; Samuels *et al.* 1991) should be retained in *Fusarium* is discussed by Seifert (this volume).

Although there is a vast literature about the biology and genetics of *Gibberella*, mainly under the name of *Fusarium,* little effort has been expended on characterizing the perithecia, asci or ascospores of the species of this genus. In this paper, we discuss how to recognize a *Gibberella* perithecium and the background to the taxonomy of the genus. We also discuss recent research in the definition of biological and 'phylogenetic' species within *Gibberella*. Finally, we present a key to the *Gibberella* species that are proven to have *Fusarium* anamorphs.

RECOGNIZING THE GENUS AND TAXONOMIC STATUS

Gibberella was proposed by Saccardo in 1877 and distinguished from *Botryosphaeria* Ces. & de Not. and *Lisea* Sacc. on the basis of ascospore septation. Species of all three genera are described as having dark blue or violaceous to black perithecia. Ascospores in *Botryosphaeria* are aseptate; they are 1-septate in *Lisea* and 3-or-more-septate in *Gibberella*. Today *Botryosphaeria* is recognized to be a loculoascomycete classified in the Dothideales. *Lisea* Sacc. is often considered a synonym of *Gibberella*. *Lisea* was first neotypified with *L. buxi* (Fuckel) Sacc. (= *G. buxi* (Fuckel) Winter) by Clements and Shear (1931), however this neotypification is incorrect because *L. buxi* is not an original species of *Lisea*. Müller and Arx (1962) are apparently the first to have selected *L. nemorosa* (Sacc.) Sacc., one of the two original species, as the type of *Lisea* and we take this to be effective lectotypification of the genus. Wollenweber (1931) included *L. nemorosa* in *Gibberella* as *G. nemorosa* (Fuckel) Wollenw. The illustration provided for this species by Wollenweber (1930: 821), which was taken from material collected on *Clematis* at the type locality, agrees with the type specimen on *Cytisus* that we studied (PADOVA), thus confirming the identity of *Lisea* with *Gibberella*.

Gibberella perithecia are dark purple, appearing black by reflected light (Fig. 1). They become red in 3% potassium hydroxide and yellow in lactic acid. They are ovoidal to subglobose and roughened to a greater or lesser extent by warts on the perithecial surface (Figs. 1-5). In nature, the inconspicuous and easily overlooked perithecia are gregarious and superficial on the substratum (Fig. 1); they are not obviously stromatic but they are difficult to remove from the substratum and may be formed on a weakly developed stroma. Asci are narrowly clavate and thin-walled, most often lacking an apical discharge mechanism. Ascospores are fusoid, straight or sometimes curved and 1-3 septate when mature. They are colorless when still in asci, but they become pale brown after discharge from the perithecium. Although perithecial anatomy of only a few species of *Gibberella* has been studied (Samuels *et al.*, 1990; Seifert, 1996; Klittich *et al.*, 1997; Nirenberg and O'Donnell, 1998), there appears to be little variation (Fig. 2). The perithecial wall is formed of 2-3 intergrading regions of cells (Figs. 3-5). Cells of the outer region are globose to angular, 15-30 x 10-20 µm and have thickened and pigmented walls. Cells of the middle region are elliptic and have thinner, non-pigmented walls. Cells of the inner region are elongated and very thin-walled and hyaline.

The only exception to this pattern may be *G. xylarioides* Heim & Saccas, the teleomorph of *F. xylaroiodes* Steyaert (1948). Perithecia of this species were originally described as being formed on a conspicuous stroma that is erumpent through bark (Heim, 1950). Booth (1971) redescribed *G. xylarioides* and its anamorph. However this redescription may have been based on misidentified material or on a mixed culture, as the illustrations of the perithecia and anamorph are not consistent with the original descriptions of either. Booth ascribed male and female strains to *G. xylarioides* and said that there was sex-linked dimorphism of the conidia. Conidia in his Fig. 33a (female strain) are similar to what was originally described for *F. xylarioides* by Heim & Saccas (Heim , 1950) but the conidia in Fig. 33b (male strain) and Fig. 32 may not be *F. xylarioides.* Further, Booth reported a very slow rate of growth and a slimy colony for the species whereas *F. xylarioides* was originally described as growing fast (on PDA) and having abundant aerial mycelium.

Approximately 100 taxa (species and varieties) of *Gibberella* have been proposed (see Reed and Farr, 1993; and Index of Fungi and Petrak's Lists; and the ISPP Subcommission on *Fusarium* Systematics database at the following URL: http://www.cbs.knaw.nl/www/fusarium/database.html). Most species of *Gibberella* have not been described from agricultural settings and they have not been reevaluated since they were described, mostly in the late 19th and early 20th centuries. Because very little synonymy is reported within *Gibberella*, there may be older names for more recently described species. Examination of type specimens has generally been neglected in *Fusarium* taxonomy, and has also been overlooked in *Gibberella*, although Wollenweber (1917, 1926) documented type specimens of many *Gibberella* and *Fusarium* species. In some instances, however, type specimens apparently were not saved and thoughtful and considered neotypification will be critical for stabilizing nomenclature and usage of names.

In 1981, Booth listed only thirteen taxa of *Gibberella* that were proven teleomorphs of *Fusarium.* Today only twenty-one names are commonly used in taxonomic treatments of *Fusarium* (Booth, 1971; Gerlach & Nirenberg, 1982; Nelson *et al.*, 1983).

THE NEW TAXONOMY

An unstated understanding by most contemporary *Fusarium* taxonomists is that taxonomically useful differences in *Gibberella* species are manifested in cultures and conidia rather than in perithecia. Given the few *Gibberella* species for which perithecia have been adequately characterized, it may be premature to eliminate the perithecium as a source of taxonomically useful characters. Perithecial anatomy in the few species that have recently been documented appears to be homogeneous. Nevertheless, Kuhlman (1982) reported statistically significant differences in perithecial diameter and ascospore length among the four members of the *G. fujikuroi* complex that he studied. These observations based on perithecia developed *in vitro* warrant repeating, in particular with material collected in nature. Another potential taxonomic problem with teleomorphs known primarily from mating experiments is that a limited range of morphological expression may be imposed by 'funelling' the expressed phenetic characters through the narrow, morphological space of the mating-type test strains. Thus, it may be difficult to make meaningful morphological comparisons between perithecia developed *in vivo* and *in vitro* until comparative studies are done.

Teleomorphs are known for all but three of the sections of *Fusarium* that are accepted by Gerlach and Nirenberg (1982) and Nelson *et al.* (1983) (Table 1). Recent evidence from DNA sequences (see O'Donnell, 1993, 1996) confirms conclusions derived from observations of the teleomorphs (Samuels *et al.*, 1991) that sections *Eupionnotes*, *Macroconia*, *Submicrocera*, *Pseudomicrocera*, and *Arachnites* cannot be distinguished. These teleomorphs should be classified in *Cosmospora* Ces. & de Not. (Rossman *et al.*, 1998). Guadet *et al.* (1989) clearly demonstrated that *Nectria rigidiuscula* Berk. & Broome, *N. haematococca* and *Gibberella* form a clade that is phylogenetically distinct from *N. cinnabarina* (Tode: Fr.) Fr., the type species of *Nectria* Fr. Within this clade, *N. rigidiuscula* is basal and *N. haematococca* and *Gibberella* are sister groups. Because each of these groups is easily distinguished through its teleomorph, new genera are proposed for each of them in Rossman *et al.* (1998). Furthermore, results of DNA sequences indicate that at least some of the currently recognized sections of the genus *Fusarium* that have *Gibberella* teleomorphs, such as sect. *Liseola*, are paraphyletic or polyphyletic as they are presently defined (O'Donnell *et al.*, 1998).

Although classical *Fusarium* taxonomists have all but ignored the *Gibberella* perithecium, reproductively isolated biological species (see Kuhlman, 1982; Desjardins and Nelson, 1995; Leslie, 1991, 1995) and monophyletic lineages (see O'Donnell, 1996; O'Donnell *et al.*, 1998) within the genus have been defined using genetic and molecular techniques. Most known *Gibberella* species are heterothallic and compatible mating partners must be crossed on the appropriate medium and under the appropriate conditions for the teleomorph to appear in culture. Only *G. zeae* is known to be homothallic. Some *Gibberella* species produce perithecia readily in artificial culture on a variety of media (for example carrot agar by Leslie, 1991; twigs of *Morus alba* (mulberry) by Desjardins and Nelson, 1995; wheat straw by Booth, 1971), usually with relatively stringent temperature and lighting requirements. This has permitted genetic analysis, population studies and the discovery of mating groups in some groups. Other *Gibberella* species rarely if ever produce perithecia in culture and are known primarily from natural collections. Successful fruiting of these species may require or be enhanced by the addition of special nutrients, perhaps lipids such as linoleic acid, as has been shown for one mating population of *Nectria haematococca* and other ascomycetes (Dyer *et al.*, 1993).

The *G. fujikuroi* species complex (*Fusarium* sect. *Liseola*) has been the object of intense study (see reviews in Kuhlman, 1982; Leslie, 1991, 1995; Nirenberg, 1976; O'Donnell *et al.*, 1998). Species of this complex are common on maize, sorghum and sugar-cane, where they cause diseases and also may produce fumonisin, moniliformin and beauvericin toxins. Today seven intersterile mating populations (MP *A-G)* are recognized (Leslie, 1991, 1995), most of which have been described formally as *Gibberella* species (Table 2). Only mating population *B* has not been given a name. This mating population is isolated from *Saccharum* and its anamorph is *F. sacchari* (Butler) W. Gams. Perithecia of a species of *Gibberella* have been produced in crossed cultures of *F. sacchari*, but have not been described; thus this species is not included in the key that is presented below. Mating population *D* is *Gibberella fujikuroi* var. *intermedia* Kuhlman (*F. proliferatum* (Matsushima) Nirenberg. Because the mating populations are recognized to represent distinct species, we elevate this variety to species rank as *Gibberella intermedia* (Kuhlman) Samuels, Nirenberg & Seifert stat. nov., comb. nov. (basionym: *Gibberella fujikuroi* var. *intermedia* Kuhlman, Mycologia 74: 766. 1982). The mating populations are usually regarded as being reproductively isolated from each other, although there is some evidence that the reproductive barriers are incomplete. Each mating population in the *G. fujikuroi* complex can be distinguished by various biochemical and nucleic acid-derived traits (see Leslie, 1995).

In a study of sexual intercompatibility among field strains of the *F. sambucinum* Fuckel complex (*Fusarium* sect. *Discolor*), thirteen strains were compatible with tester strains of *G. pulicaris (F. sambucinum sensu stricto*). Twenty-seven strains were not fertile when paired with *G. pulicaris*, most of which were excluded from that species on the basis of their morphological characters. Nirenberg (1995) formally described these populations and ascribed a possible *Gibberella* teleomorph to one of them, *F. torulosum* (*G. pulicaris* var. *minor* Wollenw.); no teleomorph was reported for the new species *F. venenatum* Nirenberg (Table 3).

IDENTIFICATION OF *GIBBERELLA* SPECIES

The identities of *G. gordonii* Booth and *G. cyanea* (Sollm.) Wollenw. and their anamorphs are uncertain. Booth (1971) reported *G. gordonii* to be the teleomorph of *F. heterosporum* (Booth, 1971), with *F. reticulatum* Mont. as a synonym. Booth (1971) stated that the species occurs on gramineous hosts. Gerlach and Nirenberg (1982) gave G*. gordonii* as a possible synonym of *G. cyanea*, the teleomorph of *F. reticulatum*, following Booth's synonymy of *F. reticulatum* with *F. heterosporum*. They maintained *F. heterosporum* as a distinct species on gramineous hosts for which they knew no teleomorph. According to Booth (1971), ascospores of the teleomorph of *F. heterosporum* (*G. gordonii:* 15-18.5 x 4-4.5 µm) are smaller than ascospores of *G. cyanea* (17-22 x 6-7 µm). This size difference would certainly indicate that two species are involved. However, Sollman (1863) did not report ascospore measurements in the protologue to *Sphaeria cyanea* Sollm. Because Booth was not able to locate type material for the species, ascospore sizes that he reported are taken from the illustration provided by Sollman. We have reexamined those illustrations and have found that measurements of the sixteen ascospores that we could measure were 12.5--20 x 3.7--8.7 µm, but of these sixteen ascospores, nine were shown as germinating and might be expected to be wider than nongerminating ascospores. Indeed, the width of the ungerminated ascospores is 3.7--6.2 µm, indicating that at least on the basis of ascospore measurements, *G. gordonii* falls within the range given by Wollenweber

(1926) for *G. cyanea* (13--20 x 4.25--5.25 µm). Booth's concept of *G. gordonii* is based on mating experiments that W. L. Gordon performed. None of the cultures that Gordon used as mating partners (DAOM 194229, 194230, 194231, 194234 and 194235) came from hosts in the *Gramineae*; all were from woody hosts. The conclusion that we draw from this is that *G. cyanea* is the anamorph of *F. reticulatum* (Gerlach and Nirenberg, 1982; Nelson *et al.*, 1983) and the species occurs on woody substrata. *Gibberella gordonii* is a probable synonym of *G. cyanea.* Despite the reports of Booth (1971), followed by Nelson *et al.* (1983), that *G. gordonii* is its teleomorph, no teleomorph can yet be linked to *F. heterosporum.*

It must be noted that not all of the teleomorph-anamorph combinations that we recognize in this work are proven, i. e. that the entire life cycle of the fungus has not yet been achieved in culture. This is true for the following species: *G. stilboides* Gordon ex Booth/F*. stilboides* Wollenw*., G. heterochroma* Wollenw./F*. flocciferum* Corda, and *G. pseudopulicaris* Wollenw./F*. sarcochroum* (Desm.) Sacc.

A further interesting result was found when shape and septation of the ascospores were used for the key. Straight, 1-septate ascospores are found only in the *G. fujikuroi* complex (sections *Liseola* and *Dlaminia;* O'Donnell *et al.*, 1998). Mostly straight ascospores with 1 and/or 3 septa are found in sects. *Lateritium, Roseum,* and *Sporotrichiella*, which places *F. tricinctum* (*G. tricincta)* in the vicinity of *F. avenaceum* and *F. heterosporum*, and close to members of sect. *Lateritium*. Slightly curved and mainly 3-septate ascospores are known to be produced only by species of sects. *Discolor* and *Gibbosum* with the exception of *F. sarcochroum*. This misplacement of *F. sarcochroum* (*G. pseudopulicaris*) in our key in the sense of sectional grouping gives us a further hint that there might be something wrong with its identification or the teleomorph-anamorph combination.

In the key that follows we include all *Gibberella* species that are encountered in three major taxonomic treatments of *Fusarium* (Booth, 1971; Gerlach and Nirenberg, 1982; Nelson *et al.*, 1983). In addition we have included several more recently described species. The *Gibberella* species included in the key are those that are commonly found in agricultural settings.

KEY TO *GIBBERELLA (FUSARIUM)* SPECIES ENCOUNTERED IN AGRICULTURAL SETTINGS

1. Ascospores either straight and 1-septate or predominantly straight and 1- and/or up to 3-septate **2**
1. Ascospores slightly curved, mostly 3-septate (sects. *Discolor*, *Gibbosum*) **15**

2. Ascospores predominantly 1-septate (Sects. *Liseola*, *Dlaminia*) **3**
2. Ascospores 1-3-septate (Sects. *Lateritium*, *Roseum*) **10**

3. Conidiogenous cells in aerial mycelium (on primary c'phores) monophialidic only **4**
3. Conidiogenous cells in aerial mycelium (on primary c'phores) mono and polyphialidic …... **5**

4. Colonies on PDA grayish vinaceous, conidia formed in chains in aerial mycelium, clavate, sporodochial conidia 3-5-septate, 47-58 x 3.0-3.5 µm (mean 54.2 x 3.5 µm) when 5-septate; ascospores 15-19 x 4-5 µm; mainly on maize .... ***G. moniliformis*** Wineland, (*F. verticillioides* (Sacc.) Nirenberg) (Wineland, 1924; Nirenberg, 1976; Kuhlman, 1982)

4. Colony on PDA with a conspicuous diffusing yellow pigment; conidia formed in long chains in aerial mycelium, clavate; macroconidia mainly 5-septate, 24-64 x 3-4 µm (mean 47 x 3.5 µm); ascospores 12-22 x 4-8 µm. Mainly on *Sorghum*. .... ***G. thapsina*** Klittich *et al.* (*F. thapsinum* Klittich *et al.*) (Klittich *et al.*, 1997)

5. Conidia in aerial mycelium in chains or in chains and heads **6**
5. Conidia in aerial mycelium in heads only **8**

6. Conidia in aerial mycelium in heads and long chains, clavate, sometimes few pyriform conidia in the chain, polyphialides conspicuous, sporodochial conidia 3-5-septate, 47-58 x 3.5-4.5 µm when 5-septate; chlamydospores not produced; ascospores (10-)15(-21) x (3-)5(-7) µm. On various hosts, including orchids and *Asparagus* .... ***G. intermedia*** (Kuhlmann) Samuels *et al.* (*F. proliferatum* (Matsushima) Nirenberg) (Kuhlman, 1982).
6. Conidia in aerial mycelium in heads and short chains **7**

7. Conidia in aerial mycelium clavate, very few polyphialides formed; sporodochial conidia 50-59 x 3.5-4.0 µm; chlamydospores not produced; ascospores 7-20 x 3.0-7.0 µm. On rice .... ***G. fujikuroi*** (Sawada) Wollenw. (*F. fujikuroi* Nirenberg) (Nirenberg**,** 1976**;** Kuhlman, 1982).

7. Conidia in aerial mycelium obovoid, polyphialides abundant; sporodochial conidia mainly 3-septate, 25-54 x 2.5-3.5 µm; chlamydospores formed in chains and clusters; ascospores (8.5-)14(-20) x (4-)5.5(-8) µm. On hosts in the Gramineae, including rice and maize .... ***G. nygamai*** Klaasen & Nelson (*F. nygamai* Burgess & Timboli) (Klaasen & Nelson, 1996).

8. Conidiophores in aerial mycelium short and infrequently branched with few polyphialides, conidia oval to allantoid; sporodochial conidia with uncinate apical and basal cells, mostly 3-septate, 20-32 x 2.5-3.5 µm; chlamydospores formed in chains and clusters; ascospores 10-17 x 5-7 µm. On *Cajanus* .... ***G. indica*** B. Rai & R. S. Upadhyay (*F. udum* Butler) (Rai and Upadhyay, 1982).
8. Conidiophores long and conspiciously branched, with abundant polyphialides, conidia of aerial mycelium oval or fusiform; sporodochial conidia not uncinate; chlamydospores not produced **9**

9. Conidia in aerial mycelium fusiform, 0-1-septate; sterile coiled hyphae on the agar; sporodochial conidia 3-5-septate, (32-)34-43(-48) x (3.0-)3.5-4.0 µm; ascospores (9.5-)11-14(-16) x (4.5-)4.5-5.5(-6.0)µm. On *Pinus* .... ***G. circinata*** Nirenberg & O'Donnell (*F. circinatum* Nirenberg & O'Donnell) (Nirenberg and O'Donnell, 1998).
9. Conidia in aerial mycelium oval to fusiform, 0- to 3-septate; no sterile coiled hyphae in or on the agar; sporodochial conidia 3(-5)-septate (32-)34.5-41.5(48.0) x (3.0-)4.0-4.0(-5.0) µm; ascospores (11.0-)16.5(-21.0) x (3.5-)5.0(-6.0) µm. On hosts in the Gramineae, mainly maize .... ***G. subglutinans*** Nelson *et al.* (*F. subglutinans* (Wollenw. & Reinking) Nelson *et al.*) (Edwards, 1935).

10. Conidia formed in aerial mycelium **11**
10. No conidia formed in aerial mycelium **13**

11. Fusiform, 0-5-septate conidia produced in aerial mycelium **12**

11. Pyriform and citriform conidia produced in aerial mycelium; sporodochial conidia 3(-5)-septate, 24-46 x 3.0-4.0 µm when 3-septate; ascospores 12.5-20.0 x 4.9-7.5 µm when 3-septate. Usually on hosts in the Gramineae .... ***G. tricincta*** El-Gholl *et al.* (*F. tricinctum* (Corda) Sacc., El-Gholl *et al.*, 1978).

12. Sporodochial conidia sickle-shaped with an elongated apical cell, mostly 3-5-septate, slender, 8-50 x 3.5-4.5 µm; ascospores primarily 1-septate, 13-19 x 4-5 µm when 1-septate, 13-25 x 4.0-6.5 µm when 3-septate. On diverse substrates including members of the *Gramineae* .... ***G. avenacea*** Cook (*F. avenaceum* (Corda)Sacc.) (Cook, 1967; Booth, 1971)

12. Sporodochial conidia almost straight with a slightly hooked apical cell, mostly 5-7-septate, 57-85 x 4-5 µm when 5-septate; ascospores 12-18 x 4.0-5.5 µm Mainly on *Citrus* and *Coffea* ... *G. stilboides* Gordon ex Booth (*F. stilboides* Wollenw.) (Booth, 1971).

13. Cultures on PDA growing medium fast, with an even margin, red, pionnotal; sporodochial conidia sharply curved to lunate, 1-3-septate, 23-30 x 2.5-3.0 µm when 3-septate; ascospores 9-16 x 4-6 µm. On *Coffea* .... ***G. xylarioides*** Heim & Saccas (*F. xylarioides* Steyaert) (Heim, 1950 but see note above.

13. Cultures on PDA growing slowly, with a lobed margin **14**

14. Cultures red, lanose, not pionnotal; sporodochial conidia straight or slightly curved, mostly with a hooked apical cell, 3-7-septate, 46-64 x 3.5-4.5 µm when 5-septate; ascospores 17-21 x 7-8 µm. On *Buxus* .... ***G. buxi*** (Fuck.) Wint. (*F. lateritium* Nees var. *buxi* Booth) (Booth, 1971).

14. Cultures not red, but orange with brownish or bluish tinges; sporodochial conidia straight or slightly curved with a hooked apical cell, 3(-5)-septate, 21-42 x 3.0-4.5 µm when 3-septate. On diverse woody hosts .... ***G. baccata*** (Wallr.) Sacc. (*F. lateritium* Nees). (Booth, 1971).

15. Ascospores averaging <20 µm in length; sporodochial conidia with apical cells abruptly narrowed, almost pointed, 3-5-septate, 34-46 x 3.5-4.5 µm when 5-septate; 1-septate ascospores 13-20 x 4.5-5 µm, 3-septate ascospores 17-20 x 4-5 µm. From woody plants and soil and roots of various plants .... ***G. cyanea*** (Sollm.) Wollenw. (*F. reticulatum* Mont.) (Wollenweber, 1917: 39)

15. Ascospores averaging > 20 µm in length **16**

16. Ascospores averaging < 5 µm in width **17**

16. Ascospores averaging > 5 µm in width **18**

17. Colonies on PDA growing quite slowly, 2.0-3.5 cm in 4 days on PDA at 25 C, margin lobed; sporodochial conidia produced only when grown under black light, predominantly 3-5-septate, 36-50 x 4.5-5.0 µm when 5-septate, apical cell coming abruptly to a point; chlamydsopores abundantly produced in clusters; sclerotial bodies present; ascospores 20-25 x 4-5 µm. On various hosts and in soil .... ***G. heterochroma*** Wollenw. (*F. flocciferum* Corda) (Wollenweber, 1917, 1926: figs. 40-42).

17. Colonies on PDA growing fast, 7.5- 8.0 cm in 4 days on PDA at 25 C, margin even, whitish, pinkish, golden yellow, ochraceous to grayish rose, crimson, finally becoming dark purple to vinaceous with a dash of brown; sporodochial conidia (3-)5-6(-9)-septate, 41-60 x 4.5-5.0 µm when 5-septate; homothallic; ascospores 20-29 x 3.5-4.5 µm. On hosts in the *Gramineae* .... ***G. zeae*** (Schw.) Petch (*F. graminearum* Schw.) (Booth, 1971; Seifert, 1996).

18. Colonies on PDA never producing red pigments; sporodochial conidia > 6 µm wide, usually 3-9-septate, 34-61 x 6.0-10.0 µm when 5-septate; heterothallic; ascospores (25-)29-36(-39) x 5.5-7.5(-8.5) µm. On *Leguminosae*, especially *Cytisus* and *Ulex* .... ***G. tumida*** Broadhurst & Johnston (*F. tumidum* Sherb.) (Broadhurst and Johnston, 1994).
18. Sporodochial conidia < 6 µm wide **19**

19. Chlamydospores produced **20**
19. Chlamydospores not produced **21**

20. Colonies on PDA never producing red pigments; sporodochial conidia dorsiventrally curved, apical cell attenuated and bent, 3-5-septate, 31-47 x 4.0-5.0 µm when 5-septate; ascospores 22-27-33 x 4.0-6.5-5.5 µm. On diverse substrates including *Gramineae* …………………. ***G. intricans*** Wollenw. (*F. bullatum* Sherb.) (Wollenweber, 1930: figs. 810, 917 a,b; 1931; Booth, 1971).
20. Colonies on PDA always with some red pigments; sporodochial conidia, sickle-shaped, almost lunate, (3-)5-septate, 34-54 x 3.0-4.5 µm when 5-septate; ascospores 22-26 x 5-8 µm. On various plants and in soil .... ***G. acuminata*** Wollenw. (*F. acuminatum* Ellis & Kellerm.) (Wollenweber and Reinking, 1935; Booth, 1971, as *G. acuminata* Booth)

21. Sporodochial conidia (1-)3-5(-6)-septate, 28-45 x 4.5-6 µm when 5-septate; colonies on PDA whitish, cream, yellowish, peach to ochraceous, buff-brown, finally slightly cinnamon colored, sometimes distinct red or carmine, never purple or violet; ascospores 20-25 x 5-7 µm. On diverse plants, especially potato .... ***G. pulicaris*** (Fr.) Sacc. var. ***pulicaris*** (*F. sambucinum* Fuckel) (Booth, 1971).
21. Sporodochial conidia (3-)5(-7)-septate, 37-53 x 3.5-5.5 µm when 5-septate; colony reverse on PDA whitish, beige, pink to yellowish, ochraceous, finally buff-brown to chestnut, red pigments absent; sclerotial bodies abundant; ascospores 18-26 x 5-7 µm. On bark of trees and bushes .... ***G. pseudopulicaris*** Wollenw. (*F. sarcochroum* [Desm.] Sacc.) (Wollenweber, 1926, fig. 30; 1930, fig. 817; 1931).

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Table 1. *Fusarium* sections and their corresponding teleomorphs.

SECTION	TELEOMORPH GENUS
Eupionnotes	*Cosmospora* pro parte, (Rossman *et al.*, 1998), *Plectosporium* pro parte (Phyllachorales), Palm *et al.* 1995
Macroconia	*Cosmospora* pro parte, (Rossman *et al.*, 1998)
Submicrocera	*Cosmospora* pro parte (Rossman *et al.*, 1998)
Pseudomicrocera	*Cosmospora* pro parte (Rossman *et al.*, 1998)
Spicarioides	*”Nectria" rigidiuscula*
Arachnites	*Monographella* pro parte (Amphisphaeriales), Samuels and Hallett, 1984; *Cosmospora* pro parte (Rossman *et al.*, 1998)
Sporotrichiella	none known
Roseum	*Gibberella*
Arthrosporiella	none known
Gibbosum	*Gibberella*
Fusarium (=Discolor)	*Gibberella*
Lateritium	*Gibberella*
Liseola	*Gibberella*
Elegans	none known
Martiella	*”Nectria” haematococca*

Table 2. Biological species within the *Gibberella fujikuroi* complex.

Mating population	*Fusarium* anamorph	*Gibberella* teleomorph	Teleomorph reference
A	*verticillioides*	*moniliformis*	Wineland 1924
B	*sacchari*	*"subglutinans"*	Nelson *et al.*, 1983
C	*fujikuroi*	*fujikuroi*	Nirenberg, 1976
D	*proliferatum*	*intermedia*	Kuhlman, 1982 and herewith
E	*subglutinans*	*subglutinans*	Nelson *et al.*, 1983
F	*thapsinum*	*thapsina*	Klittich *et al.,* 1997
G	*nygamai*	*nygamai*	Klaasen and Nelson, 1996

Table 3. *Gibberella pulicaris* complex.

Gibberella teleomorph	*Fusarium* anamorph
cyanea	*reticulatum*
gordonii	*heterosporum*
pulicaris	*sambucinum*
? pulicaris var*. minor*	*torulosum*
heterochroma	*flocciferum*
zeae	*graminearum*
tumida	*tumidum*

LEGENDS TO FIGURES

Fig. 1. *Gibberella zeae*, perithecia formed on wheat straw (DAOM 213220).

Figs. 2-5. *Gibberella zeae*, perithecial anatomy. 2. Median longitudinal section of a mature perithecium, x160. 3. Detail of lateral wall, x 640. 4. Detail of cells around the ostiole, x 640. 5. Detail of lateral wall, with asci in centrum, x. 640. All from lectotype specimen from Kew.

i in centrum, x. 640. All from lectotype specimen from Kew.