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STACKS

Studies on *Diplodia* and *Diplodia*-like Fungi

VII. Criteria for Classification

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Variation encountered in cultures resulting from single pycnidiospores of representative isolates of the Phaeodidymous:Sphaeropsidales was analyzed. Spore morphology, ornamentation, and size are proposed as the most stable characters for use in future taxonomic treatments of this group. The genus *Diplodia* is broadened to include all fungi that produce dark, two-celled spores within a pycnidium.

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VII. Criteria for Classification^{1,2}

INTRODUCTION

MANY ECONOMICALLY IMPORTANT plant pathogens belong to the group of fungi known as the Phaeodidymous: Sphaeropsidales (F. L. Stevens, 1913; Grove, 1937). Identification is difficult and sometimes impossible because various workers have used unstable taxonomic characters to delimit both genera and species. The primary criterion for placing fungi in this group is the production of dark, two-celled spores in a pycnidium.

The genus *Diplodia* was originally described by Fries, and was distinguished primarily by the morphology and nature of the pycnidium in which the dark, two-celled pycnidiospores are produced. Numerous similar genera have since been described as belonging to the Phaeodidymous: Sphaeropsidales, and have been included in subsequent taxonomic works. For example, Saccardo's *Sylloge Fungorum* lists 17 genera, Clements (1909) 11, F. L. Stevens (1913) 10, Grove (1937) five, Buchwald (1939) three, Barnett (1960) two, and Bender (1934) 14. Most of these works distinguish genera on the basis of pycnidial characters, such as beaked or not beaked, hairy or smooth, separate or grouped, superficial or submerged in host tissue, presence or absence of stromata and subicle, and the type of ostiole. Pycnidiospore characters utilized have included size, ornamentation, presence or absence of a constriction at the septum, and mode of extrusion, whether wet or dry. In many

cases, characters used by one author to distinguish genera are used by another to distinguish species of a single genus.

Attempts to distinguish species in this group are complicated not only by the fact that no clear agreement exists regarding genus concepts but also by the extensive misuse, in our opinion, of host occurrence as a primary criterion. A notable example is found in Wehmeyer (1964), in which he states: "In this genus again so many species have been described with similar or overlapping characters but differing only in host occurrence that occurrences on new hosts cannot be definitely placed but must be erected as a new species to complicate the confusion."

We encountered similar difficulty when we attempted to identify a fungus first isolated in 1960 from rotting green grapes and later from mature grapes, canes, and truck wood of the grapevine. Each of the isolates appeared similar in culture on potato-dextrose-agar. Furthermore, spores from fruiting bodies in grapevine canes and wood were similar. We found, however, that a single-spore colony of the fungus could be classified "correctly" in the available literature (depending on the media on which it was cultured and on temperature and light conditions) in any of four or more genera, such as *Diplodia*, *Rhyncodiplodia*, *Botryodiplodia*, and *Chaetodiplodia* (unpublished data). Therefore, we classified the fungus as *Diplodia viticola* Desm.

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(Hewitt *et al.*, 1962) simply because it was a *Diplodia*-like fungus and was isolated from *Vitis vinifera*. When grown on sterile pea-straw bits in water agar, many, but not all, of the pycnidia were hirsute, perhaps placing it in *Chaetodiplodia* Karst. Those formed near the surface were beaked and glabrous, placing it in *Pellionella* Sacc., and those in the subepidermal tissue were frequently embedded in stromatic tissue, placing the isolate in *Botryodiplodia* Sacc. When the same isolate was grown on cane tissue of grape, the pycnidia were characteristic of *Diplodia* Fries.

Later, after a more critical study of the fungus isolate from grapes, and on the basis of the presence of paraphyses in the pycnidium, spore shape, size, and ornamentation, the fungus was reclassified as *Diplodia natalensis* P. Evans (Barbe and Hewitt, 1965).

Others have had similar problems in classifying these fungi. In a study of *Diplodia* and related fungi, Taubenhuis (1915) found that *D. gossypii* Zimi. grown on sweet potato had all of the characteristics of the genera *Lasiodiplodia* Griff. et Maub., *Chaetodiplodia*, *Botryodiplodia*, and *Diplodiella* Karst. He found that *L. tubericola* Ell. Ev. performed in a similar way, and concluded that all species placed in these genera were congeneric and should be in the genus *Diplodia*. N. E. Stevens (1941) concluded that stromatic characters of these fungi are so variable that they are unreliable and not suitable for use in classification. With *D. mutila* (Fries) Mont., for example, the size of the stroma and complexity of the pycnidium spore chambers varied greatly with the substrate. The stroma formed by clones of a single-spore isolate grown on twigs of raspberry, currant, and on cornmeal agar, were different on each substrate. On raspberry the fungus formed thin-walled, uniloculate pycnidia; on the thicker bark of currant it formed thick-walled, multilocu-

late pycnidia; and on cornmeal agar the stroma were loose-textured and thick. N. E. Stevens (1933) reported that humidity also influenced the characteristic of the pycnidium.

Voorhees (1942), in a paper on the life history and taxonomy of *Physalospora rhodina*, concluded that the morphology of the stroma pycnidia was extremely variable, but that of the conidia was more constant.

N. E. Stevens (1941) showed that many species of *Diplodia* and related genera are facultatively parasitic and that the morphology of fruiting structures was modified by the nature of the host tissue. He expressed the opinion that many names have probably been given the same fungus grown on different substrates.

Goos, Cox, and Stotzky (1961) found that some isolates of *Botryodiplodia theobromae* Pat. produced only simple pycnidia on potato-dextrose-agar, whereas other isolates of the same fungus, grown under the same conditions, formed large, columnar stroma containing several pycnidia.

The only apparent extensive taxonomic revision of the group was that of Zambettakis (1953, 1954a,b). In these works, 1,524 described species and forms, representing 40 genera, were reduced to 248 species and forms in 23 genera. Zambettakis retained 15 genera—7 *in sensu nobis*, 2 emended, and 6 unaltered; 20 others were reduced to synonymy, and 8 new genera were erected. Although Zambettakis examined over 2,000 herbarium specimens, he studied only 53 in culture, representing 11 genera and 49 species. Zambettakis used many of the characters employed by Bender (1934), plus paraphyses and pycnidiospore ornamentation. He failed, however, to establish the stability of characters and their natural range of variation.

We have concluded that three main factors account for the difficulties ex-

Plate I. Pycnidiospores representing variation in size and morphology observed among the isolates of *Diplodia* and *Diplodia*-like fungi. Size differences are relative. Name given here is that assigned by contributor of the culture. 1. *Diplodia zaeae*; 2. *D. maydis*; 3. *Diplodia* sp.; 4. *D. pinea*; 5. *Diplodia* sp.; 6. *Diplodia* sp.; 7. *D. oleae*; 8. *Lasiodiplodia theobromae*; 9. *D. natalensis*.

perienced in classifying fungi belonging to this group: (1) the choice of characters upon which the previous systems are based; (2) inadequate knowledge of the effects of various environments and substrates on the morphology of those characters; and (3) inadequate knowledge of the range of variation that individual isolates are capable of displaying when submitted to single-spore analysis.

In our laboratory we have attempted to evaluate critically the taxonomic characters that have been used by various authors to classify this group of fungi. The stability and range of variation of the characters have been tested under a number of different cultural conditions and nutrient regimes, including effects of carbon sources (Satour, Webster, and Hewitt, 1969a), nitrogen

sources (Satour, Webster, and Hewitt, 1969b), pH, temperature, light, and vitamins (Hewitt, Webster, and Satour, 1971), carbon:nitrogen ratio (Webster, Hewitt, and Satour, 1971), natural substrates (Webster and Hewitt, 1971); and the natural variation in *Diplodia natalensis* isolates from grape in California (Webster, Hewitt, and Polach, 1969).

This paper presents the results of an extensive analysis of single spores, and shows the natural variation encountered when members of this group of fungi are grown under similarly controlled conditions. The results are compared with those of earlier studies, and guidelines for future taxonomic attempts are proposed.

MATERIALS AND METHODS

In carrying out these studies we drew from a collection of over 250 isolates of fungi belonging to the Phaeodidymous:Sphaeropsidales taxon. Representative isolates are listed in table 1. (All tables follow p. 457.) The isolates were obtained from various collections and authors, from many different host plants from different parts of the world. The name of each isolate was retained as it was received. The following genera were represented among the isolates: *Diplodia*, *Botryodiplodia*, *Rhyncodiplodia*, *Macrodiplodia*, *Microdiplodia*, *Lasiodiplodia*, *Pellionella*, *Schizodiplodia*,

Macrophoma, *Physalospora*, *Botryosphaeria*, and *Sphaeropsis*.

All media and culture conditions have been described previously (Webster, Hewitt, and Polach, 1969; Webster and Hewitt, 1971). Except where noted, results reported here were obtained from cultures grown on potato-dextrose-agar (PDA) at $24^{\circ} \pm 2^{\circ}\text{C}$.

Methods used for isolating single spores, making observations, and measuring characters have been described previously (Webster, Hewitt, and Polach, 1969).

RESULTS

Earlier studies on the Phaeodidymous:Sphaeropsidales have shown that pycnidiospore characters, such as gross morphology, ornamentation, and size, are the most stable under varied cultural conditions. Therefore we have

concluded that they are the most useful characters for distinguishing genera and species. Table 1 shows comparison of 50 individual pycnidiospores from a single-spore culture of each of 75 separate isolates representing 10 genera

Plate II. 10. *Microdiplodia myriospora*; 11. *Diplodia warburgiana*; 12. *D. subsecta*; 13. *Diplodia pyrethri*; 14. *Microdiplodia osmanthi*; 15. *Rhyncodiplodia* sp.; 16. *Macrophoma* sp.; 17. *Diplodia* sp.; 18. *Pellionella tetonensis*; 19. *Lasiodiplodia theobromae*; 20. *Microdiplodia* sp.; 21. *D. philodendri*.

and over 45 species. (The names used are those assigned by contributing authors.) A summary of the nature of the pycnidium is also included.

As seen in table 1, many isolates submitted to us as different genera as well as species are clearly identical when pycnidiospores are compared (see isolates 47, 108, 103). It is also clear that various workers differed in their opinions on isolates submitted to us, because some with the same name are obviously different—for example, see 93 and 60, and 120 and 122.

To determine if the differences in size ($W \times L$) of pycnidiospores between and within the isolates is a consistent character, single spores were separated from each isolate, and cultures were established under uniform conditions on PDA. Twenty-five pycnidiospores were measured from each of the single-spore cultures. Statistical analysis with the Burroughs 7700 computer revealed that length and width were variable to the extent that, in some cases, significant F values were obtained for spore measurements between colonies originating from single spores taken from the same pycnidium (table 2).

To further test the range of natural variation that could be observed, 19 isolates of *Diplodia zeae*, the one species

most easily identified in this group, were subjected to a similar analysis. The results (table 3) again show that natural variation in spore size varied significantly in most pycnidia examined.

Throughout our studies we have routinely examined and photographed the gross morphology of pycnidiospores produced by the various isolates. In addition to width and length, surface characters (i.e., striations and granulations vs. smooth) and presence or absence of a constriction at the septum are the most consistent and recognizable. The range of pycnidiospore morphology encountered within the collection studied is represented in Plates I and II. A general description follows: Conidia characteristically dark, one-septate, but occasionally some may have two septa. Conidia may be smooth, granular, or striated. Granulation or striation is seen only in mature spores, while immature spores begin as smooth and usually hyaline. Conidia may be constricted or not constricted at the septum, depending on the isolate. The two cells may or may not be symmetrical. Length-to-width ratios range from 1.5:1 to 5.2:1, but in general there is a poor correlation, r (tables 1, 2, and 3), between mean lengths and widths of the samples observed from each isolate.

DISCUSSION

Results presented here and in earlier publications have led us to the conclusion that characters chosen to classify this group of fungi must meet the following conditions if a system of universal utility is to evolve;

(1) A worker should be able to identify a specimen whether it be living or dead, and provided, in the case of living material, that it is cultured on a standard medium under conditions available to all.

(2) Either the characters used should

be constant or the range of variation should be well enough understood that it can be taken into account.

(3) Since members of this group occur almost as frequently as saprophytes as they do as facultative parasites, host occurrence should not be used as a genus or species criterion. Physiologic specialization, if it is observed, would be determined by appropriate experimentation.

We have examined all of the characters used previously in attempts to clas-

sify these fungi, and have concluded that pycnidiospore characters best meet the stated conditions.

We propose that fungi producing dark, two-celled spores in a pycnidium be included in the genus *Diplodia*. The priority for this is substantiated by the chronological listing (table 4) of genera that have been proposed for this group. *Diplodia* Fr. (Fries, 1849) was founded in 1849, and characterized at that time by scattered pycnidia, subcutaneous to erumpent, black, papillate, with one-septate brown to black spores. Taubenhaus (1915) broadened this description to: "Pycnidia black, subcutaneous to erumpent or superficial, scattered or in groups, coespitose or in a stroma; hirsute or glabrous, paraphyses present or absent, spores hyaline, one-celled when young, but one-septate, brown to dark when mature." Zambettakis maintained *Diplodia* in *sensu nobis*, and reserved it for species with smooth spores, paraphyses and stromata absent, and separate, ostiolated, smooth (glabrous), fleshy-walled pycnidia without necks.

We concur with Taubenhaus (1915) in regard to pycnidial characters, but believe that the spore types of the genus should be expanded to include ornamentation (i.e., striation and granulation) and a consideration of the size of pycnidiospores. We therefore visualize the genus *Diplodia* as follows:

Diplodia Fr. (emend. Taubenhaus, 1915) emend. Webster, Hewitt, & Barbe.

Pycnidia black, subcutaneous to erumpent or superficial, scattered or in groups, coespitose or in or on a stroma, hirsute or glabrous; paraphyses present or absent; when young, spores hyaline and one-celled; at maturity, characteristically dark and one-septate. Mature spores may or may not be symmetrical, or constricted at the septum; smooth, striated or granulose. Length-to-width ratios range from 1.5:1 to 6.5:1.

In delimiting genera in this group, Zambettakis relied heavily on the presence or absence of paraphyses, spore ornamentation, position of pycnidia and whether they were glabrous or hirsute, and characters of the ostiole. With the emended description of the genus *Diplodia* offered above, those genera listed in table 4 become synonymous. It is proposed that spore shape, ornamentation, and size be used as species characters in the future.

Zambettakis has listed the synonymy of species that results from his proposal to retain 23 genera in this group. Since observations on the characters we propose to employ are not readily available, it is not possible at this time to formulate a key for species. We hope to achieve a sorting out of species synonymy in the future, based on both herbarium specimens and descriptions in the literature.

Although further study may possibly reveal characters acceptable for use in separating these fungi, such characters have not yet been discovered, particularly if considered in the light of the suggested guidelines.

Originally, mycologists recognized that the imperfect fungi were assembled in this class as a matter of convenience to allow researchers to recognize them and communicate studies dealing with them. We believe that, philosophically, mycologists agree that the groupings proposed under the *Fungi imperfecti* do not represent natural assemblages. Traditionally, however, workers have sought taxonomic systems for this group based on opinions of similarity due to relatedness. We do not disagree with recent proposals to attempt to classify the imperfect fungi on the basis of relatedness, because a high correlation has been observed between such systems and those used to classify the known perfect states. We do, however, feel that such systems are not at this time applicable to the Sphaeropsidales.

TABLE 1
OBSERVATIONS ON TAXONOMIC CHARACTERS IN SINGLE-SPORE CULTURES
OF SEVENTY-FIVE ISOLATES OF *DIPLODIA* AND *DIPLODIA*-LIKE FUNGI

Name (as received)	Isolate No.	Spore length (μ)		Spore width (μ)		Ornamen- tation	Number of septa	Constrict- ion at septa*	Pycnidia	
		Mean	Std. dev.	Mean	Std. dev.				Multi- or single- loculate	Para- physes*
<i>Diplodina coloradensis</i>	47	4.88	0.7257	2.68	0.4761	smooth	1	—	single	—
<i>Diplodina castaneae</i>	108	5.04	0.7348	3.52	0.5099	smooth	1	—	single	—
<i>Diplodia warburgiana</i>	63	5.56	1.0033	3.40	0.5774	smooth	0	—	single	—
<i>Microdiplodia</i> sp.	103	5.92	1.0770	4.36	0.4899	smooth	1	—	single	—
<i>Diplodina lycopersicae</i>	46	6.04	1.2741	2.92	0.7594	smooth & granular	0,1	+	both	—
<i>Diplodina frazzini</i>	48	6.68	1.0296	3.16	0.6880	smooth	0	—	single	—
<i>Microdiplodia myriospora</i>	238	7.00	1.4434	3.92	0.8622	smooth	1	—	single	—
<i>Diplodia pyrethri</i>	49	7.36	1.3808	5.12	1.2014	smooth	1	+	both	—
<i>Microdiplodia osmanthi</i>	92	7.84	0.9434	3.40	0.5774	smooth	1	—	single	—
<i>Microdiplodia perpusilla</i>	109	8.00	1.0801	4.00	0.5000	smooth	1	—	single	—
<i>Rhynchoiplodia ursusiformae</i>	93	9.04	1.2410	3.44	0.6506	smooth	1	+	single	—
<i>Sphaeropsis malorum</i>	61	9.24	0.7789	7.76	0.7789	smooth	0	—	single	—
<i>Diplodia subiecta</i>	241	9.48	0.8226	4.00	0.5774	smooth	1	—	both	—
<i>Phyalospora ilicis</i>	87	9.56	1.0832	6.76	0.6633	smooth & granular	0	—	multi	—
<i>Pellionella tetonensis</i>	75	10.12	1.4526	4.64	1.0360	smooth	0,1	slight	both	—
<i>Macrophoma</i> sp.	95	11.32	1.3760	6.24	1.8092	smooth	0,1	—	both	—
<i>Diplodia</i> sp.	14	13.88	1.4526	4.56	0.7118	smooth	1-3	slight	both	—
<i>Diplodia philodendri</i>	97	15.52	2.5515	8.40	1.6073	smooth	1	—	single	—
<i>Phyalospora obtusa</i>	258	16.84	2.3216	10.60	1.6330	smooth & granular	1,0	—	single	—
<i>Diplodia natalensis</i>	147	18.96	1.6951	11.16	0.6245	smooth & striated	1	—	single	+
<i>Diplodia</i> sp.	15	20.60	1.2583	11.76	1.0116	smooth & striated	1	—	both	+
<i>Phyalospora obtusa</i>	146	20.92	3.0676	5.44	0.8206	smooth & granular	1,0	—	both	—
<i>Phyalospora zeicola</i>	73	21.28	2.3721	11.00	0.7071	smooth & striated	1	—	both	—
<i>Diplodia tubericola</i>	148	21.48	1.7823	11.40	0.8660	striated	1	—	both	+
<i>Botryodiplodia</i> sp.	259	21.48	1.9880	11.40	0.7638	smooth & striated	1	—	multi	+

<i>Diplodia maydis</i>	145	21.60	2.9155	5.44	0.8206	smooth	1	slight	single	—
<i>Physalospora obtusa</i>	256	21.96	2.2635	10.92	1.1150	smooth	1	—	both	+
<i>Diplodia gossypina</i>	122	22.00	1.7795	10.32	0.6272	striated	1	—	single	—
<i>Diplodia</i> sp.	19-3	22.16	1.9079	11.52	0.8226	smooth	1	—	single	+
<i>Diplodia ursusiformae</i>	60	22.40	2.7988	12.88	1.0132	striated	1	—	both	—
<i>Diplodia zeae</i>	225	22.40	3.5000	5.36	0.4899	smooth	1	—	single	—
<i>Diplodia</i> sp.	18	22.68	1.9942	10.44	1.4457	smooth	1	—	single	—
<i>Diplodia zeae</i>	139	22.68	2.2121	5.16	0.3742	smooth	1	+	single	—
<i>Diplodia gossypina</i>	120	22.76	2.2598	13.00	1.1902	smooth & striated	1	—	multi	+
<i>Diplodia</i> sp.	12-2	23.12	1.9647	12.28	0.9798	smooth & striated	1	—	single	+
<i>Microdiplodia agaveae</i>	113	23.12	2.8036	11.88	1.0924	smooth	1	—	both	—
<i>Diplodia natalensis</i>	175	23.24	2.2038	11.72	0.9798	smooth & striated	1	—	both	+
<i>Diplodia natalensis</i>	230	23.32	1.9732,	11.84	0.8000	smooth & striated	1	—	both	+
<i>Botryosphaeria</i> sp.	257	23.56	2.5671	5.04	0.5385	smooth & granular	0,1,2	—	both	+
<i>Diplodia zeae</i>	22	23.64	3.2130	4.96	0.4546	smooth	1	+,—	single	—
<i>Diplodia natalensis</i>	9	23.88	1.6912	10.44	0.7681	smooth & striated	1	—	both	+
<i>Diplodia gossypina</i>	117	23.88	2.6820	12.24	0.9256	smooth & striated	1	—	single	+
<i>Diplodia zeae</i>	132	24.16	2.7791	5.32	0.4761	smooth	1	+,1	single	—
<i>Diplodia</i> sp.	17	24.20	1.9579	11.84	0.9434	smooth & striated	1	—	multi	+
<i>Microdiplodia myriospora</i>	240	24.32	2.6413	6.72	1.2423	smooth & granular	1,2	—	multi	+
<i>Diplodia</i> sp.	249	24.52	1.7108	12.04	0.7348	smooth & striated	1	—	multi	+
<i>Diplodia zeae</i>	25	24.56	4.1541	5.24	0.4359	smooth	1	—	both	—
<i>Diplodia zeae</i>	129	24.72	2.1703	5.23	0.6272	smooth	1	—	both	—
<i>Diplodia natalensis</i>	163	24.76	2.0265	12.60	1.0000	striated	1	—	both	+
<i>Diplodia zeae</i>	143	25.04	2.9366	5.20	0.4082	smooth	1	—	single	—
<i>Diplodia zeae</i>	133	25.28	2.4920	5.40	0.8165	smooth	1	+,—	single	—
<i>Diplodia zeae</i>	229	25.28	2.3188	5.48	0.5859	smooth	1	—	both	—
<i>Diplodia zeae</i>	140	25.32	4.6879	5.20	0.6455	smooth	1	—	single	—

Continued

TABLE 1 (Cont'd)

Name (as received)	Isolate No.	Spore length (μ)		Spore width (μ)		Ornamen- tation	Number of septa	Constriction at septa*	Pycnidia	
		Mean	Std. dev.	Mean	Std. dev.				Multi- or single- loculate	Para- physes*
<i>Botryodiplodia theobromae</i>	123	25.40	2.1409	13.48	1.3577	striated & smooth	1	—	both	+
<i>Diplodia</i> sp.	19-2	25.44	1.9596	11.12	1.1662	smooth	1	—	single	+
<i>Diplodia zeae</i>	227	25.48	2.3650	5.52	0.7141	smooth	1	+, —	both	—
Unknown	261	25.56	3.3302	11.08	0.7024	smooth & striated	1	—	both	+
<i>Diplodia natalensis</i>	11	25.64	1.2543	13.64	1.0755	smooth & striated	1	—	single	+
<i>Physalospora rhodina</i>	86	25.72	2.9933	13.12	1.2689	smooth & striated	1	—	both	+
<i>Botryosphaeria ribis</i>	254	25.72	2.6223	4.60	1.3229	smooth & granular	0,1,2	—	both	+
<i>Diplodia zeae</i>	144	25.76	3.8867	5.12	0.4397	smooth	1	—	both	—
<i>Diplodia natalensis</i>	157	26.36	1.5780	11.80	0.8165	striated	1	—	both	+
<i>Diplodia zeae</i>	142	26.48	3.7094	5.40	0.5774	smooth	1	—	both	—
<i>Diplodia zeae</i>	131	27.00	3.0414	5.24	0.7234	smooth	1	—	both	—
<i>Diplodia zeae</i>	134	27.08	2.7677	5.24	0.5228	smooth	1	—	both	+
<i>Diplodia zeae</i>	135	27.08	2.6602	6.76	6.9659	smooth	1	+, —	both	—
<i>Diplodia natalensis</i>	156	27.28	2.4413	13.00	1.1547	smooth & striated	1	—	both	+
<i>Diplodia zeae</i>	138	27.40	2.1985	5.76	0.6633	smooth	1	—	both	—
<i>Diplodia zeae</i>	141	27.52	2.7252	5.20	0.4082	smooth	1	—	both	—
Unknown	260	27.68	1.8193	13.20	1.5546	smooth & striated	1	—	both	+
<i>Diplodia zeae</i>	137	27.76	3.7225	5.68	0.7483	smooth	1	—	multi	+
<i>Diplodia zeae</i>	136	28.36	2.8119	5.40	0.6455	smooth	1	—	both	—
<i>Physalospora tucumanensis</i>	155	28.92	2.7526	5.36	0.7000	smooth & granular	1	—	both	—
<i>Diplodia pinea</i>	1	29.04	3.9421	11.16	1.2477	smooth & granular	1	—	both	+
<i>Diplodia zeae</i>	130	29.72	3.2726	5.00	—0.000	smooth	1	+, —	both	—

* + = present; — absent.

TABLE 2

SINGLE-SPORE ANALYSIS OF VARIATION IN WIDTH AND LENGTH OF PYCNIDIOSPORES OF SELECTED ISOLATES OF *DIPLODIA*-LIKE FUNGI

Name (as received)	Isolate no.	No. single-spore colonies	Length (μ)		Obs. F	Width (μ)		Obs. F	Corr. coeff. r	L:W ratio
			Mean	Std. dev.		Mean	Std. dev.			
<i>Diplodia coloradensis</i>	47	12	4.917	0.894	19.094	2.643	0.706	13.647	0.435	1.860
<i>Microdiplodia myriospora</i>	238	21	5.326	1.121	6.430	2.792	0.702	4.905	0.350	1.908
<i>Diplodia pyrethri</i>	49	22	7.013	1.537	4.587	3.958	0.724	5.638	0.522	1.772
<i>Microdiplodia osmanthi</i>	92	22	7.318	1.168	4.291	3.027	0.742	13.865	0.208	2.418
<i>Microdiplodia perpusilla</i>	109	20	7.972	1.381	4.878	3.716	1.1375	45.806	0.355	2.145
<i>Diplodia subsecta</i>	241	22	8.715	1.040	4.523	3.651	0.605	4.086	0.027	2.387
<i>Sphaeropsis malorum</i>	61	13	9.219	0.925	5.434	7.385	0.880	1.635	0.317	1.248
<i>Rhynchodiplodia ursusiformae</i>	93	20	9.644	1.162	4.772	3.390	0.674	7.901	0.402	2.845
<i>Pellionella tetonensis</i>	75	13	10.132	1.766	2.123	4.560	0.658	2.016	0.167	2.222
<i>Macrophoma</i> sp.	95	14	10.157	1.468	11.156	5.029	0.737	4.815	0.369	2.020
<i>Rhynchodiplodia ursusiformae</i>	59	26	10.490	1.819	7.958	4.917	0.958	5.564	0.424	2.133
<i>Diplodia</i> ?	14	13	12.046	2.603	3.887	4.637	0.631	2.458	0.444	2.598
<i>Physalospora</i> sp.	21	2	14.020	0.979	17.401	8.900	0.886	14.264	0.449	1.575
<i>Diplodia philodendri</i>	97	12	16.166	2.735	2.184	8.223	1.454	2.267	0.567	1.966
<i>Botryosphaera hypodermia</i>	29	5	21.048	2.261	12.353	14.560	1.628	10.787	0.201	1.446
<i>Diplodia</i> sp.	15	16	21.315	2.261	3.521	11.235	0.909	3.127	0.096	1.897
<i>Diplodia zeae</i>	132	17	21.429	2.867	2.812	5.221	0.459	1.125	-0.261	4.104
<i>Diplodia</i> sp.	19	14	23.100	2.118	2.457	11.949	1.067	2.630	0.086	1.933
<i>Diplodia tubericola</i>	148	23	23.186	2.025	5.566	12.144	1.178	13.367	0.151	1.909
<i>Diplodia</i> sp.	60	22	23.218	2.227	2.920	13.180	1.333	2.362	0.099	1.762
<i>Physalospora zeicola</i>	73	18	23.356	2.135	1.922	11.711	1.003	2.306	0.166	1.994
<i>Diplodia</i> sp.	16	14	23.434	2.230	3.091	11.720	0.991	2.627	0.055	1.999
<i>Physalospora obtusa</i>	146	10	23.464	2.155	8.597	9.800	0.994	3.480	0.060	2.394
<i>Botryodiplodia theobromae</i>	123	21	24.381	2.187	6.443	12.282	1.143	5.877	0.738	1.985
<i>Diplodia maydis</i>	145	22	23.964	3.596	1.943	5.120	0.336	1.956	-0.102	4.680
<i>Physalospora rhodina</i>	86	8	24.330	1.879	0.421	12.510	1.103	5.904	0.032	1.945
<i>Diplodia oleae</i>	34	14	24.349	2.014	6.872	12.077	1.288	14.076	0.235	2.016
<i>Botryodiplodia theobromae</i>	43	21	24.381	2.187	6.443	12.282	1.143	5.877	0.738	1.985
<i>Diplodia gossypina</i>	117	3	24.853	2.135	5.223	11.600	1.197	13.584	0.310	2.143
<i>Microdiplodia agavae</i>	113	17	25.127	1.7219	2.067	12.993	1.884	68.598	0.138	1.934
<i>Diplodia</i> sp.	249	26	25.271	2.368	6.216	11.694	0.894	2.115	0.047	2.161
<i>Diplodia</i> sp.	260	9	25.951	1.965	6.803	12.782	1.363	4.639	-0.019	2.030

TABLE 3
SINGLE-SPORE ANALYSIS OF VARIATION IN WIDTH AND LENGTH OF PYCNIDIOSPORES OF SELECTED
ISOLATES OF *DIPLODIA* FROM CORN (*ZEA MAYS* L.)

Name (as received)	Isolate No.	spore colonies No. Single-	Length (μ)		Obs. F	Width (μ)		Obs. F	Corr. coeff. r	L:W ratio
			Mean	Std. dev.		Mean	Std. dev.			
<i>Diplodia zeae</i>	132	17	21.429	2.867	2.812	5.221	0.0459	1.125	-0.261	4.104
<i>D. zeae</i>	227	19	21.625	3.279	2.300	5.194	0.436	3.167	-0.234	4.163
<i>D. zeae</i>	26	15	21.933	4.511	18.409	4.787	0.765	4.909	-0.128	4.582
<i>D. zeae</i>	65	20	22.214	3.561	8.014	4.956	0.501	1.892	-0.139	4.482
<i>D. zeae</i>	137	14	22.863	3.567	3.303	5.114	0.336	1.667	-0.166	4.471
<i>D. zeae</i>	22	15	23.013	3.410	4.064	5.213	0.436	0.921	-0.175	4.415
<i>D. zeae</i>	138	20	23.056	3.974	8.514	5.164	0.407	1.584	-0.272	4.465
<i>D. zeae</i>	19	14	23.100	2.118	2.457	11.949	1.067	2.630	0.086	1.933
<i>D. zeae</i>	229	26	23.468	3.301	2.175	5.139	0.470	1.108	-0.226	4.567
<i>D. zeae</i>	223	12	23.543	3.699	6.632	5.147	0.565	5.564	-0.270	4.574
<i>D. zeae</i>	228	23	23.884	3.433	3.228	5.087	0.333	1.706	-0.243	4.695
<i>D. maydis</i>	145	22	23.964	3.596	1.943	5.120	0.336	1.956	-0.102	4.680
<i>D. zeae</i>	143	22	24.431	4.527	6.552	5.178	0.537	3.232	-0.323	4.718
<i>D. zeae</i>	142	28	24.556	3.489	4.464	4.890	0.544	1.706	0.011	5.022
<i>D. zeae</i>	135	20	25.110	3.254	1.390	5.116	0.339	0.611	-0.186	4.908
<i>D. zeae</i>	134	14	25.277	3.732	6.235	5.123	0.329	1.911	-0.264	4.954
<i>D. zeae</i>	130	22	25.546	3.698	4.585	5.140	0.373	1.268	-0.259	4.970
<i>Diplodia</i> sp.	260	9	25.951	1.965	6.803	12.782	1.363	4.639	-0.019	2.030
<i>D. zeae</i>	141	28	27.050	4.237	7.042	5.114	0.500	6.380	-0.079	5.289

TABLE 4

CHRONOLOGY OF GENERA IN THE PHAEODIDYMAE:SPHAEROPSIDALES

Year	Genus and Author	Reference
1849	<i>Diplodia</i> Fries	Summa Vegetabilium Scand., p. 416
1880	<i>Botryodiplodia</i> Saccardo	Michelia 2:7
1884	<i>Chaetodiplodia</i> Karsten	Hedwigia 23:62
1884	<i>Macrodiplodia</i> Saccardo	Syll. Fung. 3:374
1884	<i>Diplodiella</i> Karsten	Hedwigia 23:62
1896	<i>Pellionella</i> Saccardo	Bull. Soc. Myc. Fr. 12:68
1903	<i>Microdiplodia</i> Allesches	Rabenhort Kryptogamen Flora, I. 7:78
1904	<i>Diplodiopsis</i> P. Henn	Hedwigia 43:386-87
1907	<i>Rhynchodiplodia</i> Briosi et Farneti	Atti Inst. Bot. di Pav.
1909	<i>Chaetoconis</i> Clements	Syll. Fung. 25:317
1909	<i>Lasiodiplodia</i> Griff. et Maub (Ell & Everhart)	Bull. Soc. Myc. France 70:330
1911	<i>Didymosporiella</i> Trav. et Mig.	
1916	<i>Placodiplodia</i> Bubak	Ber. Deut. Bot. Gaz. 34:305
1916	<i>Syndiplodia</i> Peyronel	Men. R. Acad. Sc. Torino Ser II. 66:55
1918	<i>Diblostospermella</i> Spegaz.	Nat. mic. in Physics, IV:291
1918	<i>Leprieurina</i> Arnaud	Ann. Ecole Nat. Agr. Montpel 16:210
1927	<i>Nemadiplodia</i> Sibilis	Boll. R. St. Pat. Veg. Nouv. Ser. 7:433
1937	<i>Metadiplodia</i> Sydow	Ann. Mycol. 35:359
1947	<i>Zernya</i> Petrak	Sydowia 5:277
1951	<i>Microbotryodiplodia</i> Comara	Myc. Aliquot. Lusit., Agr. Lusit. 13(3):206
1954	<i>Granulodiplodia</i> Zambett.	Bull. Soc. Myc. France 70:330
1954	<i>Hemiodiplodia</i> Zambett.	Bull. Soc. Myc. France 70:224
1954	<i>Lasiodiplodiella</i> Zambett.	Bull. Soc. Myc. France 70:229
1954	<i>Paradiplodiella</i> Zambett.	Bull. Soc. Myc. France 70:320
1954	<i>Schizodiplodiella</i> Zambett.	Bull. Soc. Myc. France 70:302
1954	<i>Striodiplodia</i> Zambett.	Bull. Soc. Myc. France 70:334
1954	<i>Strionemadiplodia</i> Zambett.	Bull. Soc. Myc. France 70:233
1954	<i>Synnemadiplodia</i> Zambett.	Bull. Soc. Myc. France 70:230

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