[Reprinted from PHYTOPATHOLOGY, September, 1934, Vol. XXIV, No. 9, pp. 953–983.]

PHYTOPATHOLOGICAL AND TAXONOMIC ASPECTS OF OPHIOBOLUS, PYRENOPHORA, HELMINTHOSPORIUM, AND A NEW GENUS, COCHLIOBOLUS

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(Accepted for publication December 13, 1933)

OPHIOBOLUS HERPOTRICHUS AND O. GRAMINIS

The genus Ophiobolus, erected by Riess (65) in 1854, was extended into the sphere of phytopathological interest in 1881 with the transfer to it by Saccardo (66) of the fungus described by him (67) only 6 years earlier as *Rhaphidophora graminis* together with the form that, originally described by Fries (26, v. 2, p. 504) as *Sphaeria herpotricha,* later had been cited as *Rhaphidospora herpotricha* (Fries) by Fuckel (28), and as *Rhaphidophora herpotricha* by the Tuslasne brothers (73). The transfer, as is evident from a statement of somewhat later date (68, v. 2, p. 337), was carried out because of nomenclatorial necessity, the genera Rhaphidospora Fries and Rhaphidophora Ces. and De Not., assuming they can be regarded as separate taxonomic entities on strictly formal grounds, having been found homonymous with genera of seed plants erected earlier by Nees and Hasskarl, respectively.

The earlier descriptive literature of the 2 fungi conveys little intimation of pathogenic relationships, the only direct intimation, indeed, here being contained in the somewhat reluctant statement by the Tulasne brothers that they had found *Ophiobolus herpotrichus* on fading wheat culms as early as the end of June, its appearance there being associated with subsequent premature yellowing of the heads and blackening of the stems. In 1880 Cugini (6) found a wheat disease in Italy, associated with blackening and killing of the roots, and with the development of a black incrustation over the surface of the stem. This disease he attributed to *Rhaphidospora herpotricha,* on the strength of an identification by Passerini; and the same fungus, referred to as *O. herpotrichus,* was held responsible for a similar disease encountered by Cugini (7) in 1889. In the meantime Morini (55), in investigating the causes of a new disease of wheat in Italy, had discovered, though apparently only on a single diseased specimen, a fungus that he held to agree well with *O. herpotrichus* except in having shorter asci and

ascospores, these structures measuring only 90–114 μ and 75–84 μ, respectively. This fungus he had described as *O. herpotrichus* var. *breviasci.*

The dimensions given by Morini together with his characterization of the ascospores as pale yellowish make it hard to avoid the conclusion that he was dealing not with *Ophiobolus herpotrichus* at all, but with *O. graminis.* Of the latter species he makes no mention, a fact that, under the circumstances, is difficult to explain except on the assumption that he was unaware of its having been described. For that matter neither of Cugini's papers makes mention of *O. graminis,* though the statement in the later one to the effect that Saccardo had said in the "Sylloge fungorum" that the species involved (presumably *O. herpotrichus*) was found on Cynodon and Agrostis, indicates that Cugini may have inadvertently confused or, perhaps, purposely integrated the portion of Saccardo's diagnosis of *O. graminis,* referring to habitat (in which Cynodon and Agropyron were cited as hosts) with the diagnosis of *O. herpotrichus.* It is possible therefore that Cugini's exclusive preoccupation with *O. herpotrichus* may have been due less to lack of knowledge concerning the other form reported on graminaceous hosts than to doubt as to the independence of that form from the much older and better established species the graminicolous character of which apparently had already become somewhat a matter of accepted tradition.

Such doubt, at all events, would seem to have prevailed after Prillieux and Delacroix (61) in 1890 reported *Ophiobolus graminis* as the cause of the wheat disease in France long known there as *piétin* or *maladie du pied.* For Frank (22), in reporting *O. herpotrichus* as responsible for serious damage to wheat in Germany in 1894, stated not only that the fungus had been known for some time in Italy, but also that it had a few years earlier been observed in the region surrounding Paris, there having occasioned the same injuries as in Germany. Any possible uncertainty as to which French report was alluded to in the statement, was dispelled in two later publications (23; 24, v. 2, p. 306–307) in the second of which, especially, the paper by Prillieux and Delacroix was explicitly cited in connection with the representation that *O. herpotrichus* had been found in France as the cause of *piétin* or *maladie du pied.* As the French authors had clearly set forth that their identification of the parasite causing *piétin* was based on its correspondence to Saccardo's description of *O. graminis,* especially with respect to dimensions of asci and ascospores, and as Frank was evidently cognizant of the different dimensions attributed to *O. herpotrichus,* since he cited them in one of his publications (24), it may be inferred that he regarded the 2 species as one in spite of knowledge of the differences in morphology ascribed to them.

This inclusive species concept became of moment in phytopathological

literature when in Frank's several publications *Ophiobolus herpotrichus* was set forth as one of the most destructive parasites of wheat in Germany, with the imputed destructiveness being, moreover, vividly brought into relief in the formidable term *Weizenhalmtöter* applied to the fungus. Unfortunately, these papers contain few clues as to the extent to which their author may have been dealing with *O. herpotrichus* on the one hand and with *O. graminis* on the other. The most tangible clue undoubtedly is to be found in the colored plate accompanying the last of Frank's (25) papers on the *Weizenhalmtöter,* which it may be presumed was prepared under his direction or must at least have met with his approval. In this plate the figures of the asci and ascospores show proportions assuredly much more suggestive of *O. graminis* than of *O. herpotrichus.* Later, to be sure, Krüger (41), on the basis of actual identifications, concluded that *O. herpotrichus,* evidently in its true restricted sense, was, in spite of unimpressive pathogenicity under experimental conditions, the species generally concerned in Germany, and he held this conclusion to confirm an assumption to the same effect that he credited to Frank. Whatever assumptions may be credited to Frank would, however, judging from his published works, need to be predicated on an *O. herpotrichus* including within its limits both the *O. herpotrichus* and the *O. graminis* of other authors. In contrast to Krüger, McAlpine evidently fully understood Frank's ambiguous application of *O. herpotrichus.* This author, who at first (45) considered the "wheat-stem-killer (*Ophiobolus herpotrichus*)" in relation to "take-all," which had long been destructive to wheat in Australia, later (46) referred the disease to *O. graminis,* explaining that the fungus in question was identical with the wheat-stem-killer determined by Frank in 1894, as well as with the parasite found by Prillieux and Delacroix to be the cause of footrot in France. It is not apparent that the ambiguity was recognized by van Hall (30), whose extended account of a disease of wheat in Holland, which he attributed to the *tarwehalmdooder,* added to the reputation of *O. herpotrichus* as a serious pathogen.

This reputation, however, during the 3 succeeding decades, has not been fully sustained, though Crüger (5), as late as 1929, attributed to *Ophiobolus herpotrichus* an important rôle in the causation of foot disease. Owing to the unimpressive performance of the fungus under ordinary experimental conditions, Foex and Rosella (20, 21) in France, van de Laar (43) in The Netherlands and Schaffnit (69) in Germany, have come to regard it as a parasite of secondary importance. Rather curiously *O. herpotrichus* has, hitherto, apparently never been recorded as occurring in the United States, though the writer has found a fungus morphologically agreeing with and evidently referable to that species regularly occurring in great abundance on quack grass (*Agropyron repens* (L.) Beauv.) during April, May,

and early June in Maryland, the District of Columbia, and Virginia every year from 1922 to 1933, as well as near Madison, Wis., in the corresponding seasonal periods in 1919 and 1920, and on Long Island in and about Brooklyn, N. Y., in 1921. Evidently quack grass serves, at least in the northern part of this country, as a most congenial host of *O. herpotrichus,* and but for the low esteem in which this grass is held the reputed stem-killer of central and western Europe might long have been a familiar object to American pathologists. If, as seems not unlikely, the fungus is similarly frequent in northern and central Europe, the earlier reluctance of investigators in those regions to accept *O. graminis* as a separate species has some explanation. For Saccardo's citation of Agropyron as one of the two genera representative of the hosts of *O. graminis* could hardly have failed to convey somewhat the impression that the Ophiobolus occurring so abundantly and so frequently to the exclusion of any congeneric fungus on the very widely distributed member of that host genus must somehow have been the one on which his diagnosis was based.

Although the paper of Mangin (50) published in 1899, cast doubt on the causal relationship of *Ophiobolus graminis* to *piétin* in France, Delacroix (10), 2 years later, reestablished the position of the fungus as at least one of the parasites involved in that disease. In 1901 appeared also a report by Hori (36) attributing foot rot in Japan to *O. graminis,* and in 1904 McAlpine's account, already referred to, connecting the fungus with take-all in Australia. Thereafter the destructively pathogenic character of *O. graminis* appears never to have been seriously questioned. In the United States the fungus and the disease caused by it have been treated more especially in publication by Kirby (39, 40), Davis (9), and McKinney (47); while recent European testimony to the harmful effectiveness of *O. graminis* is given by Foex and Rosella, by van de Laar, by Schaffnit, and by Moritz (56).

Such degree of confusion as earlier obtained with respect to *Ophiobolus graminis* and *O. herpotrichus* had, it may be admitted, some excuse in the resemblance in habit between the 2 fungi. Similarities such as those expressed in the rather characteristic localization of the perithecia on the basal portions of grass culms, and in the presence of the superficial network of dark hyphae over the adjacent host substratum, constitute features of parallelism that would seem to indicate a narrowly congeneric relationship. Since these features are set forth also in Tullis' (74) account of *O. oryzinus* Sacc., the cause of a rice disease in Arkansas, and are sustained here besides by general similarities in dimensions of asci, as well as in dimensions, septation, and arrangement of ascospores, there is reason to believe that this parasite, too, is included in the same intimate relationship. *O. cariceti* (B. and Br.) Sacc., described originally from *Aira caespitosa* in

England, was found by Fitzpatrick, Thomas, and Kirby (18) to resemble the take-all fungus so closely in morphology of perithecium, asci, and ascospores that they held it to be the same organism and, accordingly, favored relegation of the name *O. graminis* to synonymy. However, as the only material of *O. cariceti* used in their comparisons consisted of microscope preparations and herbarium specimens no longer in living condition and, moreover, not entirely above question in regard to authenticity, the resemblances observed by them have, in conformity with representations made by McKinney, been generally deemed insufficient to justify so important a nomenclatorial change as the one they proposed. Of course, the possibility of such identity, earlier predicated by Berlese (2, v. 2, p. 119–120) in his citation of both *O. cariceti* and *O. graminis* as synonyms of *O. eucryptus* (B. and Br.) Sacc., is not yet to be dismissed; and, in any case, the resemblances referred to together with the similarity in position on the host, also pointed out by Fitzpatrick, Thomas, and Kirby, would seem to indicate a close relationship in the same series.

It appears probable that *Ophiobolus oryzae* described by Miyake (54) from rice in Japan may likewise belong in the same group with *O. graminis* and *O. herpotrichus,* even though its occurrence on the leaves and glumes of the host plant rather than on the basal parts fails to sustain the parallelism in parasitic habit. As to various other species of Ophiobolus recorded from dead graminaceous materials, as, for example, *O. medusae* E. and E. on culms of *Spartina* sp. in New Jersey, *O. festucae* Tracy and Earle on dead leaves of *Festuca* sp. in Colorado, *O. trichosporus* Ell. and Ev. on grass stems in Canada, *O.* (later *Ophiochaeta*) *trichellus* Bomm. Rouss. Sacc. on the lower leaves of *Psamma arenaria* Roem. and Schult. in Belgium, *O. seriatus* Syd. on dead stems of *Bambusa* sp. in the Philippines, *O. graffianus* Sacc. on the decaying caryopsis of *Coix lacrima-Jobi* L. in the Philippines, and *O. panici* Syd. on dead sheaths of *Panicum miliaceum* in the Philippines, the available information is too scanty for any conjecture as to their more intimate affinities. In the main, no doubt, these species owe their assignment to Ophiobolus much more to gross conformity with the broad Saccardian application of the genus, than to their degree of similarity to the 2 parasites through which the genus has become familiar to plant pathologists.

HISTORICAL AND TAXONOMIC ASPECTS OF THE GENUS OPHIOBOLUS IN GENERAL

For, although *Ophiobolus graminis* and *O. herpotrichus* have occupied prominent places in mycological literature, their influence on the taxonomic history of the genus in which they are now included has remained unimportant. Indeed, in their present systematic setting, there is little historical

justification for regarding either the one or the other as a pivotal species. Ophiobolus was erected on a fungus found presumably in saprophytic relationship on *Carduus arvensis* Robs., and described as new by Riess under the name *Ophiobolus disseminans.* The newness of the species, to be sure, failed to convince contemporaneous writers some of whom, like Duby (63, no. 57), evidently considered it to be identical with the fungus that Sowerby (71, v. 3, pl. 394, fig. 3) had much earlier found "scattered on the stalk of a thistle" and described rather inadequately as *Sphaeria acuminata,* while others held it to be the same as Wallroth's (77) *Sphaeria carduorum,* of which the host substratum was only slightly more definitely indicated in the words "*ad caules Carduorum siccos.*" Apart from the question of specific identity the fungus, according to Riess' description, was certainly not devoid of morphological distinctiveness, the many-septate ascospores being set forth as originating joined end to end in pairs, later to become separated individually at a commissure located between two swollen segments, and thus finally appear with the characteristic snakelike terminal swelling signalized in the generic name. Yet neither the rather astonishing development ascribed to the ascospores, which now would more likely be interpreted as representing disarticulation of a single ascospore into halves, nor the arresting nodosity of the inflated spore segments appears to have impressed writers of the time as constituting a character of generic significance. The disesteem in which both the genus and species launched by Riess soon came to be held is reflected in the use of the various binomials applied presumably to the same fungus, Rabenhorst (63, no. 530) citing it as *Rhaphidospora disseminans,* the Tulasne brothers as *Rhaphidophora carduorum* and Fuckel as *Rhaphidospora carduorum.*

In the same publication with the latter citation Fuckel further cited under Rhaphidospora, *R. rudis* (Riess) and *R. rubella* (P.), thereby in effect merging with Rhaphidospora, in addition to Ophiobolus, the 2 genera typified in these species. Of these 2 genera Entodesmium had been erected by Riess in 1854 on the newly described *E. rude,* the spores of which were set forth as being produced within clavate asci in chains of approximately 16 individuals,—a characterization now more aptly interpreted as referring to ascospores with approximately 15 septa disarticulating into their component segments. Leptospora, the second of the amalgamated genera, had been erected by Rabenhorst (62) in 1854 on a fungus he regarded as identical with the *Sphaeria porphyrogena* described as new by Tode (72) in 1791, but treated by Persoon (60) in 1801 as a variety of *Sphaeria rubella.* The distinctive feature setting his genus apart from Rhaphidospora was found, according to Rabenhorst, in the non-septate character of the ascospores, but as early as in 1863, Cesati and De Notaris (3), whether from doubt as to the reality or as to the significance of this imputed feature, cited the presumptive type species as *Rhaphidophora porphyrogena.*

In any case it is apparent that long before the publication of the *Sylloge fungorum* began, species of types sufficiently distinctive to have led earlier to the proposal of several separate genera had wisely or unwisely been brought into the same fold. Favored no doubt by the distinguished example set by the Tulasne brothers, the term Rhaphidophora apparently proposed by Cesati and De Notaris as a mere modification to avoid homonymy with Nees' genus, continued for about 2 decades to hold the field, though the earlier term reappeared now and then, as in Fuckel's meritorious work already cited. When it was finally realized that, curiously enough, the substituted term was a homonym no less than the one it displaced, Saccardo, as has been noted previously, revived Ophiobolus, applying it, of course, not only to the forms corresponding closely to the type on which it was erected, but also to the multitude of forms corresponding to the several other types with which its original type had in the meantime become agglutinated. In the second volume of the "Sylloge fungorum," although a number of species of the abandoned Rhaphidophora were committed to a new Saccardian genus Ophioceras, 63 species were compiled in Ophiobolus, and additions in subsequent volumes have more than trebled this number, even if allowance is made for the 7 species with more or less chaetose perithecia transferred to another Saccardian genus, Ophiochaeta, in 1895.

The very considerable increase in number of species assigned to it could hardly have failed to bring into relief the rather indiscriminating inclusiveness of the rehabilitated genus. Yet it was more from motives of taxonomic correctness than of expediency that Höhnel (34), in 1918, submitted a remedy in proposing to reestablish Entodesmium and Leptospora as genera independent of Ophiobolus, assignment of the various species to be governed by their similarity to the 3 historical types, *E. rude, L. poryphyrogona* and *O. acuminatus,* respectively. From his discussion it may be inferred that he regarded the complete disarticulation of the ascospores prevalent in the first of these types as an essential feature of Entodesmium, and median disarticulation between 2 swollen segments set forth in Riess' account of the second type, and also illustrated by Berlese in all the species figured by him under his Leptosphaeriopsis, as an essential feature of Ophiobolus. Each of these modes of disarticulation would seem to occur in only a relatively small proportion of the species compiled in Ophiobolus in the *Sylloge fungorum,* and it seems quite possible that their occurrence here may indeed constitute a feature representative of such thoroughgoing parallelism as distinguishes the members of natural genera. Leptospora, however, was apparently left by Höhnel in a more ambiguous state, for although it was to be constructed about *L. porphyrogona,* it was evidently to serve at the same time as repository for all forms included by Saccardo in Ophiobolus

that have spores, whether nodose or not nodose, that on maturation remain filamentous, that is, do not in any normal way become disarticulated. Manifestly this disposition would have transferred to Leptospora, with only relatively small reduction, the main mass of forms compiled in Ophiobolus. What Rabenhorst had emphasized as a distinctive feature of Leptospora, an imputed unicellular condition of the ascospores, was omitted from discussion, and not without justification from factual considerations, since Winter had described the spores of *O. porphyrogonus* in at least their later stages as being provided with many cross walls.

In a second paper Höhnel (35) applied to the genera under discussion the moot structural distinction between discrete fruiting bodies, of which he was a most persistent exponent. Finding the type species of Leptospora to be of "sphaeriaceous" structure, he made such structure a requirement for the retention of any fungus in the genus, the forms to be excluded by reason of their "dothideaceous" character being provided for in a new genus, Leptosporopsis. Since *Ophiobolus herpotrichus* also was revealed as being *"ganz deutlich dothideal,"* it may be inferred that inclusion in Leptosporopsis is to be counted among the events in the taxonomic history of that economically important species. Examination of *Entodesmium rude* likewise showed dothideaceous structure, whereas *O. acuminatus* was recognized as truly sphaeriaceous,—these findings, to be sure, not altering the narrow limits adopted by Höhnel for the 2 genera concerned in them. A rather considerable widening of the limits of Ophiobolus would seem to have been involved, however, in the later recommendation by Weese (78) that the species with 1 or 2 nodes and not given to disarticulation, which Höhnel had preferred to include in Leptospora, be transferred to the former genus.

The dispositions of Höhnel and of Weese appear to have proceeded from an assumption that if the species in Ophiobolus as applied by Saccardo were distributed judiciously mainly among the 3 historical genera and the new Leptosporopsis the resulting arrangement would somehow approximate, if not actually constitute, a natural one. Such as assumption would seem at least premature, for, on the basis of our present knowledge, only a relatively small number of the species can with tolerable certainty be assimilated as natural congeners to the type species of the historical genera, leaving, therefore, a large residue of unassimilated forms, which will continue to require an obviously collective genus. Now, since Ophiobolus has served as collective genus for a half century, its rehabilitation as a restricted genus would entail shifting of this function elsewhere with numerous changes in established binomials. Considerations of expediency may, therefore, be expected to militate strongly against such rehabilitation, possibly with the result that the group involved may again be integrated, even if

somewhat in defiance of strict priority, in Berlese's genus Leptosphaeriopsis. Revival of Leptospora and Entodesmium, neither of which has in any serious degree been compromised nomenclatorially, would entail no similar difficulty, and might well serve a good purpose, though, evidently, only if through study more detailed than routine examination of mostly dead herbarium specimens, their memberships were maintained in acceptable homogeneity.

Even if the elevation of Ophiochaeta to generic rank in 1895 relieved Ophiobolus as first applied by Saccardo of only relatively few species, it yet came to affect the nomenclature of both the take-all fungus and the reputed wheat stem killer. Hara (31), in 1916, made reference to the former of these parasites under the binomial *Ophiochaeta graminis* (Sacc.) Hara, and the latter was cited in 1930 by Clements and Shear (4, p. 277) under the binomial *O. herpotricha* (Fr.) Sacc. as the type species of the genus Ophiochaeta. The aptness of these dispositions would seem somewhat doubtful, for, judging from Berlese's figures of *Ophiochaeta helminthospora* (Rehm) Sacc. and of *Ophiochaeta penicillus* (Schmidt) Sacc. as well as from the illustrations of *Ophiochaeta chaetophora* (Crouan) Sacc. given by Malbranche and Niel (49), the perithecial setae of at least 3 of the forms Saccardo definitely referred to Ophiochaeta were represented by apparently rigid, rather stiffly radiating bristles. Bristles of such character are not readily identified with the flexible filaments that, although often attached here and there to the fruiting bodies of the two graminicolous parasites, have much the appearance of the hyphae that make up the mycelial plate. Berlese (2, v. 2, p. 127) recognized the distinction clearly and held that *O. herpotrichus* could not be referred to Ophiochaeta. Nor is it clear that Saccardo ever actually transferred *Ophiobolus herpotrichus* to Ophiochaeta, though his statement that this species must be more fully investigated indicates that he had considered such a transfer. In respect to shape of ascospores none of the 3 species of Ophiochaeta figured by Berlese and by Malbranche and Niel show close similarity to *Ophiobolus graminis* and *O. herpotrichus,* or for that matter, to one another. The genus as constituted gives the impression of being a heterogeneous assemblage of species and, therefore, as Weese intimated, might perhaps just as well have remained in Ophiobolus.

MORPHOLOGICAL FEATURES OF THE HELICOID ASCIGEROUS SERIES

In 1925, through the discovery of the ascigerous stage of a fungus causing leaf spot of maize in the warmer regions of the world (13), the genus Ophiobolus in the broad Saccardian sense was brought into relation with a second field of phytopathological interest, certainly no less important than the first. The maize parasite directly concerned was one of the rather

numerous series of graminicolous species of Helminthosporium distinguished by conidia of typically elongated-elliptical outline that germinate by the production of 2 polar germ tubes, one from the apex, and the other from a narrow zone immediately surrounding the basal scar. As the thoroughgoing parallelism between most known members of the series was fairly obvious from their morphology as well as from their cultural and pathogenic behavior, it was inferred that, when perfect stages should be discovered for other members of the series, they very probably would show intimate morphological similarity with the one then described as *Ophiobolus heterostrophus* Drechsl. The correctness of this inference has since been confirmed. In 1927 Ito and Kuribayashi (38) described under the binomial *Ophiobolus miyabeanus* the ascigerous stage of *H. oryzae* B. de H. A year later Nisikado (57) described under the binomial *Ophiobolus kusanoi* the perfect stage of a fungus causing leaf blight of *Eragrostis major* Host, the conidial condition of which was referred to as *H. kusanoi.* In 1929 Ito and Kuribayashi (42) issued the description of *Ophiobolus sativus,* the ascigerous condition of the widely destructive *H. sativum* Pamm., King and Bakke and, in 1930, followed this with a description (37) of *Ophiobolus setariae,* the ascigerous stage of *H. setariae* Sawada. Martin (51), in a report published in 1931, stated that C. W. Carpenter had obtained the ascigerous stage of the fungus causing brown stripe of sugar cane, *H. stenospilum* Drechsl., and found it to be referable to Ophiobolus. As far as can be determined from the rather immature perithecial fructifications that the writer has obtained in cultures of *H. micropus* Drechsl., a parasite on *Paspalum boscianum* Flügge, widely distributed in the Southeastern States, this member of the series provides no departure from the morphological trend of the others.

This morphological trend is manifested conspicuously in pronounced helicoid arrangement of the ascospores within the ascus, taken together with rather unusual dimensional relationships that in part ensue therefrom. Even in *Ophiobolus kusanoi,* the smallest of the 5 ascigerous forms known in detail, the diameter of the ascospore (5 μ) exceeds the homologous dimension in the general run of species assigned to Ophiobolus, while the ranges of values given for *O. heterostrophus* (6–9 μ) are comparable with the asci rather than with the ascospores of a large proportion of the species compiled in the genus, and, indeed, in not a few cases even exceed them. Obviously, an ascus to contain a full complement of 8 such spores would, under any circumstances, need to be of proportionately greater diameter, but here, owing to the additional spatial requirements entailed in the helicoid arrangement of the spores, it needs to be of a diameter exceeding the corresponding dimension of Ophiobolus species generally, in a measure, more than proportional to the greater widths of the ascospores. It is not

surprising, therefore, that the published values for diameter of ascus in *O. heterostrophus* (24–28 μ), *O. setariae* (22–32 μ), *O. miyabeanus* (25–32 μ), and *O. sativus* (32–45 μ) are unequalled among the corresponding values given under the genus in the *Sylloge Fungorum,* and that only a few of the latter are comparable even with the values (14–18 μ) given for *O. kusanoi.* As the spiral arrangement permits the ascospores to attain a length considerably greater than that of the ascus, spores of unusual length (the maximum value given for this dimension in *O. miyabeanus,* 468 μ, would be regarded as extraordinary in any group of fungi), as well as of respectable diameter are borne in asci that, among scolecosporous groups, appear more remarkable for width than for length.

It is, of course, not to be asserted that the features largely giving character to the ascigerous series under consideration are entirely unknown among the numerous unsifted saprophytic forms compiled in Ophiobolus. As was pointed out earlier in the discussion of the parasite causing leaf spot of maize, helicoid arrangement of ascospores, besides being well illustrated in Berlese's figures of *Ophiobolus camptosporus* Sacc., has been attributed to both *Ophiobolus helicosporus* (B. and Br.) Sacc. and to *Ophiobolus galii* Rich., not to mention *Ophiobolus chaetophorus* (Crouan) Sacc., later transferred to Ophiochaeta. A fairly pronounced spiral condition with the direction of rotation reversing several times has been observed in especially well-developed material of a fungus collected near Clarendon, Virginia, with exceptionally long asci and longer ascospores, which, otherwise, in a general way, conforms morphologically to the species or series of species customarily referred to as *Ophiobolus porphyrogonus.* However, in none of these forms is the one feature of similarity sustained by others in a degree making for a parallelism indicative of close relationship with the helicoid graminicolous series. The single, median, nodose cells present in the spiral ascospores of *O. camptosporus* precludes a more complete similarity, and the dimensions of this species are hardly of an order to provide a close parallelism. As measurements of *O. chaetophorus, O. helicosporus* and *O. galii* have apparently never been published, information in regard to dimensional relationships is not here available. The very slender and conspicuously filamentous spores of *O. porphyrogonus* and of species closely related to it, differ so markedly from those of any of the helicoid graminicolous series that an intimate connection would seem rather definitely out of question. In many species of Ophiobolus a spiral tendency is often or occasionally evident in the upper portions of the ascospores, even where these structures are for the most part straight and disposed parallel to one another. Such a tendency represented, for example, in 2 specimens deposited in Mycological Collections of the Bureau of Plant Industry under covers labelled:

Sydow, Mycotheca germanica. 2343. *Ophiobolus ulnosporus* (Cke.) Sacc. Auf Stengeln von *Ballota nigra*, Brandenburg: Tamsel. 24. 7. 1927.

Fungi Dakotenses, Brenckle. 237. *Ophiobolus claviger* Harkn. On *Artemisia biennis*. Kulm, N. Dak., Aug. 18, 1913.

rarely entails more than a half turn of rather wide pitch, so that the ascospores are only infrequently if ever appreciably longer than the asci in which they are contained.

ASEXUAL REPRODUCTION IN THE HELICOID SERIES AND IN OPHIOBOLUS

Although the series of strongly helicoid graminicolous species thus exhibits fairly distinctive features in the ascigerous stage, it will undoubtedly continue to be known mainly through the conidial stage achieved in the widely familiar group of forms within the genus Helminthosporium characterized by the special type of germination to which reference has been made. In general, the conidia here are produced abundantly on the natural substrata, and with few exceptions, also on artificial media, so that membership in the series is ordinarily very easily determined, even though identification of the individual species may require detailed comparisons. Yet the literature on Ophiobolus, outside of the publications dealing with *O. heterostrophus, O. kusanoi, O. miyabeanus, O. sativus, O. setariae,* and the brown-stripe parasite, makes no mention of any conidial condition suggestive of Helminthosporium. Indeed, relatively few contributions on subsidiary stages of any kind are to be found, and of these not all are in as complete harmony as might be desired.

The Tulasne brothers in their account of the fungus or fungi that they treated as *Rhaphidophora herpotricha* included as a stage in the life history set forth therein a pycnidial form producing elongated 6- to 10-celled stylospores measuring 25 to 35 μ long by 3.5 to 5 μ wide. It is not apparent that *Hendersonia herpotricha* Sacc. with 8-septate spores, 36 μ long and 6 μ wide, later cited by Saccardo as the pycnidial stage of *Ophiobolus herpotrichus,* was intended to have reference to the same sphaeropsidaceous form; or for that matter, whether so intended or not, that it actually had such reference. Hiltner (32), in 1912, asserted his continued belief in the association of a pycnidial form designated by him as *Hendersonia herpotrichoides* Sacc. that had appeared in 1894, following incubation in a damp chamber, on affected wheat plants originating in Saxony that year, with the Ophiobolus perithecia that had later developed thereon. Frank (23) considered it likely that a species of Phoma that he called *P. tritici* was associated with his *Weizenhalmtöter.* The genetic connection mentioned by Frank has no more received confirmation than has that mentioned by Hiltner; and in both cases uncertainty as to the identity of the species of Ophio-

bolus concerned is present as a disturbing consideration. Similarly dubious circumstances surround the report by Voges (76) of a connection between *O. herpotrichus* and *Acremonium alternatum* Link. On the one hand, as van de Laar strongly hinted, the measurements of length and maximum width of swollen ascospores, 66–74 × 4 μ, given by Voges, certainly indicate *O. graminis* rather than *O. herpotrichus;* and on the other, the relationship of *A. alternatum* to either of these species of Ophiobolus has never been confirmed. The pure cultures of *O. herpotrichus* isolated by the writer from different lots of quack grass collected in Clarendon, Va., have so far failed to reveal sporulation of any kind, sexual or asexual.

Subsidiary reproductive stages have been attributed also to *Ophiobolus graminis.* McAlpine (46), in 1904, was strongly inclined to regard a pycnidial form newly described by him under the name *Hendersonia graminis,* but later transferred to the genus Wojnowicia by Saccardo and D. Saccardo (68, v. 18, p. 367–368), as connected with the take-all fungus. McKinney and Johnson (48), however, on comparing the two forms in pure culture, found no close similarity between them, and were, therefore, led to question the probability of a genetic connection. Guyot's (29) studies later definitely established *Wojnowicia graminis* as a separate fungus. Mangin's claim of a connection between *O. graminis* and a species of Coniosporium somewhat doubtfully identified as *C. rhizophilum* (Preuss) Sacc. has likewise remained without confirmation. On the other hand, the production frequently of minute falcate sporidia in the germination of the ascospores of *O. graminis,* first reported by Mangin, was later confirmed by Foex (19), by Kirby (40), and by Foex and Rosella (21).

The Tulasne brothers attributed to the fungus discussed by them under the name *Rhaphidophora carduorum* pycnidia filled with cylindrical curved conidia as well as spermogonia producing cylindrical curved spermatia. Fuckel listed *Phoma acutum* and *Phoma complanatum* under *Rhaphidospora pellita, Phoma acutum* under *R. urticae,* and *Phoma dictamni* under *R. dictamni.* Höhnel (33), in 1915, stated that the asexual stages thus listed by Fuckel certainly did not belong to the ascigerous species to which they had been referred and held as questionable the association of pycnidial and spermogonial fungi with *Ophiobolus herpotrichus* and *O. carduorum* set forth by the Tulasne brothers. He considered as certain a connection between *O. porphyrogonus* and a pycnidial form, *Pleurophoma porphyrogena* Höhnel, having pycnidia measuring 150 to 250 μ in diameter that gave rise to rod-shaped hyaline spores 5 to 6.5 μ in length and 0.8 μ in width. In the *Sylloge Fungorum, Phoma rudis* Sacc. is mentioned, evidently on the authority of Karsten, as possibly a spermogonial phase and *Septoria rudis* Sacc. as possibly a pycnidial stage of *O. rudis; Phoma hesperidis* Sacc. is cited as the spermogonial phase of *O. hesperidis* Sacc.;

Chalara monticellica Sacc. is indicated as a conidial stage of *O. monticellicus* Sacc.; and reference is made to accessory reproductive phases in the diagnoses of *O. glomus* (B. and C.) Sacc., *O. rhagadoli* Passer. and *O. claviger* Harkn.

In the hope that some information might be obtained that would supply a clue as to the merit of these different references to subsidiary stages, the writer collected during May, 1932, living material of about a dozen species of Ophiobolus on the dead remains of various coarsely herbaceous plants. Pure cultures of each species were obtained readily by making dilution plate cultures from ascospores crushed out of the perithecia, care being taken to avoid contamination from admixed fungi. All showed satisfactory vegetative development on maize-meal decoction agar. Submerged sclerotia were developed in cultures of several forms of the type usually referred to as *O. porphyrogonus.* Scattered sclerotia representing probably immature fruiting bodies were formed in cultures of the well-characterized species occurring on stems of *Ambrosia trifida* L., the ascospores of which exhibit at their distal end a contour strongly suggestive of the head of a snake. The fungus was identified with the *O. anguillides* (Cooke) Sacc. reported on the same host substratum from Indiana by Fink and Fusan (17) as it was found to agree very well with specimens deposited in Mycological Collections of the Bureau of Plant Industry under the following labels:

> Fungi dakotensis, Brenckle. 236. *Ophiobolus anguillides* (Cke.) Sacc. On *Ambrosia trifida.* Aug. 24, 1913.
>
> Ascomycetes of Indiana prepared by Bruce Fink and Sylvia Fusan. *Ophiobolus anguillides* (Cooke) Sacc. Near Crawfordsville. On *Ambrosia trifida.* Number 381. 9–1–1917.

Actual sporulation was observed in cultures of only 2 of the fungi isolated, these having been obtained also from stems of *A. trifida,* on which substratum their fructifications occur year after year in very considerable abundance. Examination of specimens in Mycological Collections showed that the 2 fungi have apparently never been distinguished from one another, each being dealt with separately or both together as *O. fulgidus* (C. and P.) Sacc.

Sphaeria fulgida was described from Albany, N. Y., in 1875, evidently on the authority of Clinton and Peck (59) as follows:

"Perithecia gregarious, sometimes disposed in lines, soon free, globose, black, smooth, shining, scarcely papillate, .01′–.012′ in diameter, at length collapsed; asci clavate or cylindrical; spores filiform, curved or flexuous, multinucleate, at length multiseptate, colorless, .003′ long."

The host substratum was rather indefinitely indicated at the time as being "dead stems of herbs" but not much later, material collected by Peck

at Albany in June, 1879, and distributed under the binomial *Sphaeria fulgida* as No. 583 of Ellis North American Fungi was stated on the label to represent *Artemisia trifida*. It is not known to the writer whether an error was later acknowledged in the identification of the host, but in any case the specimen is now generally filed in herbaria as being of *Ambrosia trifida*, and is evidently thus considered in the host index of Farlow and Seymour (16) as well as in the more recent host index of Seymour (70). There can be little doubt that this disposition is correct, as *Artemisia trifida* Nutt. is not recorded as occurring in the eastern United States and as, moreover, the material is entirely similar to material known to be of *Ambrosia trifida*. A correction in identification of the host genus, impaired somewhat through an apparent garbling of the specific term, would seem to be implied in the citation of *Ambrosia trifolia* as host plant on the label of specimens of *Sphaeria fulgida* collected by Peck in June, 1880, and distributed as No. 1742 of de Thümen's Mycotheca Universalis.

The specimens of *Sphaeria fulgida*, distributed as No. 583 of North American Fungi, contain both of the species of Ophiobolus that were found to produce asexual reproductive stages in culture. From the close agreement with respect to size and shape of perithecium (Fig. 1, A, B), to length of ascus (Fig. 1, C), and to length and nearly colorless condition of ascospores (Fig. 1, D, *a–i*) it is evident that the description by Clinton and Peck was based on the smaller of the 2 species. It may be added that the ascospores that are rather regularly and typically 7-septate, and measure 55 to 95 μ in length by 3 to 3.5 μ in diameter, when freshly crushed out of the perithecium (Fig. 1, D, *a,b,c,f*) show such swelling in a water mount that a diameter of 4 to 6 μ (Fig. 1, D, *d,e,g,h,i*) is usually soon attained, the swelling often taking place even when the spores are retained within the ascus. On maize-meal-agar plate cultures the fungus gives rise to a scattering of rather dark, globose pycnidia (Fig. 1, E) from 0.1 mm. to 0.3 mm. in diameter, the exteriors of which reveal pseudoparenchymatous structure. The colorless hyaline pycnospores (Fig. 1, F), which are irregularly ellipsoidal in shape and measure 4 to 7 μ in length by 2.5 to 4 μ in width, are liberated from an ostiolar opening situated on the upper side of the pycnidium, sometimes in the center of a crater-like depression.

Although evidently the fungus with 7-septate, nearly colorless ascospores must be regarded as the one to which the binomial *Ophiobolus fulgidus* is correctly to be applied, it is not the one most frequently encountered under this name in herbarium collections. In Mycological Collections of the Bureau of Plant Industry this form has been recognized in only one specimen besides the specimen already referred to, that additional specimen being the one distributed as No. 3824 of the Fungi Columbiana, consisting of old stems of *Ambrosia trifida* collected by J. Dearness at London, On-

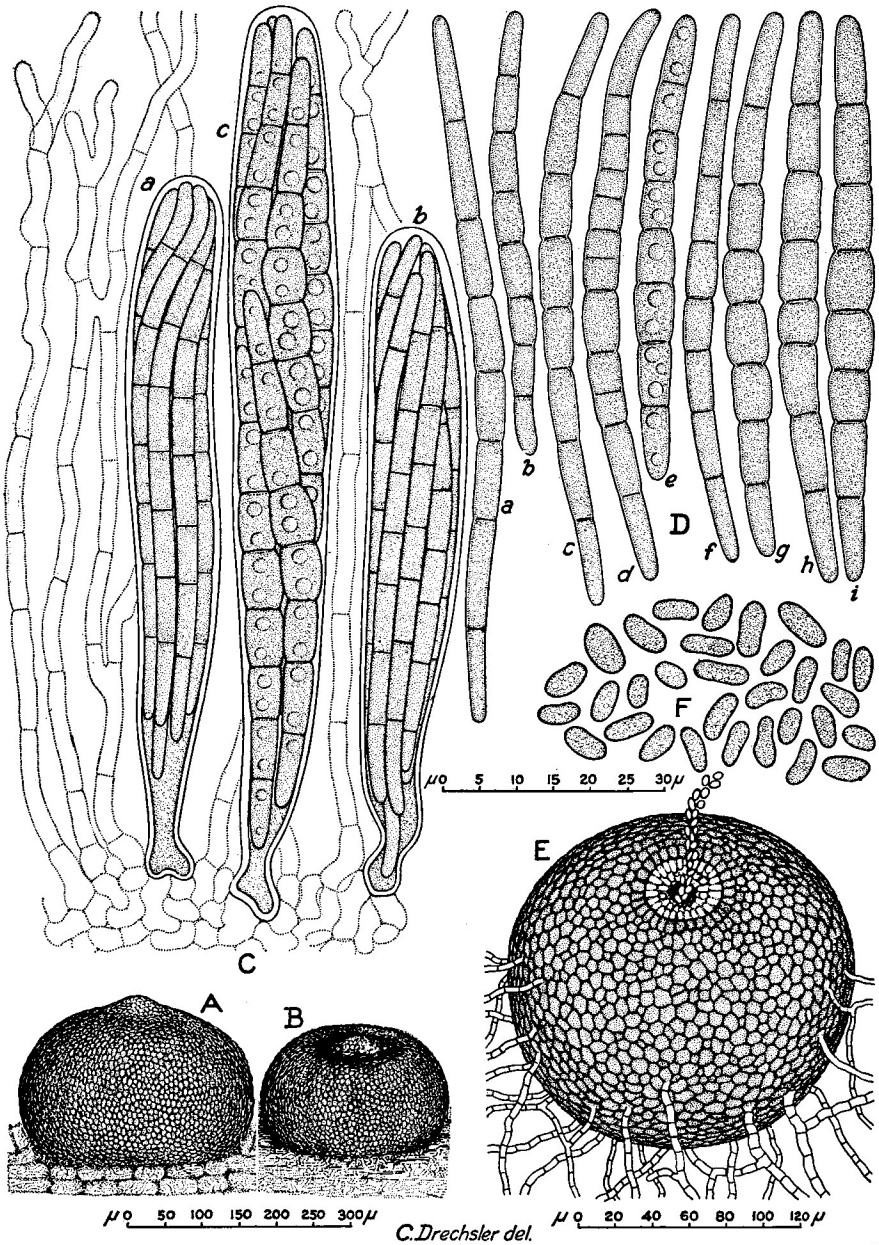

FIG. 1. *Ophiobolus fulgidus*. A. Perithecium on host substratum, viewed in profile. ×100. B. Perithecium on host substratum, showing apex somewhat collapsed. ×100. C. Asci, the spores within two, *a* and *b*, showing no swelling; the spores within *c* beginning to swell. ×1000. D. Ascospores, showing variation in size and shape, *a,b,c,* and *f* not swollen; *d,e,g,h,* and *i* somewhat swollen. ×1000. E. Pycnidium produced in pure culture. ×250. F. Pycnospores. ×1000.

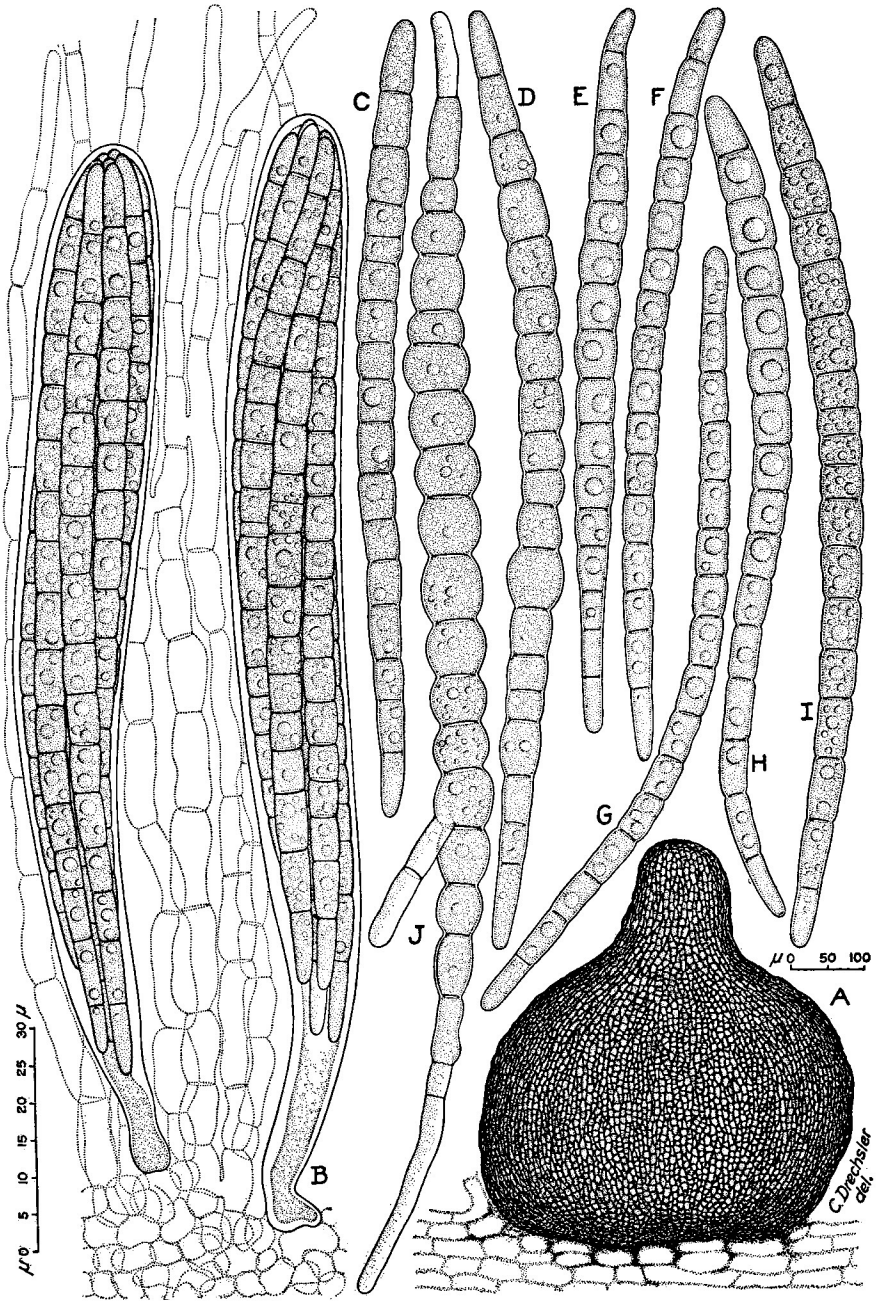

FIG. 2. *Ophiobolus* sp., often identified incorrectly as *O. fulgidus*. A. Perithecium on host substratum in profile. ×100. B. Asci, the ascospores not perceptibly swollen. ×1000. C–I. Free ascospores. ×1000. J. Germinating ascospore. ×1000.

tario, May, 1911. Microscope preparations of all other specimens designated as *O. fulgidus* and citing *A. trifida* as host, were found to represent the larger species included in Peck's specimen collected in June, 1879. The globose perithecia here measure mostly .35 to .5 mm. in diameter and are provided usually with a recognizable ostiolar beak, though this modification is generally not so prominent as in the fructification shown in figure 2, A. As there is little tendency toward collapse, the fruiting bodies of this species, which occur often in large numbers in close, somewhat linear arrangement, may be distinguished from those of the first form considered not only by their larger size but also by their more marked protrusion from the substratum. The asci (Fig. 2, B), on maturity, are 100 to 150 μ long by 13 to 17 μ wide and contain 8 spores of distinctly yellow coloration, which measure from 85 to 125 μ in length by 4 to 4.5 μ in diameter. The spores (Fig. 2, C–I) are usually and typically 15-septate, though the number of cross walls may be as low as 10 or 12 in unusually short individuals, or as high as 18 in unusually long ones. In a water mount living spores, after being liberated from the perithecium, swell to a diameter of 7 or 8 μ, evidently as a preliminary step toward germination, which ensues generally within a few hours (Fig. 2, J).

In pure culture on maize-meal-agar plates the fungus with 15-septate ascospores exhibits 2 subsidiary reproductive stages. Tawny pycnidia (Fig. 3, A, B) measuring from 25 to 125 μ in diameter are formed usually more or less superficially on the substratum, mostly in groups readily visible to the naked eye as flesh-colored masses. The pycnidia show externally a pseudoparenchymatous structure, though often and more especially in the smaller individuals (Fig. 3, B) the mycelial origin of this structure may be rather readily apparent. The orifice through which the spores are extruded in a cohesive mass is sometimes surrounded by a fringe of hyphal processes of variable lengths (Fig. 3, A). The pycnospores (Fig. 3, B), which are hyaline, colorless, and ellipsoidal, measure usually 2 to 3.5 μ in length by 1 μ in diameter and would seem, therefore, to be somewhat smaller than those of *Phyllosticta ambrosiae,* described by Davis (8) as causing a leaf spot of the giant ragweed in Wisconsin, though the difference in size is hardly sufficient to dismiss entirely the possibility of identity.

A second type of asexual reproduction (Fig. 3, C, D, E) is found in the production of spherical unicellular conidia in usually somewhat tortuous chains terminally on aerial hyphal elements that are mostly not well differentiated from the aerial mycelium generally. Rather curiously, the sporulating elements here are not of approximately uniform widths, as in most similar fungi, but vary in diameter from 1.5 to 4 μ. With this variation in the conidiophorous hyphae is associated a corresponding variation in the conidia, the more delicate hyphal elements bearing chains of conidia

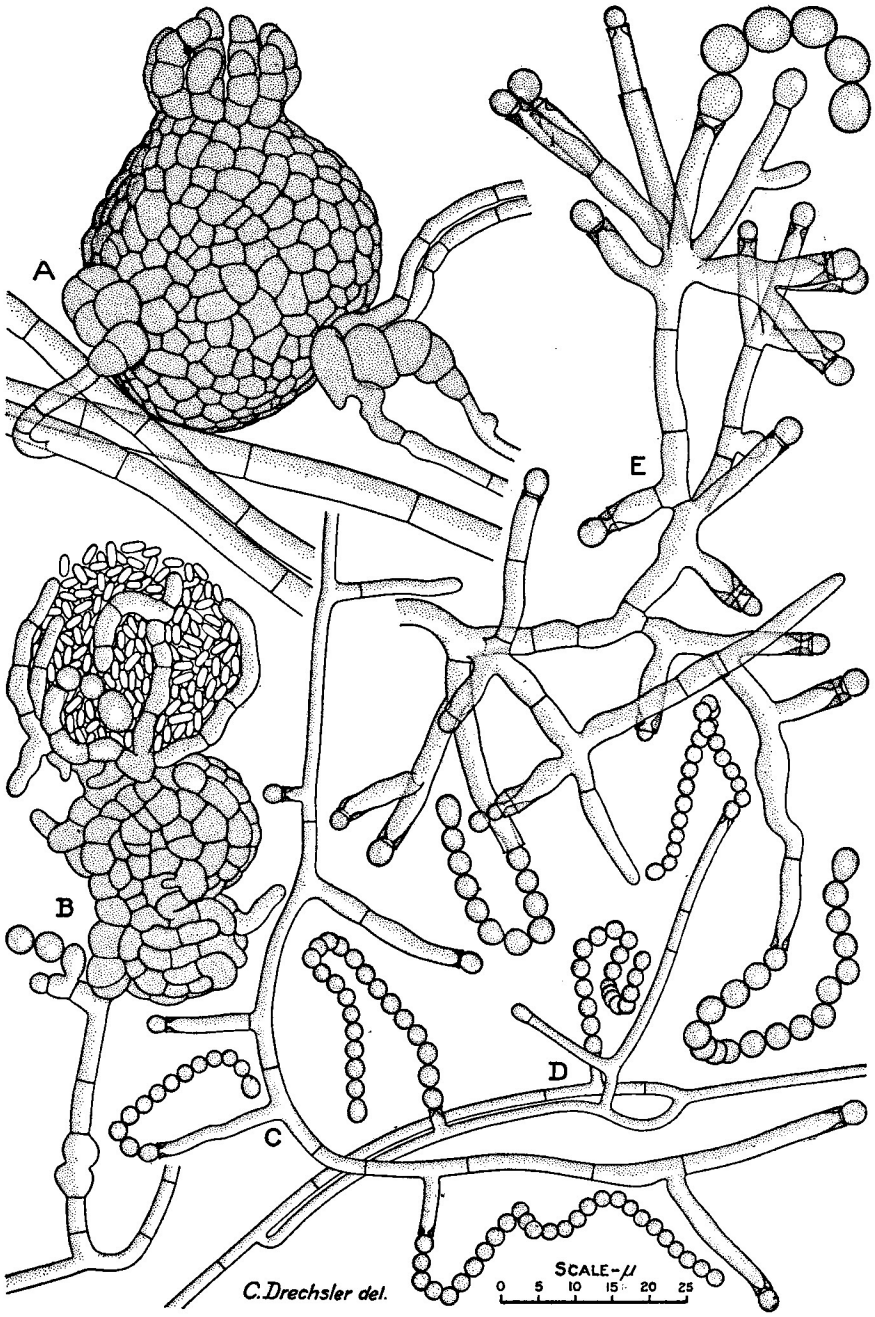

FIG. 3. *Ophiobolus* sp., often identified incorrectly as *O. fulgidus*. ×1000. A. Pycnidium of moderate size developed in pure culture. B. Small pycnidium. C–E. Aerial hyphae with sporiferous branches producing chains of aerial subspherical conidia, showing cuplike character of some sporulating tips, development of several successive rings at tips, and variation in diameters of conidia and conidiophorous branches; only the basal spore of a chain being shown in most cases.

2 μ in diameter, whereas the sturdier ones give rise to chains composed of individuals up to 6 μ in diameter. The production of each successive conidium following the first, entails a characteristic modification of the hyphal tip that becomes increasingly pronounced as the process is repeated again and again. On each occasion the peripheral wall at the tip for a short distance downward is slightly thickened on the inside, with the result that a thick rim soon comes to surround a narrowing isthmus through which the new spores are protruded as buds one after another. Often the isthmus comes to recede into the cup-like rim, so that the conidia are formed, as it were, partly endogenously, somewhat after the manner described by Andrus and Harter (1) for *Ceratostomella fimbriata* (Ell. and Hals.) Elliott, or by Woronin (80) for *Sordaria coprophila* De Not. Not infrequently, after the lumen of a sporulating tip has become much reduced, the hypha grows out vegetatively a short distance, establishing a new apex in which internal thickening again takes place. As a noticeable ring or collar remains to mark the position of the earlier tip, repetition of the process results in an annulated termination somewhat reminiscent of the conidiophores figured by Ducomet (15, pl. 31) for *Fusicladium dendriticum* (Wallr.) Fuckel, the conidial stage of *Venturia inequalis* (Cooke) Aderhold.

It would, in all probability, be going too far to interpret the tendency toward endogenous development of conidia just described as evidence of parallelism with the association supposed to obtain between *Chalara monticellica* and *Ophiobolus monticellicus*. As chains of conidia are usually much too fragile to withstand the handling incident to collection and removal to a laboratory, circumstances have been generally unfavorable for the recognition of catenulate sporulating stages as associated with asciger-ous fructifications on material gathered in field or forest. On the other hand, as has been noted, homologues of the more durable pycnidia found produced in pure cultures of the 2 species cited under the binomial *Ophiobolus fulgidus,* have been recorded in the literature for various species of Ophiobolus as members of the form-genus Phoma. Genetic relationship with Phoma and allied sphaeropsidaceous types may thus represent an attribute shared rather widely among the many fungi occurring on the dead remains of coarsely herbaceous plants that provide the bulk of species subsumed under Ophiobolus. Since Phoma and the essentially similar Phyllosticta include numerous forms parasitic on the higher plants, it is possible that some of the unsifted species of Ophiobolus, now known as saprophytes, may ultimately be revealed as disease-producing organisms.

THE HELICOID ASCIGEROUS SERIES SET APART AS A NEW GENUS COCHLIOBOLUS

In any case it appears significant that none of the dozen or more species of Ophiobolus grown in pure culture from ascospores gave rise to any co-

nidial stage resembling the series of graminicolous Helminthosporium forms with bipolar germination. As, conversely, this Helminthosporium series has never been found connected with species of Phoma or with any other sphaeropsidaceous stage, its separateness from what would seem to be the general run of species in Ophiobolus, appears fairly obvious, at least with respect to life-history associations. The series furthermore has apparently no intimate connection with the widely known plant pathogens, *O. graminis* and *O. herpotrichus,* even though its members, rather curiously, occur in part as parasites on the same graminaceous hosts, bringing about somewhat similar, though not identical, pathological changes. In order that confusion may be obviated between the helicoid ascigerous series corresponding to the Helminthosporium forms on the one hand and the take-all and stem-killing fungi on the other, it seems expedient to set apart the former as a separate genus for which a term referring to the spiral disposition of the ascospores is proposed.

Cochliobolus, gen. nov.

Perithecia sparsa, globulosa, coriaceo-membranacea, ostiolo papillato, atra, glabra aut hyphis sterilis vel hyphis conidiophoris vestita. Asci cylindracei, brevi-stipitati, saepius ad maturitatem plus minusve inflati, typice octospori. Sporidia filiformia, multiseptata, hyalina vel praeprimis ad maturitatem flavo-fumaginea, stipata, vehementer et regulariter spiraliter convoluta. Conidiophora rigidula, simplicia vel ramosa, saepius fusca, pluriseptata, geniculata. Conidia typice elongato-ellipsoidea, recta vel curvata, pluriseptata, hyalino-fumiginea vel fusca saepius olivacea, hyphis duabus germinantia quarum altera ex apice altera hilum juxta emergens.

Perithecia scattered, black, submembranaceous to subcoriaceous, smooth or covered more or less with flexuous vegetative filaments or with somewhat more bristling conidiophorous hyphae, globose, usually with evident paraboloid or short cylindrical ostiolar beak. Asci subcylindrical, short-stipitate, often becoming more or less distended especially previous to dehiscence. Ascospores 1 to 8 in number, colorless or especially at maturity somewhat colored, filamentous, provided with many septa, crowded, disposed in strongly helicoid arrangement. Conidiophore simple or somewhat branched, mostly olivaceous, septate, producing first conidium some distance from base and following repeated subterminal elongation successive conidia at intervals later often marked by geniculations. Conidia elongated-ellipsoidal or sometimes somewhat fusoid, straight or curved, nearly colorless to deep olivaceous, provided with plural septa, germinating by the production of 2 polar germ-tubes, one from the apex and the other from a zone immediately surrounding the basal scar.

The type species is **Cochliobolus heterostrophus,** nov. comb. (= *Ophio-*

bolus heterostrophus Drechsl., Jour. Agr. Research, v. 31, p. 701–726, 1925; and Phytopathology, v. 17, p. 414, 1927).

The new genus thus defined in both its sexual and asexual stages is intended to include only species that through a thoroughgoing parallelism in morphology and life history can safely be regarded as narrowly and naturally congeneric with the parasite causing leaf spot of maize designated as the type species. As undoubtedly the ascigerous stages of more Helminthosporium forms with bipolar germination will become known, in addition to the half dozen already described or reported in the literature, the scope of Cochliobolus with respect to number of likely members would seem, even with scrupulous application, to be a sufficiently ample one. Beside the 18 graminicolous species occurring in Japan that were cited by Nisikado (58) under his conidial subgenus eu-Helminthosporium, with which in the main the proposed ascigerous genus corresponds, the literature of other countries contains references to an approximately equal number of additional Helminthosporium forms parasitic on graminaceous hosts that are evidently referable to the same category. The writer has encountered on hosts other than grasses species that have every appearance of belonging here, the rather frequent occurrence of such forms, especially on dead or fading foliage of sedges, giving grounds for a suspicion that the destructiveness occasioned by the series of fungi in question among the Gramineae may in some measure be duplicated among the Cyperaceae. Conidial forms apparently of the same series have also been recognized on dead materials representing a goodly variety of woody and herbaceous plants, after incubation in a damp chamber, their occurrence, on the whole, indicating a fairly widespread distribution in nature, apparently in saprophytic as well as parasitic relationships.

On the other hand it is hardly to be assumed that the numerous species described from woody and herbaceous substrata that make up the main mass of forms compiled in Helminthosporium have representation in the series achieving the perfect stage in Cochliobolus in any proportion approximating the representation here of the graminicolous species of Helminthosporium. For, judging from the illustrations given by different authors, it appears rather improbable that either of the 2 main series that largely account for the graminicolous species account in comparable measure for the large body of unsifted fungi included under Helminthosporium in the *Sylloge Fungorum*. It may not be superfluous to emphasize that not all of even the graminicolous species can be assigned to one or the other of the 2 main series. In mode of germination and production of a Hormodendron-like sporulating stage, *Helminthosporium giganteum* H. and W., as was pointed out earlier (14), certainly departs widely from the series having its ascigerous phase in Pyrenophora Fries. The demonstration recently by

Tullis (75) of a connection between *H. sigmoideum* Cav. and *Leptosphaeria salvinii* Catt. has brought to light a third ascomycetous relationship within the group. The short sterigmata on the conidiophores of *H. sigmoideum* figured by Tullis, on which the conidia are borne directly, have no counterpart among the generality of graminicolous species of Helminthosporium and may, therefore, have value as a characteristic indicating similar pleomorphic association in other conidial forms. Nor are spherical sclerotia of the type represented in *Sclerotium oryzae* Catt., which is now revealed by Tullis as another phase in the life cycle of the same species of Leptosphaeria, known among the members of the 2 main graminicolous series. Even the decidedly different cylindrical sclerotia produced in culture by *H. cyclops* Drechsl. arouse misgivings concerning the affinities of that species, though the discrete conidiophores and the conidia here conform tolerably well in morphology to the homologous structures of known species of Cochliobolus. Apparently similar columnar or filamentous sclerotia occur frequently in a series of species, including forms like *H. geniculatum* T. and E. and *H. inequale* Shear, that are distinguished further by smaller, often geniculate conidia, the swollen middle cells of which are usually darker than the end segments. Whether the series, which is often recognized on grounds well set forth by Mason (52), as a separate genus, Acrothecium Preuss (?), falls outside the scope of Cochliobolus, must remain in doubt until the ascigerous condition of one of its members has been discovered. Of the arrangement of the conidia in a terminal whorl, which is customarily cited as the most distinctive feature of the series or genus, the present writer has seen little evidence, since, in all cultures of the group examined by him, the arrangement was found exactly as in cultures, for example, of *H. sativum*. Indeed, to the extent to which any difference was observed, it was rather the smaller species that produced the more prolonged and more abundantly laden spike-like racemose sporophores.

In characterizing the perithecium in Cochliobolus as glabrous or as bearing sterile hyphae or even conidiophores, it is intended to dispose of a feature that has been brought into undue relief through the Saccardian practice of using the presence of setae on the fruiting body, or their absence therefrom, for the separation of genera. The criterion very probably acquired its impetus by virtue of its actual merit in instances where the setae represent special structures pertaining definitely to the reproductive body in question; and it undoubtedly continues to serve well wherever such special structures are involved. However, in application even the occasional presence of adventitious hyphal filaments has sometimes been interpreted as constituting a setose condition. In *C. heterostrophus* the perithecium in some cases is thoroughly glabrous, but in other cases it shows a variable development of undifferentiated hyphae as well as of conidio-

phorous filaments. Such development should, of course, not be interpreted as pertaining to the sexual stage at all, but rather as intrusion of the vegetative and the asexual reproductive phases, brought on by appropriate environmental conditions.

HELMINTHOSPORIUM, PYRENOPHORA, AND PLEOSPORA

In this connection it may be appropriate to consider the distinction between the genera Pyrenophora and Pleospora Rab. In an earlier paper (12) the writer transferred the ascigerous stages of *Helminthosporium teres* Sacc., *H. tritici-repentis* Died. and *H. bromi* Died. from the latter to the former genus, though the transfer entailed the making of several new combinations. The change was made not without the knowledge that as competent an authority as Winter (79) had regarded as inadequate for the separate maintenance of the 2 genera, the distinction based on the presence or absence of setae, emphasized in the works of Saccardo (68) and of Lindau (44). Indeed, it was recognized that Winter's view regarding the inadequacy of this distinction in itself had very considerable justification, for, although sterile bristles not readily to be confused with vegetative hyphae were usually found on the perithecia of the 3 fungi mentioned, their irregular occurrence and occasional suppression argued against their interpretation as structures of primary significance. A circumstance disturbing to Winter's dispositions was apparent in that, if the 2 genera were to be treated as a single genus, the term Pyrenophora dating from 1849 might deserve preference on the score of priority over the term Pleospora, originating in 1857.

However, when the 2 genera are considered in regard to the life history and the perithecial structure represented in each of their respective types, more substantial reasons for their separation are revealed. The genus Pleospora was erected on *P. herbarum* (Pers.) Rab., a species that has become widely known in both saprophytic and parasitic relationships. Since the time when Miyabe (53) definitely determined the parasite on onions (*Allium cepa* L.), which host has apparently as good a claim as any to be considered the type source of the species, to be connected with *Macrosporium parasiticum* Thüm., the same or at least very similar conidial form has been repeatedly shown to be the asexual reproductive stage of the fungus by other workers. In short, an altogether sufficient body of evidence—which the present writer had occasion to corroborate successfully—has accumulated, showing that *P. herbarum* has as its conidial stage a Macrosporium species of the "sarcinula" type, for which Mason submitted the name *M. sarcinula* Berk. emend Bolle as the most acceptable one.

When the genus Pyrenophora was established, Fries (27) listed in it 3 species under the following names: *P. paradoxa* Fr., *P. inclusa* (Kunz sub

Sclerot.) and *P. phaeocomes* Reb. Concerning the first and second of these species not much information has ever become available, and it is very doubtful whether either of the 2 names could now be definitely referred to any particular fungus. As a result *P. phaeocomes* is left as the obvious type of the genus and is properly listed as type by Clements and Shear. The sclerotia of this fungus were described by Rebentisch (64) in 1804 as *Sphaeria phaeocomes,* the host substratum mentioned being withering leaves of *Holcus mollis* L. The habit sketch supplementing the description, showing imbedded sclerotia distributed over the blade of the grass leaf, like the more recent habit sketch of Berlese, is strongly reminiscent of withered leaves of *Bromus inermis* Leyss. bearing sclerotia of *P. bromi,* such as may be observed in southern Wisconsin during late summer and autumn. Herbarium specimens in the Mycological Collections of the Bureau of Plant Industry, representing collections made in recent times in various European localities and consisting of leaves of *Holcus lanatus* L. and *Holcus mollis* with sclerotia in them scattered much after the manner illustrated in Rebentisch's figures, leave no doubt that the relatively ancient species enjoys an exceptionally consistent application. Though the fungus might well be expected to occur on *H. lanatus* in some of our northern States, the writer has not succeeded in obtaining freshly collected living material of it and, therefore, has been unable to ascertain more precisely the details of its life history. Fuckel, who presumably saw favorable material, stated that its conidial stage was similar to that of *Pyrenophora relicina,* without, however, giving further particulars concerning the morphology of the conidial stage of either species. Yet, since he cited *Pleospora polytricha* Tul. as a synonym of his *Pyrenophora relicina,* his statement is manifestly to be interpreted as implying resemblance to the conidial stage set forth in the account of *Pleospora polytricha* given by the French mycologists. The illustrations of conidia and conidiophores in the plate supplementing this account are perhaps most readily referred to a Helminthosporium occurring abundantly every year on overwintered oat straw during May and June in Maryland, Delaware, and Virginia in association with a Pyrenophora having ascospores with 5 transverse septa. Though the substratum obviously suggests identity of this Helminthosporium with *H. avenae* Eidem, the conidia on the overwintered straw are in general smaller (40–100 $\mu \times 12$–15 μ), darker (sometimes olivaceous), and less frequently (usually 2 to 7 times) septate than conidia from the leaf-stripe lesions developing on the foliage of oats, often in some abundance, late in June and early in July. In any case the illustrations of the Tulasne brothers leave no doubt that the conidial stage of their *Pleospora polytricha* belongs to the Helminthosporium series with indiscriminate germination from any or all segments, familiar as pathogens concerned in the causation of important

diseases of cereal-crop plants. Fuckel's statement thus testifies to a parallelism in the asexual reproductive stage between Rebentisch's historically important species and the disease-producing series under consideration.

The supplementary parallelism in the sexual stage is expressed especially in the hard sclerotioid texture of the immature perithecium, and in the usually delayed and somewhat protracted development of the asci within. These features were very properly cited by Fuckel in his definition of Pyrenophora, which must be reckoned as a very happy one, whether or not the texture and development in question, together with peculiarities in internal perithecial structure associated therewith, can be regarded as requiring inclusion of the genus in the Dothidiaceae, or, for that matter, in the Pseudosphaeriaceae of some more recent writers. The intimate relationship of the species which Fuckel definitely referred to the genus, including besides *P. phaeocomes* and *P. relicina,* the collective *P. trichostoma* (Fr.) Fuckel (from which latter Diedicke (11) later correctly segregated a number of integral species, among them the ascigerous stages of *Helminthosporium teres, H. bromi,* and *H. tritici-repentis*), was recognized by Saccardo and Winter in retaining them in a subgenus eu-Pyrenophora. When Saccardo amalgamated this distinctive group with the more miscellaneous nonsclerotioid setose forms in his subgenus Chaetoplea, the larger genus Pyrenophora that resulted manifestly represented a collective genus. The recent elevation of Chaetoplea to generic rank by Clements (4, p. 275) remedies this undesirable disposition, in effecting the rehabilitation of Pyrenophora as a natural genus in the sense in which it was defined and applied by Fuckel. And to this sense it would seem to be highly desirable that future usage and application should rigorously conform.

SUMMARY

Of the 2 graminicolous species, *Ophiobolus herpotrichus* and *O. graminis,* through which the genus Ophiobolus became widely known among plant pathologists, the former long retained a reputation as a pathogen in excess of its actual destructiveness. The description of *O. graminis* by Saccardo apparently remained for many years unknown to the earlier observers of cereal-crop diseases, and later, when the description must have been known, Frank, presumably from doubts as to the separateness of the fungus in question from the older *O. herpotrichus,* apparently assigned Ophiobolus injury in general to the latter species, and brought the composite concept into prominence through the term *Weizenhalmtöter.* The formidable parasitic character implied in the term adhered to the binomial with which Frank brought it into association, long after the separateness of the 2 species which this author manifestly considered identical, was generally admitted.

Ophiobolus herpotrichus, though not hitherto reported in the United States, has been found to occur very generally and in quantity on dead stems of quack grass during April, May, and early June in Wisconsin, New York, Maryland, and Virginia.

Ophiobolus herpotrichus and *O. graminis* are probably to be regarded as narrowly related members of a series to which *O. oryzinus* also seems to belong. This series would seem to have no intimate relationship to the generality of forms compiled in Ophiobolus nor to the apparently equally independent and phytopathologically important helicoid ascigerous series corresponding to the series of forms in Helminthosporium with bipolar germination.

Of the general run of species in Ophiobolus, more asexual stages are recorded in Phoma than in any other genus. Corroborative evidence of the reality of this pleomorphic association was found in the production of pycnidia in pure cultures of 2 species from dead stems of the giant ragweed, both of which have been treated—the smaller one correctly, the larger one incorrectly, even if more frequently—under the binomial *O. fulgidus.* Of more than a dozen miscellaneous Ophiobolus species from various herbaceous host substrata, none gave rise in culture to a Helminthosporium stage and none showed any family resemblance in cultural and mycelial habit to species of Helminthosporium. It is concluded, therefore, that the helicoid ascigerous series constitutes a separate natural genus, which is accordingly described under the name Cochliobolus; the fungus causing leaf spot of maize, *C. heterostrophus,* being designated as type species.

The filamentous outgrowths sometimes present on perithecia of Cochliobolus are to be regarded as intrusions of the vegetative and the asexual reproductive stages, rather than as pertaining to the ascigerous stage itself. Excessive emphasis on the presence or absence of setose outgrowths as criterion for distinguishing Pyrenophora and Pleospora has obscured the much more important difference in life histories present here. Recently rehabilitated as a natural genus through the elevation of Chaetoplea to generic rank, Pyrenophora again conforms to Fuckel's definition, being properly reserved for the hard sclerotioid perithecial forms having their asexual stages in the Helminthosporium series with indiscriminate germination corresponding broadly with the subgenus Cylindro-Helminthosporium of Nisikado and the genus Drechslera of Ito.

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