

THE CYPERICOLOUS AND JUNCICOLOUS SPECIES OF *SCLEROTINIA*

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During the spring and summer of 1930 I took the opportunity afforded by sabbatic leave to collect and study species of the *Sclerotiniaceae* in Europe. My travels carried me through England, Holland, Switzerland, France, Germany, Denmark, Sweden and Norway. Through the kind co-operation of colleagues² in these countries I was enabled to make invaluable collections and studies of many species in their natural habitat. I was also afforded every courtesy and assistance in the examination of specimens of these cup fungi preserved in the herbaria of most of the important botanical institutions in the countries visited.

Stimulated by my early studies on the species of *Sclerotinia* found in northeastern United States on species of *Carex* (Whetzel 1929) I took special pains to collect and study the species of this genus occurring on sedges and rushes in western Europe. I was exceptionally fortunate in finding in nature most such species recorded by European mycologists.

A manuscript presenting the results of my studies on these species was partially prepared during my stay in Europe. On my return, teaching duties prevented the completion of this paper, and only recently have I been able to take up the work again and complete the studies which are here presented. This delay has not been without its compensations in certain respects. During the years that have passed, while much of the freshness and some of the details of my European observations have faded

¹ This manuscript was received and edited before Professor Whetzel's death on November 30, 1944. Realizing that he might not live to see the appearance of his paper, the author made all arrangements for its publication, including a generous gift to cover the extra cost of the halftone plates.

² *Acknowledgments:* The researches on which this paper is based, especially those undertaken in Europe in 1930, were made possible largely by grants from the Heckscher Foundation for the Advancement of Research at Cornell University. I am especially indebted to Dr. Cynthia Westcott, who as my research assistant gave invaluable help on my European trip. For access to herbarium specimens and for expert advice and assistance I am greatly indebted to Drs. David H. Linder and W. L. White of the Farlow Herbarium; to Dr. John A. Stevenson of the U.S.D.A.; to Dr. W. G. Solheim of the University of Wyoming; to Dr. J. Ramsbottom of the British Museum; to Dr. A. D. Cotton and Miss E. M. Wakefield of the Royal Herbarium, Kew; to Dr. J. A. Nannfeldt, University of Upsala; and to Mr. Ernst Gram, Dr. C. Ferdinandsen, and Mr. Johs. Grøntved of the University of Copenhagen. My best thanks are also due Miss Charlotte Dill and Mr. Carlos Garcés for preparation of the drawings for the text figures and to Dr. Rolf Singer of the Farlow Herbarium who has kindly prepared the Latin descriptions. Mr. W. R. Fisher prepared the photographs. The writer is indebted to so many other friends and colleagues both in this country and in Europe for assistance and favors that it is useless to attempt to list them all here. To everyone who has thus contributed to the consummation of these investigations I here express my thanks and gratitude.

from my memory, there have come to hand, now and then, specimens and information on species of this group that have corrected some of my earlier conclusions, confirmed others, and have added three species to those known to me at the time of my 1930 visit in Europe.

THE GENUS *SCLEROTINIA*

The generic name, *Sclerotinia*, should be restricted to those species in which the apothecium arises from a tuberoid sclerotium as in *S. sclerotiorum* (Lib.) De Bary, which is to be taken as the type of the genus. In this genus the sclerotia originate and develop upon the surface of the substrate or in lysigenous cavities within the organs of the suspect. They rarely and only incidentally enclose in their pseudoparenchyma bits of the tissue of the suspect. The sclerotia when freely formed upon the surface of the substratum are approximately loaf-shaped or globose. Even those species which form characteristically shaped sclerotia regularly within the organs of their suspects, when grown on artificial culture media produce sclerotia which tend to be globose in shape. None of them are true parasites. They must kill the cells of the invaded tissues before they are able to extract the nourishment they seek. They are necrogenic saprophytes. They have no conidial stage. All have spermatia (microconidia) produced endogenously from the tips of obclavate spermatophores, fasciculately massed into mucilaginous spermodochia, borne free on the aerial mycelium or enclosed in lysigenous cavities in the tissues of the suspect.

The species here discussed are the only ones known to me on sedges and rushes that may be properly referred to the genus *Sclerotinia* as above characterized. A number of species of Discomycetes, recorded on various species of these plants and referred to the genus *Sclerotinia*, do not qualify. These in so far as they are known to me are listed and briefly discussed at the end of this paper.

SPECIES TREATED IN THIS PAPER

As a stimulus to the reader to plunge into the details of my observations and conclusions on the species treated in this paper, it may be well to present here a list of these together with the sedges and rushes which they inhabit. There are ten species occurring on forty-one different suspects. These species are largely restricted each to a distinct suspect or set of suspects. Only among the four species on *Carex* have there been found a few cases of suspects common to two or more.

On the Cyperaceae:

1. ***Sclerotinia duriaeana***³ (Tul.) Rehm in EUROPE only, on *Carex brizoides*⁴ L.; *C. paniculata* L.; *C. disticha* Huds.; *C. chordorrhiza* Ehrh.;

³ Exercising his option under the rules, the author decapitalizes the first letter of species names.

⁴ The species names here used for the suspects have been carefully checked by my colleague Dr. R. T. Clausen.

C. acutiformis Ehrh. 2. **Sclerotinia sulcata** (Desm.) Whetzel in EUROPE on *Carex hudsonii* A. Bennett; *C. vulpina* L.; *C. gracilis* Curtis; *C. inflata* Huds.; *C. brizoides* L.; *C. nigra* (L.) Reichard; *C. disticha* Huds.; *C. paradoxa* Willd.; *C. paniculata* L.; *C. riparia* Curtis, in NORTH AMERICA on *Carex stricta* Lam.; *C. prairea* Dewey; *C. interior* Bailey; *C. hystericina* Muhl.; *C. riparia* var. *lacustris* (Willd.) Kücken; *C. flava* L.; *C. inflata* var. *utriculata* (Boott) Druce; *C. crinita* Lam.; *C. nebraskensis* Dewey. 3. **Sclerotinia longisclerotialis** Whetzel in NORTH AMERICA only, on *Carex prairea* Dewey; *C. interior* Bailey; *C. vesicaria* L.; *C. crinita* Lam.; *C. retrorsa* Schw.; *C. oligosperma* Michx. 4. **Sclerotinia caricis-ampullaceae** Nyberg in EUROPE and NORTH AMERICA on *Carex aquatilis* Wahl.; *C. aquatilis* var. *altior* (Rydb.) Fern.; *C. inflata* Huds. 5. **Sclerotinia vahliana** Rostr. in EUROPE and NORTH AMERICA on *Eriophorum scheuchzeri* Hoppe; *E. angustifolium* Roth.; *E. vaginatum* L. 6. **Sclerotinia scirpicola** Rehm in EUROPE only, on *Scirpus lacustris* L. 7. **Sclerotinia schoenicola** n.sp. in EUROPE only, on *Schoenus nigricans* L.

On the Juncaceae:

8. **Sclerotinia curreyana** (Berk. in Currey) Karst. in EUROPE only, on *Juncus effusus* L.; *J. conglomeratus* L.; *J. glaucus* Ehrh.; *J. filiformis* L.; *J. communis* E. Mey. 9. **Sclerotinia juncigena** (E. & E.) n.comb. in NORTH AMERICA only, on *Juncus effusus* L. var. *pacificus* (Fern.) Wieg. 10. **Sclerotinia luzulae** n.sp. in EUROPE only, on *Luzula pilosa* Willd.

LIFE HISTORY

The life histories of the *Sclerotinia* species attacking sedges and rushes are in their main features very much alike. The discharged ascospores, carried by air currents, fall upon the flowers of their suspects. Germination and invasion of the flowers is followed promptly by death and browning of the entire inflorescence, the affected culms never setting seed. The invading hyphae now work rather slowly down the culm forming spermodochidia⁵ (Text Figs. A, C, D) in the cortical tissues just beneath the epidermis. The increasing mass of spermatia in these fruit bodies soon burst through the epidermis in pearly white or brownish mucilaginous drops. Rain or dew and possibly insects disseminate the spermatia to the surfaces of the dying culms below wherein the sclerotia are now beginning to develop. The mechanism of fertilization is unknown but that the spermatia do function is certain. The sclerotia, at first evident as white soft cottony masses within the culm, gradually harden, enveloping the medulla in a thin black rind. This medulla is often pink at first, eventually becoming white. In the final stages of maturity in late autumn, the sclerotia usually burst the confining outer tissues of the culm. In some species they fall out of the culms onto the water or moss beneath. In other species they remain partially enclosed,

⁵ For a definition of this term see Whetzel, *Mycologia* 35: 335-338. 1943.

exposing only a part of their surface. In one species, *S. longisclerotialis* (Fig. 20), the sclerotia remain enclosed until decay of the culm tissues more or less frees them the following spring. The natural shape of the sclerotium is usually characteristic for each species, but is evidently determined to some extent by the shape of the enveloping culm. The number of sclerotia per culm varies not only with the species of *Sclerotinia* but to some extent, and within limits, in most of the species of their respective susceptibles.

The sclerotia of those species in which they are freed at maturity, float on the surface of the water, eventually finding lodgment among the mass of debris about the hummocks or shores of the swamp. In some species the sclerotia remain upright in the dead culms throughout the winter. In *S. longisclerotialis* the dead slender culms enclosing the sclerotia fall over and settle to the bottom of the pools about the hummocks.

Development and maturity of the apothecia of all the species are closely correlated with the growth and flowering of their respective susceptibles early in the spring. The ascospores are matured and discharged over a period of two weeks or so while the flowers of their susceptibles are opening and shedding their pollen. Thus for the species of *Sclerotinia* attacking sedges and rushes there is a single primary cycle of activities. So far as known, secondary cycles do not occur. Each species presents certain peculiarities and variations from the life-history picture outlined above. These will be pointed out in connection with the discussion of the different species. This outline of their life history is inferred largely from observations on their seasonal developments and the syndrome of the diseases they cause. Most of them have been grown on potato dextrose agar. Much remains to be discovered by further field studies and especially by carefully executed inoculation experiments. Several of them, no doubt, have a more extensive susceptible range than my observations indicate. They appear to have been very infrequently collected, not only in North America but also in Europe. Considering their abundance and annual reappearance in the localities where I have had them under observation, it is surprising how scanty in numbers and quantities are the specimens in the herbaria which I have visited.

SPECIES ON THE CYPERACEAE

Of the seven species of *Sclerotinia* known to me to attack members of the *Cyperaceae*, four occur on species of *Carex*, one on *Scirpus*, one on *Eriophorum*, and one on *Schoenus*. These appear to constitute a group of very closely related species. All occur in much the same type of environment, namely in wet marshes where water stands throughout the year or along the margins of lakes, ponds, and quiet streams. They appear to be restricted to the cooler parts of the north temperate zone and on up into the colder arctic regions. They usually occur in great abundance in the localities where I have found them both in America and Europe.

SPECIES ON CAREX

Four species of *Sclerotinia* pathogenic to *Carex* species have been described. Of these *S. duriaeana* (Tul.) Rehm is known only from north-western Europe, occurring widely on several species of *Carex* from France northward to Lapland in Scandinavia; *S. sulcata* (Desm.) Whetzel occurs in both Europe and America. It appears to be generally distributed over western Europe from south to north wherever its *Carex* suspects occur. It is this species which has been most frequently collected and preserved in European herbaria but almost always erroneously labeled *Sclerotinia duriaeana*, with which it has generally been confused by European mycologists. While *S. longisclerotialis* Whetzel infects many species of *Carex* in north-eastern United States it apparently does not occur in Europe. The fourth species, *S. caricis-ampullaceae* Nyberg, discovered in Finland in 1930 and first described two years later, has been collected since in Sweden as well as in North America in the high mountain swamps of Wyoming (Whetzel and Solheim 1943). This is the largest and most striking of the four species (Fig. 25). The apothecia of these four species differ chiefly in size and somewhat in shape. The differences in color of the apothecia and in the shape and size of asci and ascospores are scarcely of taxonomic significance. The species are most clearly distinguishable by the shape and size of their sclerotia together with the external appearance and arrangement of their spermodochidia.

KEY TO THE SPECIES

1. Sclerotia short, more or less fusiform, falcate or kidney-shaped.
 2. Spermodochidia in globose, equally spaced groups. ***S. duriaeana***
 2. Spermodochidia in linear, scattered groups. ***S. sulcata***
1. Sclerotia long and slender.
 3. Sclerotia of uniform diameter, truncate, more or less 3-angled

S. longisclerotialis
 3. Sclerotia obclavate, drawn out above into a slender whiplike tip

S. caricis-ampullaceae

SCLEROTINIA DURIAEANA

PLATE I & II

A clear and accurate concept of this species has long been beclouded by errors in identification of certain stages in its development and by its frequent confusion with *S. sulcata* (Desm.) Whet. by mycologists subsequent to its description by Tulasne in 1861. I have already presented (Whetzel 1929) in some detail the basic evidence for this confusion of the two species. Critical examination of specimens preserved in European herbaria together with observations in the field, in culture, and on preserved specimens of both these species personally collected on numerous species of *Carex* in Europe during 1930, has fully confirmed my earlier provisional conclusion (Whetzel 1929: 15) that the two species have commonly been confused under the name *Sclerotinia duriaeana*.

While I made numerous collections of the spermatial and sclerotial stages of this species in most of the countries visited, I was in most places too late



PLATE I

to find apothecia. Unfortunately I was unable to visit the type locality where Durieu made his collections and observations on this species. I did, however, make two collections of apothecia which appear to be those of *S. duriaeana*, one near Rambouillet, France, (CUPP 31561) and another near Lyngby, Denmark, (CUPP 31564) (see data and comments below p. 395). In neither case were many apothecia found and the circumstances under which they were taken raises some question as to their identity. Perhaps if I had found abundant fresh cups of both species, each of unquestionable identity, I might have detected some differences of specific significance in their apothecia. I doubt it. Such evidence as is available offers little expectation that they are thus distinguishable. The sclerotia of the two species cannot with confidence be told apart and the spermatial stages alone provide ready and certain identification. (Compare Figs. 1 and 13.) A more extensive comparison than I have been able to make of these two species in artificial pure culture would almost certainly also provide dependable evidence for distinguishing between them.

In view of the scattered, confused and incomplete published data and descriptions of *S. duriaeana*, it appears desirable to present here a more complete and accurate description of the species, interpreted in the light of my own studies and observations.

SCLEROTINIA DURIAEANA (Tul.) Rehm, Hedwigia **21**: 66. 1882.

Epidocium ambiens Desm. Ann. Sci. Nat. Ser. 3, **20**: 231. 1853.

Peziza duriaeana Tul. Sel. Fung. Carp. **1**: 103. 1861, and **3**: 203, pl. 22, fig. 20-24. 1865.

Sphacelia nigricans sensu Sacc. Michelia **2**: 131. 1880.

Sclerotium nigricans sensu Sacc. Michelia **2**: 134. 1880.

Sphacelia ambiens Sacc. Syll. Fung. **4**: 666. 1886.

Sclerotinia duriaeana Sacc. Syll. Fung. **8**: 199. 1889.

Sclerotinia duriaeana (Tul.) Quélet (In error. See Notes p. 395.)

Hymenoscypha duriaeana Phill. Manual Brit. Discom. p. 115. 1893.

Myrioconium ambiens V. Höhnelt. Mitt. Bot. Inst. Tech. Hochsch. Wien. **3**: 50. 1926.

Spermodochidia (Figs. 1, 3 & 7) dull black in paired groups of 3-6 at regular intervals of 5-15 mm. along upper part of culm, 5-15 paired groups per culm, groups oblong to subglobose when moist, 1-3 mm. long, arranged parallel side by side lengthwise of the culm, usually on but two sides of the 3-angled culm, sometimes encircling the culm as in *C. chordorrhiza* (Fig. 2); at maturity becoming swollen and rupturing the culm, discharging the viscid, olivaceous mass of spermatia; *spermatia* minute, globose, 2-3 μ in diam., faintly olivaceous.

The spermodochidia are formed in lysigenous cavities in the palisade parenchyma of the culm, between the vascular bundles. Each spermo-

Plate 1. *Sclerotinia duriaeana*. Fig. 1. (Left) diseased heads of *Carex paniculata* L.; (right) healthy head, with spermodochidia and sclerotia in the diseased culms. CUPP 31562. **Fig. 2.** Diseased culms of *C. chordorrhiza* Ehrh. showing the spermodochidia. CUPP 31563. **Fig. 3.** Culm of *C. paniculata* with spermodochidia and sclerotium from De Thümen's Myc. Univ. 1557. All figures natural size.

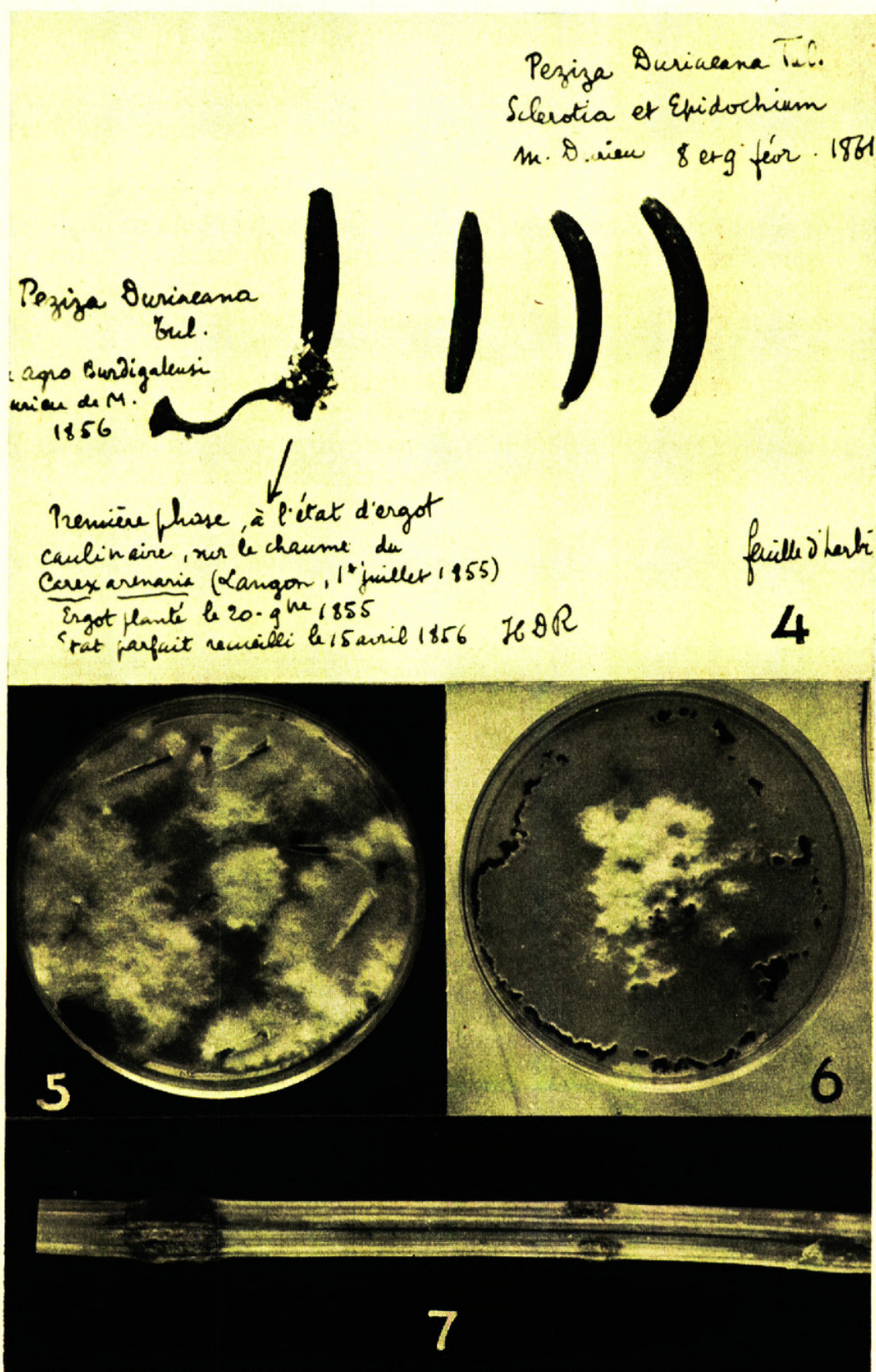


PLATE II

dochidium contains many spermodochia surrounded by masses of spermatia. (See Tulasne 1865: *pl.* 22, *fig.* 21.)

Sclerotia (Fig. 4) one to several in each culm, from which they are discharged at maturity through a slit in the culm over the sclerotium by the toppling of the upper part of the culm which bending at this point opens the sclerotial cavity; black, slender, fusiform, more or less curved when dry, when fresh plump, fusoid, slightly 3-angled, varying in length and thickness according to the size of the culm in which formed, 5–15 mm. long. The sclerotia first appear within the culm as elongate, pink, cottony masses of hyphae, which gradually darken externally as the dull black rind is formed and the densely packed thick-walled hyphae of the white medulla takes form.

Apothecia variable in size, depending upon the size of the sclerotia from which they arise, usually but one from each sclerotium; *cup*, 5–10 mm. in diam. occasionally larger, shrinking greatly on drying, deep goblet-shaped, thin, fragile, light fawn to vinaceous brown, lighter beneath due to a fine hyphal fuzz which covers the under surface when fresh; *stipe* rather short, its length usually about the diameter of the fully open cup, nearly or quite smooth; *asci*, according to Tulasne (1861: 106) are "8-spored (spores obliquely and closely uniseriate, seldom biseriate), cylindrical, obtuse, straight, 8–9.5 μ wide and about ten times as long." Boudier (1910: 274) describes them as cylindrical, rather large, slightly attenuate toward the base, 8-spored, pore blue with iodine, 210–230 x 7–10 μ ; *ascospores* are described by Tulasne (*l.c.*) as "ovate, inequilateral, obtuse at both ends and muticous, smooth, unilocular, and filled with oil the greater part measuring 10–15 x 6.5–7.5 μ , but some not exceeding 8–9.5 x 5 μ ." Boudier describes them as oblong-fusiform, colorless, usually without internal granules, but sometimes cloudy or rarely with non-oily droplets, 14–18 x 6–7 μ . Tulasne (1865: *pl.* 22, *fig.* 24) describes the discharge of the ascospores and their germination which he illustrates showing the direct formation on them of spermatophores and spermatia; *paraphyses* slender, slightly thickened at the tips, hyaline, sparingly septate, vacuolate (Boudier 1907: *pl.* 473, *fig.* 9; 1910: 274).

HABITAT: In culms of *Carex* species, growing in open swamps, marshes and wet meadows in western Europe.

TYPE SPECIMENS: Collected by Durieu de Maisonneuve in culms of *Carex brizoides* L. during the years 1855 to 1861 in the sandy meadows along the river Ciron about the ruins of the Château de Fargues not far from the towns of Langon and Bazas, France. There appears to be no

Plate 2. *Sclerotinia duriaeana*. **Fig. 4.** Photograph of Durieu's type specimens of the apothecium and sclerotia deposited in the Botanical Museum, Paris, sent me by Roger Heim; natural size. Tulasne (Sel. Fung. Carp. 3: *pl.* 22, *fig.* 23) presents a good sketch of the apothecium of this species. **Fig. 5.** Mycelial growth from bits of diseased culms of *C. paniculata* on potato dextrose agar; $\frac{1}{2}$ natural size. CUPP 31562. **Fig. 6.** Mycelium and spermodochial masses from tissue plantings from culms of *C. chordorrhiza* on potato dextrose agar; $\frac{1}{2}$ natural size. CUPP 31563. **Fig. 7.** Spermodochidia on culm of *C. chordorrhiza*, x6. CUPP 31563.

evidence that Tulasne preserved specimens of the materials on which his description of the species was based. The specimens he had in hand appear to have all been sent him by Durieu. Durieu, however, preserved what are obviously duplicate specimens of those sent Tulasne. These specimens were later, 1878, deposited in the cryptogamic herbarium of the Museum of Natural History in Paris (Fig. 4). These specimens therefore may be properly considered the type specimens of this species. These, together with rather extensive notes in Durieu's handwriting, were in 1930 mounted on herbarium sheets. Photographic copies of three of these sheets were kindly sent me by the curator, Dr. Roger Heim, after my visit to the museum. These are on file with my notes on this species. Duplicate specimens of sclerotia and infected inflorescences bearing spermodochidia from Durieu's collection of June 24 and 26, 1860, are filed in CUPP 17044. I found among Durieu's specimens but one apothecium (Fig. 4), apparently one of those developed from his first collection of sclerotia, July 1, 1855.

Since no species of *Carex* other than *C. brizoides* was found in Durieu's collections, and since this is the species pictured by Tulasne, it would appear that neither of them had in hand specimens of *S. sulcata* which they might have confused with *S. duriaeana*. Tulasne's (1861: 103) application of the name *Sclerotium sulcatum* Roberge in Desmaz. to the sclerotial stage of *S. duriaeana* was at the time a pardonable error. The only other name of the sclerotial stage of this species which has been applied is *Sclerotium nigricans* Sacc. given it by Saccardo (1880: 134, and 1899: 1153) under the erroneous impression, however, that the specimens in hand were sclerotia of *Claviceps nigricans* Tul.

DISTRIBUTION: This species is known to occur only in Europe. It has not been found in North America. Apothecia apparently appearing in May, spermodochidia June to July, sclerotia July and August. It is known to me from France, Belgium, Germany, England, Denmark and Norway.

ILLUSTRATIONS: Tulasne, Sel. Fung. Carp. 3, pl. 22, fig. 20-24. 1865. Boudier, Icon. Myc. 3: pl. 473. 1907.

MATERIAL EXAMINED: On *Carex brizoides* L. (*C. arenaria* in error): (1) Durieu's type specimens deposited in the Crypt. Herb. Mus. Nat. Hist., Paris (fully discussed above). I also found what appear to be duplicate specimens (spermodochidia and sclerotia) from Durieu's collections in the Kew Herbarium labeled "*Peziza Duriaeana* on *Carex arenaria*" from Cooke's herbarium; — (2) Krieger, Fung. Sax. 1682, "am grossen Winterberg," Germany, August 1, 1898 (spermodochidia and sclerotia). On *Carex paniculata* L.: Desmazières, Pl. Crypt. France. Ser. II, 20, "Epidocium ambiens Desm. Not. XXI. En été, sur les tiges sèches de divers Carex, à Ouystreham par M. Roberge." France (spermodochidia only); — De Thümen, Mycotheca Univ. 1575, "Epidocium ambiens Desm. f. Caricis paniculatae. Gallia. Grande Chartreuse pr. Grenoble. Aug. 1879, J. Therry." (spermodochidia and sclerotia); Roumeguère, Fungi Sel. 4682 "Sphacelia ambiens (Desm.) Sacc." (spermodochidia only); his Fungi Gallici 1200, "Sclerotium nigricans (Tul.) Sacc." (spermodochidia) all appear to have been made up from one and the same original collection by Therry; — Roumeguère, Fungi Gallici 3505, "Epidocium affine Desm. 3N.21. Chaumes du Carex paniculata. Tremonde (Belgique). Reliq. Westendorp." This is incorrectly determined. It is typical *Epidocium ambiens* Desm. The spermodochidia (no sclerotia) are typical of those of *S. duriaeana*. No date of collection is given; — Roumeguère, Fungi Sel. 4600, "Sclerotium sulcatum

Rob. A l'intérieur des chaumes secs du *Carex paniculata*. Louette Saint Pierre (Belgique). legit Aubert." (sclerotia only). No date given; — CUPP 31561, swamp near Rambouillet, France, May 6, 1930, Whetzel, Westcott & Duffrenoy. Several apothecia found lodged on hummocks of *Carex paniculata* standing in a pool of water. It is barely possible that some of these apothecia are these of *S. sulcata*. Ascospores discharged from two of them (Figs. 5, 6) gave, however, cultures quite different from cultures of *S. sulcata* (Figs. 17, 18) and like those from infected culms of the following collection; — CUPP 31562, swamp in outskirts of Faaborg, Isle of Fyn., Denmark, June 27, 1930, Whetzel & E. Gram (spermodochidia and sclerotia). On ***Carex disticha*** Huds.: Roumeguère, Fungi Selecti. Exs. 5419, "Sclerotinia Duriaeana Tul. (conidies). Sur les chaumes malades d'un *Carex* sp. King's Lynn (Angleterre), Automne 1889." Coll. Plowright (sclerotia and spermodochidia). A. J. Wilmott of the British Museum says the *Carex* is *C. disticha* Huds.; — Phillips Herbarium, Brit. Mus., three collections on one sheet. One is labeled "Peziza Duriaeana Tul. King's Lynn. July 1888," presumably collected by Plowright, showing typical spermodochidia. A. J. Wilmott identified the suspect as *Carex disticha* Huds. Two others are sclerotia which bear apothecia, labeled respectively: "Peziza Duriaeana Tul., growing from sclerotia gathered June 3, 1883 by C. B. Plowright, King's Lynn"; and "Peziza Duriaeana Tul. cultivated from sclerotia on *Carex arenaria* by C. B. Plowright, June 1, 1883." Dupl. in CUPP 33271. On ***Carex chordorrhiza*** Ehrh.: Flora Suecica, 1636, under the name *Myrioconium ambiens* (Desm.), the spermatial stage only. Collected by J. A. Nannfeldt in Torne Lappmark, Jukkäsjarvi, at Abisko above the railway station August 9, 1928. Dupl. in CUPP 31620. Apparently the first collection on this suspect; — CUPP 31563, marshy bogs near hotel at Fjellsäter above Trondhjem, Norway. July 8, 1930, Whetzel & Jørstad (spermodochidia and sclerotia). On ***Carex acutiformis*** Ehrh. (?) (new suspect): CUPP 31564, along the shore of Lyngby Sø, Lyngby, Denmark. June 5 and June 17, 1930, H. H. Whetzel (apothecia and sclerotia). The determination of the suspect by Grøntved of the University of Copenhagen is in some doubt as the single culm enclosing sclerotia is old and rotten.

In making the transfer of this species to the genus *Sclerotinia*, Rehm had before him (his *Ascomyceten* 603) specimens of *S. sulcata* which he mistakenly took to be those of Tulasne's species *Peziza duriaeana* (Whetzel 1929: 7).

The combination, *Sclerotinia duriaeana* (Tul.) Quél. appears to be a strange error, originally made by Rehm in his "Discomyceten" in Rabenh. Krypt. Flora 1³: 820. 1893. He here lists this species as "*Scl. Duriaeana* (Tul)" giving as a synonym, "Sclerotinia Duriaeana Quél. Bull. soc. myc. I. pag. 115". An examination of this reference discloses that the paper is by Boudier (not Quélet) in which he merely lists "*P[eziza] Duriaeana* Tul." as an example of species to be included in *Sclerotinia* Fckl. which Boudier makes a sub-genus of *Ciboria* Fckl. Later Boudier in his *Icones Myc.* 4: 274 writes "*Sclerotinia Duriaeana* (Tul.) Quél." without citing the place where Quélet is assumed to have made the transfer. Succeeding authors appear to have perpetuated the error.

Massee (1895: 283) cites as a synonym of *Sclerotinia duriaeana*, "*Epidodium arabicus* Desmaz. xxii. Not. in Ann. Sci. Nat., p. 19." This species name appears to be a strange error in the spelling of the name "*ambiens*." The reference he gives is obviously that of the original place of publication of *Epidodium ambiens*, the page being apparently that of a reprint instead of the original.

The names *Sphacelia nigricans* and *Sclerotium nigricans* were erected by

Saccardo who erroneously believed the sclerotia and spermodochidia in specimens (of *S. duriaeana*) on *Carex paniculata* were the sclerotia and spermoidea of *Claviceps nigricans* Tul. (Whetzel 1929: 9-10 and 1944: 426-428).

Von Höhnelt (1926a: 50-51) erroneously lists *Epidocium affine* Desm. as synonymous with his *Myrioconium ambiens*, believing it to be the same as or a variety of *Epidocium ambiens* of Desmazières.

There is considerable variation in the measurements of asci and ascospores of *S. duriaeana* as recorded by different authors. I have made measurements of asci and ascospores from three collections of apothecia with the following results: (1) Plowright's collection on *C. paniculata*: asci (6 meas.) 121.2-151.5 x 6-9.5 μ ; spores (50 meas.) 9.9-18.4 x 4.6-6.6 μ , mode 12.5 x 5.3 μ , av. 12.7 x 5.4 μ . (2) Whetzel's collection on *C. paniculata* (CUPP, 31561): asci (30 meas.) 133.3-181.8 x 8.1-10.8 μ , mode 157.5 x 8.1 μ , av. 158.9 x 8.3 μ ; spores (50 meas.) 10.5-14.5 x 4.6-7.2 μ , mode 11.8 x 5.3 μ , av. 11.9 x 5.4 μ . (3) Whetzel's collection on *C. acutiformis* (CUPP, 31564): asci (40 meas.) 127.2-169.6 x 8.1-9.5 μ , mode 151.5 x 8.1 μ , av. 147.6 x 8.7 μ ; spores (80 meas.) 9.9-15.8 x 5.3-7.9 μ , mode 13.2 x 6.6 μ , av. 13.3 x 6.5 μ . These measurements are distinctly smaller than those given by Boudier, but compare favorably with those given by Tulasne.

Although I cite Boudier's description and illustrations which he presents under the name *S. duriaeana*, I do so with some reservations. He does not specify the species of *Carex* on which his specimens occurred. His illustrations might just as well be those of *S. sulcata*. His measurements for asci and ascospores are rather large in comparison with the measurements of asci and spores of *S. duriaeana*. They more nearly approximate the maximum measurements of these structures in *S. sulcata*.

Whoever was responsible (presumably Durieu) for the identification of the *Carex* harboring the *Peziza duriaeana* which Tulasne had in hand, appears to have been in error. Culms from these collections bearing the typical spermodochidia and sclerotia as pictured by Tulasne (1865: pl. 22, fig. 20) have been critically examined by competent European taxonomists and declared to be *Carex brizoides* L., not *C. arenaria* L.

It is to be noted that of the *Carex* species on which *S. duriaeana* is known to occur only two are reported from North America. This may account for its apparent absence from the Western Hemisphere. It would appear to be most common and widely occurring on *Carex paniculata* and may yet be found on this susceptible where that occurs in the Western Hemisphere.

SCLEROTINIA SULCATA

PLATES III AND IV AND TEXT FIG. A

This species is apparently the most common and widely distributed of the *Sclerotinia* species on *Carex*. It occurs throughout northwestern Europe, northeastern United States and in the Pacific Northwest. Long confused with *S. duriaeana*, its distinct identity was first suggested by the writer (Whetzel 1929: 15). In this paper I reviewed in some detail the evidence

then available to me. My study of the species in Europe in 1930 has fully confirmed that conclusion. In that paper (*l.c.*: 19–24) I described it under the name *Sclerotinia duriaeana* ("affine form"), but anticipating the correctness of my belief that it was a species distinct from *S. duriaeana* I made the combination *S. sulcata* (*l.c.*: 15). It is here again briefly characterized under its proper name.

SCLEROTINIA SULCATA (Desm.) Whetzel, *Mycologia* **21**: 15. 1929.

Sclerotium sulcatum Roberge in Herb. Desm. (in part) *Ann. Sci. Nat. Ser. 3*, **16**: 329. 1851.

Epidocium affine Desm. (in part) *Ann. Sci. Nat. Ser. 3*, **20**: 232. 1853.

Claviceps (?) *caricina* Griffiths, *Bull. Torrey Club* **29**: 300. 1902.

Sclerotinia duriaeana "ambiens form," Whetzel, *Mycologia* **21**: 15. 1929.

Spermodochidia (Figs. 8–14) scattered irregularly along the upper part of the affected culm, usually confined to that part above the first sclerotium, sometimes a few below between sclerotia; almost always confined to two faces of the 3-angled culm; distinctly linear, 2–5 mm. long by $\frac{1}{3}$ to $\frac{1}{2}$ mm. broad; dull olivaceous brown, inconspicuous especially in dry culms, splitting longitudinally when mature to release the spermatial ooze. Their structure is illustrated in Text Fig. A; *spermatia* globose about 2 μ in diam., hyaline, produced endogenously and in succession from the tips of densely clustered obclavate spermatophores, embedded in a mucilaginous matrix.

Sclerotia (Fig. 16) one to three in each culm, fusiform, ends blunt, rounded, sulcate, at first pink, then smoky gray and finally black, variable in size, depending on the slenderness of the culm in which formed, 20–25 mm. by 3–4 mm. in the large culms of *C. riparia* var. *lacustris*, 4–5 mm. by $1\frac{1}{2}$ –2 mm. in *C. interior*. (For a more detailed description see Whetzel 1929: 20.)

Apothecia (Fig. 15) usually but one from each sclerotium, short-stipitate, fawn-colored; *cups* deep goblet-shaped to shallow funnel-shaped when fully expanded, varying in size from 2 to 10 mm. broad, about half as deep, smooth without, membranous; *stipe* relatively short, 5–20 mm. long, smooth and concolorous with cup above, darker below; *asci* slender, clavate, apex rounded, pore J+, 8-spored, spores uniseriate, 106 meas. of asci from 6 apothecia from *C. stricta* 128–183 x 7.3 x 11 μ , mode 155.8 x 9.16 μ , av. 161 x 8.6 μ ; *ascospores* hyaline, ovoid, more or less inequilateral, 205 meas. from 5 apothecia from *C. stricta* 8.8–17.5 x 5.3–8.8 μ , mode 13.1 x 7.09 μ , av. 12.6 x 6.9 μ ; *paraphyses* slender clavate, hyaline.

HABITAT: In culms of *Carex* species in swamps, wet, open marshes and along banks of slow streams and ponds. Europe and North America.

LECTOTYPE SPECIMEN: Cornell University Pl. Path. Herb. 11515 on *Carex stricta* Lam., McLean, N. Y., swamp just south of Lloyd Preserve. April 26, 1921, Whetzel. Duplicate deposited in Kew Herbarium, Kew, England.

DISTRIBUTION: Known to me in North America only from the region about Ithaca, N. Y., Delaware and the Pacific Northwest (Oregon). It will almost certainly be found when sought throughout northern United States

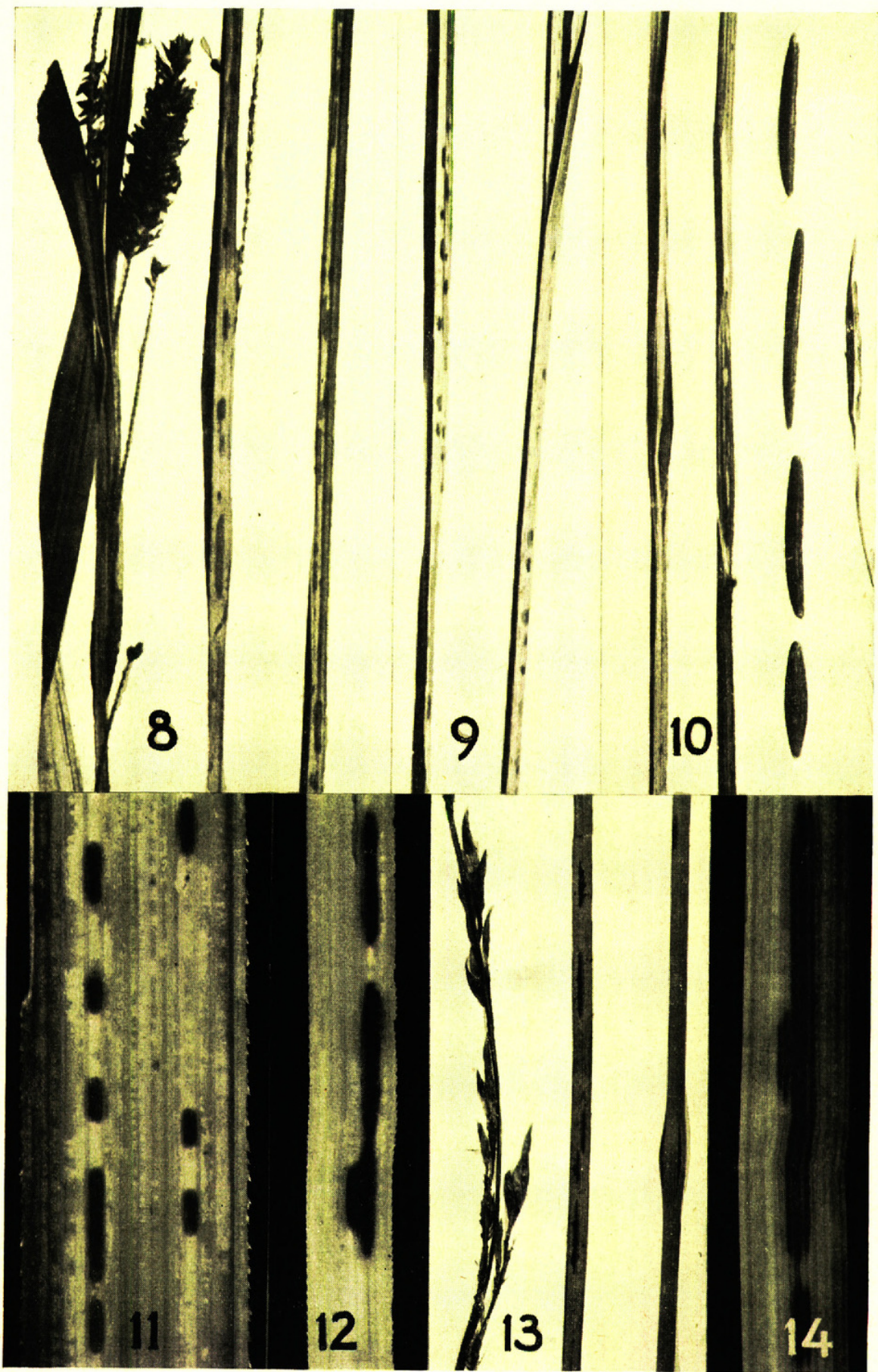


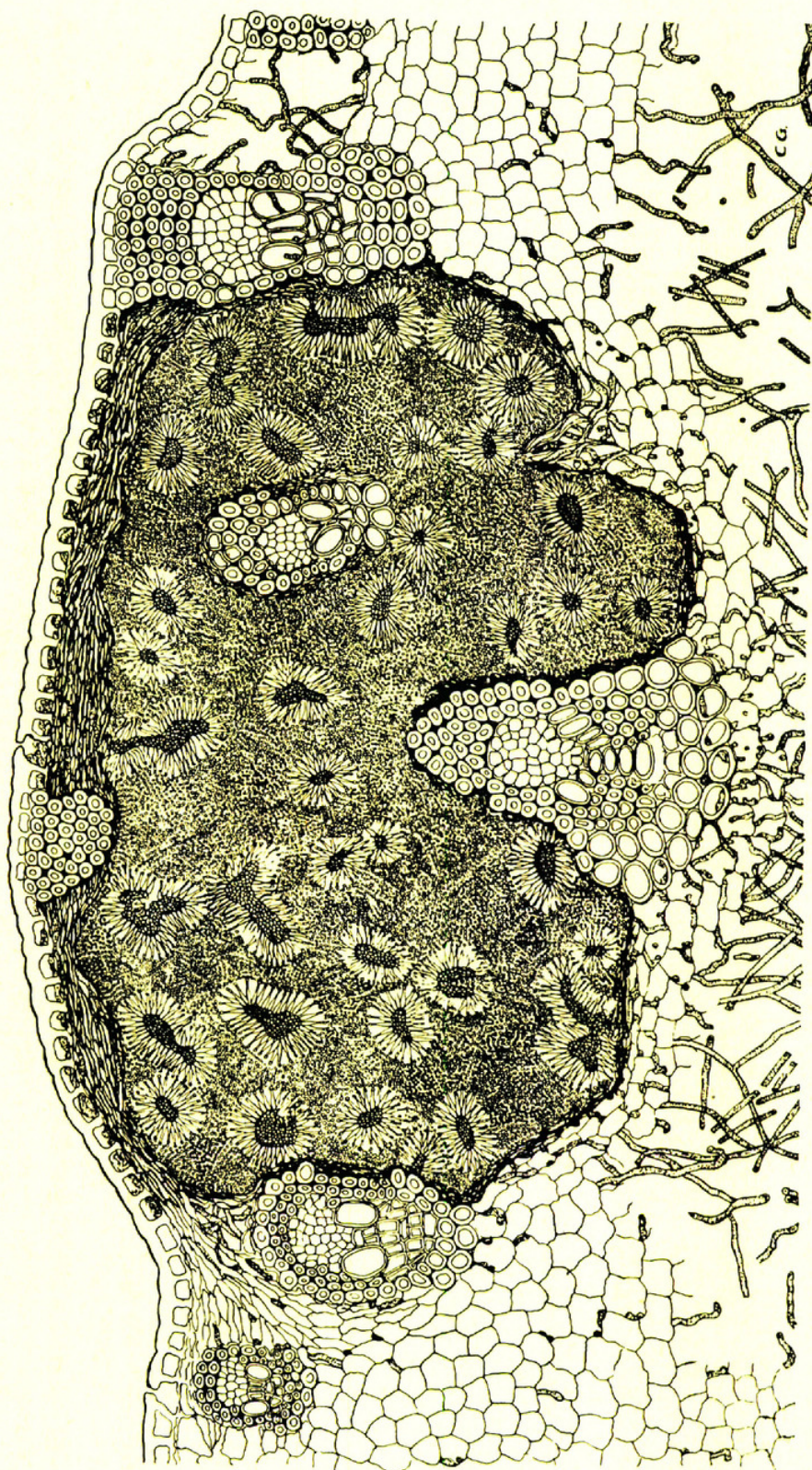
PLATE III

and Canada. It is apparently common throughout northwestern Europe as the records (below) of European specimens examined would indicate. The apothecia appear early in the spring (April–May) at the time the *Carex* susceptibles are beginning to flower. The spermodochidia and sclerotia begin to appear about a month later (June–July) and may be readily spotted in the dead bleached culms standing among the healthy.

ILLUSTRATIONS: Whetzel, *Mycologia* **21**: fig. 1–7, 14–19, 1929.

MATERIAL EXAMINED: In connection with my original description of this species (1929) I recorded the North American species of *Carex* then known to me, on which *S. sulcata* occurs. Since that time no additional collections of this species of special interest from North America have come into my hands. To round out the picture I present here the records of European collections which I have examined and studied: On ***Carex Hudsonii*** Bennett. (= *C. stricta* Good.): Desmazières, Pl. Crypt. France, Ser. II, 21. "*Epidocium affine*" (spermodochidia only); — Lindhart, Fungi hungarici, 381, "*Peziza Duriaeana* Tul." on *Carex*, Hansag, Nov. 1883 (sclerotia and spermodochidia); — Rehm, Ascomyceten, 603 a, "*Sclerotinia Duriaeana* (Tul.)" on "*Carex stricta* Good.", Diessenhofen, Thurgau, Switzerland, Apr. 1881, "Dr. Winter" (sclerotia and apothecia); — Rehm, Ascomyceten, 603 b, "*Sclerotinia Duriaeana* (Tul.) Walesellen bei Zürich, Auf faulenden Halmen, *Carex stricta*, 4/1893. Dr. V. Tavel" (apothecia and sclerotia); — Rabenhorst-Winter, Fungi Europaei, 2749. "*Sclerotinia Duriaeana* (Tul.)" on *Carex stricta* Good., Diessenhofen, Switzerland, April 1882, H. Wegelin (apothecia and sclerotia); — CUPP 31566, swamp near Fuer Sö, Jagerhuset, Denmark, June 8, 1930, Whetzel (spermodochidia and young sclerotia); — CUPP 31567, along shore of Sjael Sö, Denmark, June 20, 1930, Whetzel & Ferdinandsen (spermodochidia); — CUPP 31568, swamp on outskirts of Copenhagen, near Söburg, June 21, 1930. Whetzel & Grøntved (spermodochidia); — CUPP 31569, Ryggmossen near Upsala, Sweden, May 28, 1931, K. G. Ridehies (apothecia and sclerotia). Dupl. in Herb. Univ. Upsala, Sweden. On ***Carex vulpina*** L.: Desmazières, Pl. Crypt. France, Ser. I, Ed. 1, 2029 and Ser. I, Ed. 2, 1629. "*Sclerotium sulcatum* Rob. in herb." (spermodochidia and sclerotia); — CUPP 31576, Upper Grimley, brick pits, Worcestershire, England, August 8, 1930, Whetzel & C. Rea (spermodochidia). On ***Carex gracilis*** Curtis: CUPP 31570, Upton-on-Severn, Worcestershire, England, August 8, 1930, Whetzel & C. Rea (spermodochidia and sclerotia); — CUPP 31571, Upper Grimley, brick pits, Worcestershire, England, August 8, 1930, Whetzel & C. Rea (spermodochidia and sclerotia). On ***Carex inflata*** Huds. (= *C. rostrata* Stokes): CUPP 31572, swamp in woods at Nosten, parish of Bondhyrho near Upsala, Sweden, July 3, 1930, Whetzel & Nannfeldt (spermodochidia). On ***Carex brizoides*** L.: CUPP 31573, swamp in woods at Nosten, parish of Bondhyrho near Upsala, Sweden, July 3, 1930, Whetzel & Nannfeldt (spermodochidia). On ***Carex nigra*** (L.) Reichard (= *C. Goodenowii* Gay): CUPP 31574, swamp in woods at Nosten, parish of Bondhyrho near Upsala, Sweden, July 3, 1930, Whetzel & Nannfeldt (spermodochidia). On ***Carex disticha*** Huds.: CUPP 31575, along shore of Lyngby Sö, Lyngby, Denmark, June 21, 1930, Whetzel (spermodochidia). On ***Carex paradoxa*** Willd.: CUPP 31578, swamp near Fuer Sö, Jagerhuset, Denmark, June 24, 1930, Whetzel & Buchwald (spermodochidia). On ***Carex paniculata*** L.: CUPP 31579, marsh near Faaborg, Isle of Fyn, Denmark, June 29, 1930, Whetzel & E. Gram (spermodochidia). On ***Carex riparia*** Curtis: CUPP 31580, Knapp's brickyard, Claines, Worcestershire, England, August 7, 1930, Whetzel & C. Rea (spermodochidia and

Plate 3. *Sclerotinia sulcata*. **Figs. 8–10.** Diseased culms of *C. gracilis* showing diseased inflorescence, spermodochidia, and sclerotia; natural size. CUPP 31571. **Fig. 11.** Spermodochidia on culms of *C. vulpina*, x6. CUPP 31576. **Fig. 12.** Spermodochidia on culms of *C. paniculata*, x6. CUPP 31579. **Fig. 13.** Diseased inflorescence, spermodochidia and sclerotia on culm of *C. prairea*; natural size. CUPP 14947. **Fig. 14.** Spermodochidia on culms of *C. gracilis* x6. CUPP 31571.



Text Fig. A. Cross section through a spermodochidium of *Sclerotinia sulcata* in culm of *C. paniculata* about x325. Note that the cavity is formed by lysis of the parenchyma between the vascular bundles. Drawn by Carlos Garcés.

sclerotia); — CUPP 31581, valley of the Avon, south of Salisbury near Woodgreen, Hampshire, England, August 4, 1930, *Whetzel & Wm. Brown* (spermodochidia and sclerotia). On *Carex* sp.: Herbarium of C. Crossland (Herb. Kew, England), "*Sclerotinia Duriaeana* (Tul.) Quel. Among decaying *Carex* etc. Masham, (Yorkshire), England. May 28, 1902" (sclerotia and apothecia).

The earliest name applied to any stage of this species is *Sclerotium sulcatum* Roberge in herb. Desm. (1851). Two years later Desmazières described the spermodochidial stage under the name *Epidocium affine*. Both of these names were based on mixtures of culms of *Carex* species and *Schoenus nigricans*, the sclerotia and spermodochidia on the latter, being those of a heretofore undescribed species of *Sclerotinia*. (See p. 421). These stages as well as the apothecia of *Sclerotinia sulcata* were long confused by European mycologists with those of *S. duriaeana*. The writer (Whetzel 1929: 15) appears to have been the first to suspect its specific identity.

The only recorded collection of this species in North America, prior to 1929, as far as I have been able to discover, was made by Griffiths and Morris in August 1901 near Andrews, Oregon on *Carex nebraskensis*. Their collection consists of sclerotia and spermodochidia only. Griffiths (1902) described the fungus under the name "*Claviceps? caricina* sp. nov." Groh (1911) having had occasion to examine this collection by Griffiths and Morris which had been distributed as West American Fungi 400, referred it to Güssow who identified the fungus as *Sclerotium sulcatum* but erroneously referred the spermodochidia to *Epidocium ambiens*, the spermatial stage of *Sclerotinia duriaeana*.

It would appear from the recorded collections that *S. sulcata* is more common in Europe than *S. duriaeana* and goes to a greater number of *Carex* species. Both species are recorded on *C. brizoides*, *C. paniculata* and *C. disticha*. While *Carex paniculata* and its closely related species, *C. brizoides*, *C. disticha* and *C. chordorrhiza* appear to be the favorite suspects of *S. duriaeana* in Europe, *C. hudsonii* and its North American counterpart, *C. stricta*, appear to be the most common suspects for *S. sulcata* in North America.

SCLEROTINIA LONGISCLEROTIALIS

PLATE V

As far as I am aware, *Sclerotinia longisclerotialis* Whet. has been recorded only from North America. I kept a sharp lookout for it wherever I collected in swamps and wet marshes in western Europe during 1930, but no specimens were found which might on any grounds be referred to this species. No *Sclerotinia* species was taken there on any of the *Carex* species on which *S. longisclerotialis* is known to occur. It seems therefore probable that it is a species restricted to North America.

Although this species is described, illustrated, and discussed in full in my 1929 paper (Whetzel 1929: 24–30, fig. 10–13, 20–23) a brief description is here presented for the convenience of the reader. A complete list of the species on which it is known to occur, including a new suspect made subsequent to those already listed (Whetzel 1929: 30), is recorded below.

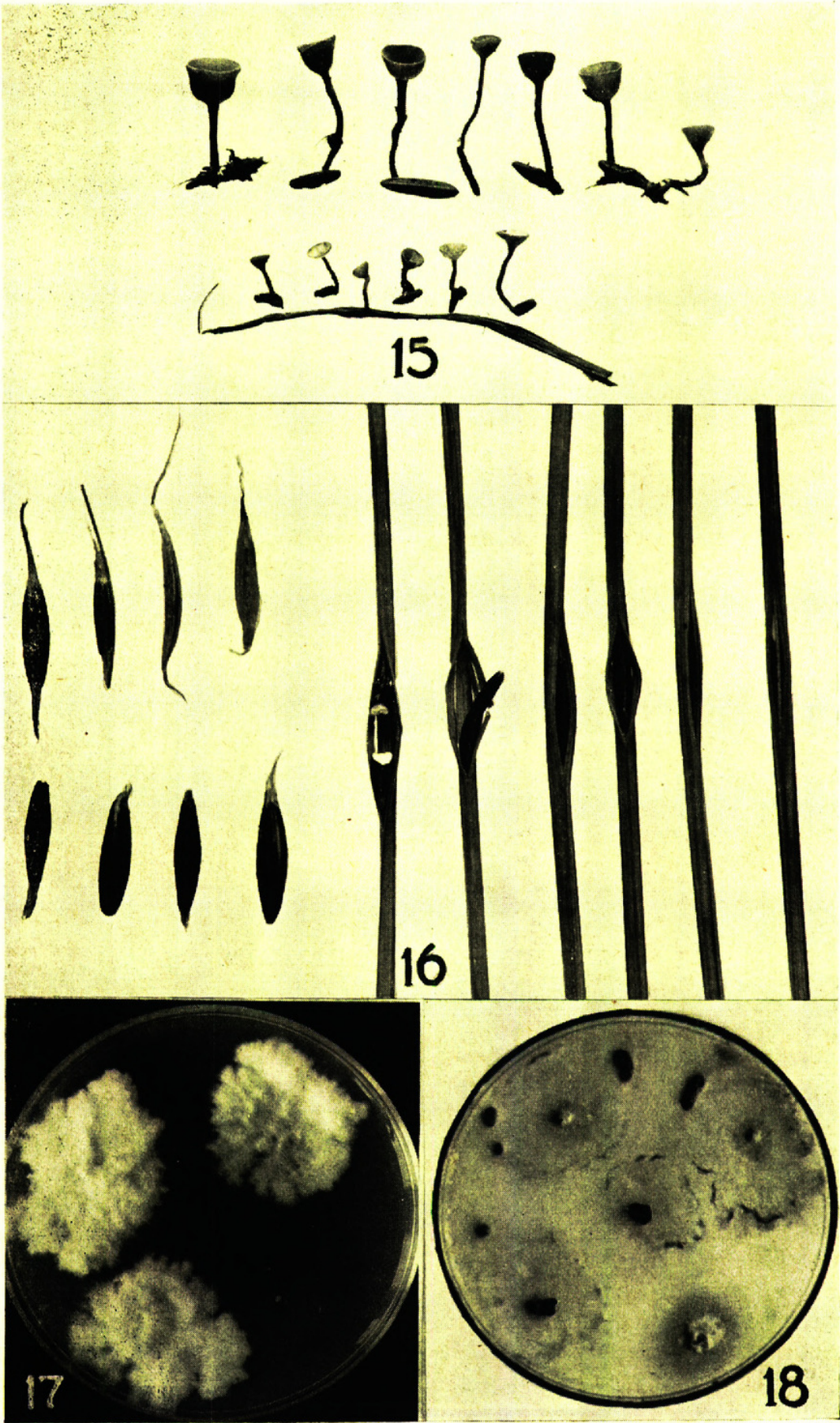


PLATE IV

SCLEROTINIA LONGISCLEROTIALIS Whetzel, Mycologia 21: 24-30. 1929.

Spermodochidial groups (Figs. 20, 21) ovate, oblong, shining black, in pairs at rather regular intervals along two faces of the culm just below the inflorescence, rarely toward the base below the sclerotium, formed within the cortical tissues of the culm, exposed by slits in the epidermis through which ooze the mucilaginous masses of spermatia; *spermatia* globose 1-2 μ in diam., hyaline, produced in succession from the tips of obclavate spermatophores. External appearance and internal structure essentially as in *S. duriaeana* (see Whetzel 1929: fig. 23).

Sclerotia (Figs. 19, 22) usually one, sometimes two or more, in culm, remaining enclosed or slightly exposed by a slit in the epidermis (Fig. 20), never freed as are the sclerotia in *S. sulcata* or *S. duriaeana*, at maturity truncate, uniform in thickness, more or less 3-angled, striate due to pressure of the vascular bundles of the culm during development, at first cottony, becoming pinkish, then smoke gray, finally dull black without, the medulla white; variable in length and diameter according to the size of the infected culm, 1 cm. long by 1 mm. thick in *C. interior*, 7 cm. long by 2 mm. thick in *C. retrorsa* and 3 to 10 cm. long in *C. prairea*.

Apothecia (Fig. 19) thistle-, funnel-, or goblet-shaped with long slender stipe, one, rarely two or more, from each sclerotium; *cup* dark fawn-colored, smooth without, membranous, mouth constricted, never opening widely, 2-5 mm. broad; *stipe* slender, 10-50 mm. long, pale and smooth above, dark tomentose below; *asci* long, cylindrical, attenuate below the middle, 136 meas. from 5 apothecia from *C. prairea* gave 170-230 x 8.8-14.3 μ , mode 194 x 10.4 μ , av. 182.1 x 10.7 μ ; *ascospores* strongly inequilateral, flat or incurved on one side, 289 meas. from 5 apothecia from *C. prairea* gave 12.6-22.8 x 5.3-12.5 μ , av. 18.3 x 8.1 μ , mode 21 x 9 μ ; *paraphyses* slender, slightly clavate, septate.

In culture on potato dextrose agar forming an appressed feathery growth of aerial mycelium (Whetzel 1929: fig. 20) with distinct minute hard spermodochial masses. No sclerotia formed.

HABITAT: Open swamps and marshes where water stands throughout the year.

TYPE LOCALITY: Swamp south of the Lloyd Preserve, McLean, N. Y.

DISTRIBUTION: U. S. A.: New York and Maine; Canada: Lake Temagami, Ontario.

TYPE SPECIMEN: CUPP 10544 on *Carex prairea* Dewey, May 16, 1918. Whetzel.

MATERIAL EXAMINED: In addition to the specimens listed in 1929 (p. 30) on *Carex prairea* Dewey, *C. interior* Bailey, *C. vesicaria* L., *C. retrorsa* Schw., and *C. crinita* Lam. may be reported: On *C. prairea*: CUPP 17499, McLean, N. Y. May 27, 1929 (apo-

Plate 4. *Sclerotinia sulcata*. Fig. 15. Apothecia from culms of *C. stricta*; natural size. CUPP 11515. **Fig. 16.** Sclerotia from culms of *C. stricta*; natural size. CUPP 14747. **Figs. 17-18.** Cultures from *C. stricta* on potato dextrose agar showing cottony aerial mycelium, and sclerotia with spermodochial masses respectively; $\frac{1}{2}$ natural size. CUPP 11515 and 14747.

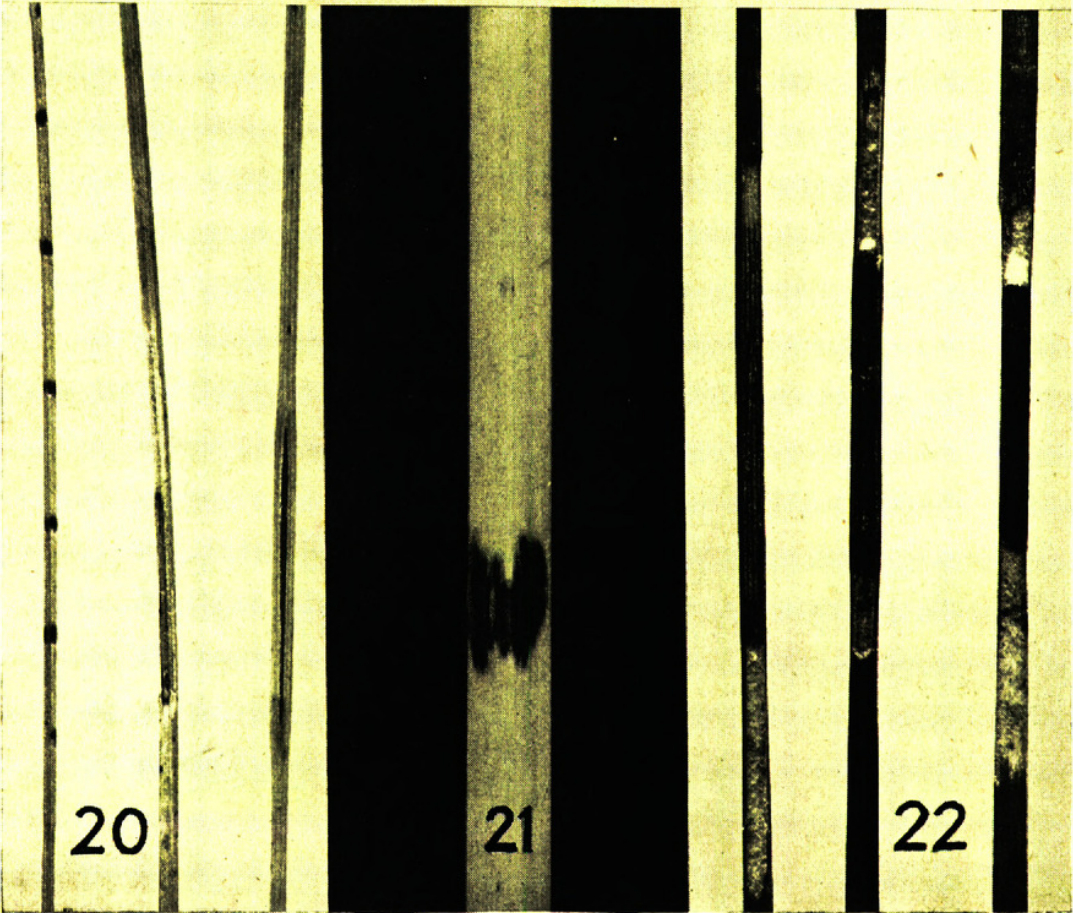
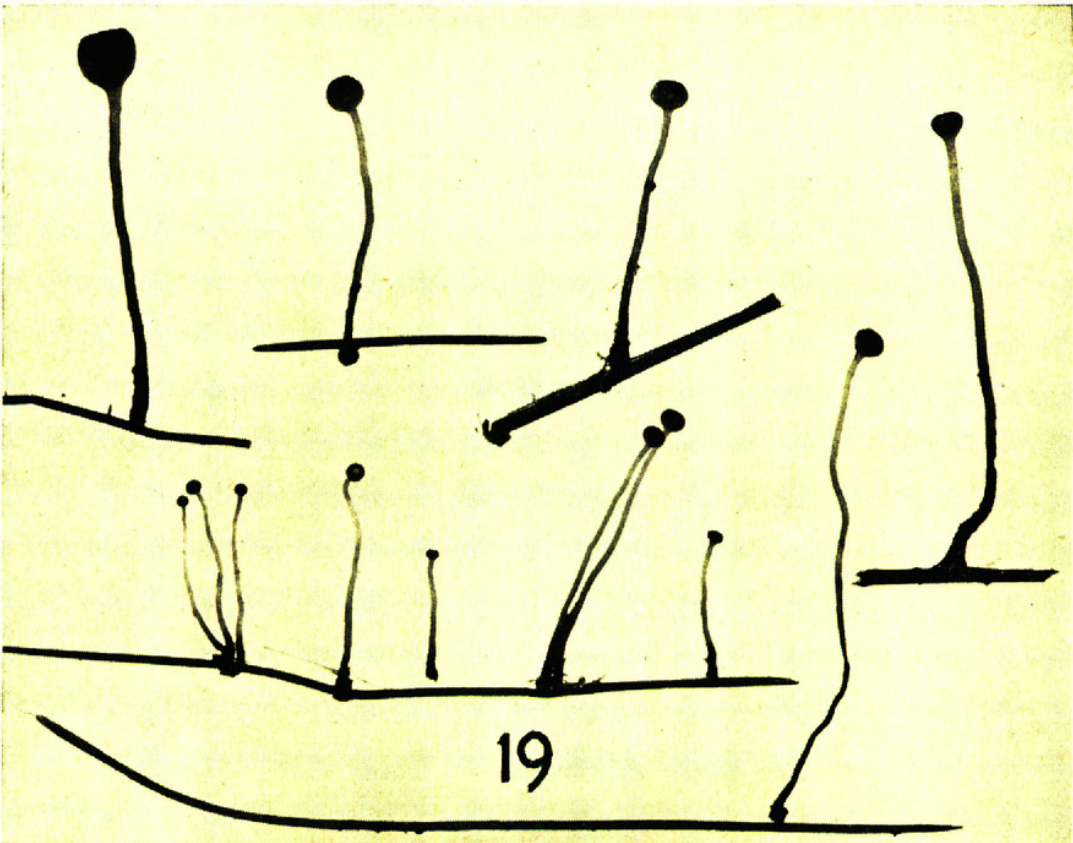


PLATE V

thecia); — CUPP 23536, McLean, N. Y. May 14, 1934 (apothecia). On *Carex oligosperma* Michx.: CUPP 17783, Sand Point, and CUPP 17784, near Bear Island, Lake Temagami, Ontario, Canada, both on September 16, 1929, H. H. Whetzel & Geo. Thompson (spermodochidia and sclerotia).

This species is doubtless common and widely distributed in northern United States and Canada. Localities where it occurs are readily discovered by looking during late summer for the dead and bleached culms with their characteristic spermodochidia and sclerotia.

Carex oligosperma Michx. is here for the first time recorded as a suspect of *S. longisclerotialis*.

SCLEROTINIA CARICIS-AMPULLACEAE

PLATE VI

Of all the species of *Sclerotinia* known to me on sedges and rushes, *S. caricis-ampullaceae* Nyberg is the largest, the most striking, and to the eye of a mycologist, the most beautiful. This species was first brought to my attention by Dr. John Nannfeldt of the University of Upsala. He sent me in February, 1933 a collection taken June 25, 1932 near Lake Gärdsjön in Sweden. I recognized it at once as an undescribed species and proposed to Dr. Nannfeldt that I publish a description of it, naming it in his honor. Fortunately I delayed the preparation of the manuscript. A year later, in February 1934, I received another specimen of this species from Dr. Nannfeldt which had been collected in Finland. Along with the specimen he sent me a preliminary description of the species prepared by the collector, Mr. Wolmar Nyberg, who was publishing it under the name the species now bears. Nyberg, amateur mycologist and banker, had discovered it in early June 1930, in a sphagnum bog on his villa grounds near Vessö in the parish of Borgä, where it appeared each succeeding spring. Nyberg's description of which he sent me a reprint appeared in the Finnish scientific journal cited below.

During the winter of 1937–38, Dr. W. G. Solheim of the University of Wyoming told me of a remarkably large and beautiful species of *Sclerotinia* on *Carex aquatilis* which his colleague, Dr. C. L. Porter, had discovered in a high mountain swamp in the Medicine Bow Mountains, in June 1937 (Fig. 25). Duplicate specimens of Porter's collection together with abundant collections made by Solheim in 1939 and in succeeding years proved it to be conspecific with the Scandinavian collections. The extraordinary size and unusual form of the sclerotia of *S. caricis-ampullaceae* distinguish it at once from the other species on *Carex*. Although known from but three localities, its occurrence in Scandinavia and the high mountains of Wy-

Plate 5. *Sclerotinia longisclerotialis*. **Fig. 19.** Apothecia attached to the sclerotia, from culms of *C. prairea*; natural size. CUPP 23536. **Fig. 20.** Spermodochidia and enclosed sclerotia, from culms of *C. interior*; natural size. CUPP 15868. **Fig. 21.** Spermodochidia, x6, from culms of *C. vesicaria*. CUPP 15860. **Fig. 22.** Young sclerotia exposed by cutting away the culm epidermis, x2, in culms of *C. prairea*. CUPP 15872.



PLATE VI

oming suggests that it is probably common wherever its suscept occur throughout the sub-arctic isothermal zone.

An extensive treatment of this species is to be found in the paper by myself and Solheim (1943).

SCLEROTINIA CARICIS-AMPULLACEAE Nyberg, Mem. Soc. pro Fauna et Flora Fenn. 10: 20-23. 1934.

Spermodochidial groups (Fig. 24) when fresh, dark colored, tuberculate, more or less spaced at intervals along the culm just below the inflorescence, exposed by slits on two faces of the culm; *spermatia* hyaline, globose to slightly ovate, 2.5-3 μ in diam., produced successively from the tips of clustered obclavate spermatophores, oozing forth in mucilaginous drops.

Sclerotia (Fig. 24) extraordinarily large, variable in size up to 20 cm. long by 1 cm. thick near the base, ventricose below with rounded or bluntly attenuated base, gradually elongated above into a slender whip-like apex, developed within the slender 3-angled culm, the base firmly nestled in the very base of the culm and the enclosing leaf bases, breaking forth through a slit in the epidermis of the culm to expose the lower half or so, the slender pointed tip remaining firmly enclosed, black without, sulcate, within pale pink to white, firm.

Apothecia (Figs. 23, 25) usually several to many, fasciculate, arising at one point on the exposed surface of the sclerotium, long-stipitate; *cup* thistle-funnel-shaped becoming more or less expanded, vinaceous brown, 4-22 mm. in diam. by 7-16 mm. deep, outside finely tomentose, relatively thin (1 mm.), membranous; *stipe* long, slender, flexuous, varying in length depending upon the depth to which the sclerotium is immersed, only the cup and upper part of the stipe protruding from the water or moss; *asci* cylindrical, attenuated below, apex rounded and thickened, pore faintly J+, 192-213 x 11.8-13.5 μ , 8-spored, spores uniseriate; *ascospores* ellipsoid, hyaline, smooth, without oil drops, 13.5-16.9 x 8.5-10 μ ; *paraphyses* fili-form, hyaline, branched below, scarcely enlarged toward the tips, 1-2 μ in diam.

HABITAT: In culms of *Carex aquatilis* Wahl., *C. aquatilis* Wahl, var. *altior* (Rydb.) Fern., and *C. inflata* Huds. in wet swamps and mossy bogs in sub-arctic or high mountain regions.

TYPE SPECIMEN: On *Carex inflata* Huds. (= *C. ampullacea* Good.), sphagnum bog near Vessö, parish of Borgå, Finland, June 19, 1931. Coll. W. Nyberg. Part of type deposited in CUPP 28912. Dupl. in Bot. Inst. Univ. Upsala, Sweden.

DISTRIBUTION: Finland, Sweden, and Wyoming, U.S.A. Apothecia June-July, spermodochidia and sclerotia late summer and autumn.

Plate 6. *Sclerotinia caricis-ampullaceae*. Fig. 23. Apothecia from sclerotia in culms of *C. aquatilis* var. *altior* (specimen from preserving solution). CUPP 28910. **Fig. 24.** Spermodochidia and sclerotia in culms of *C. aquatilis* var. *altior*; natural size. CUPP 29268. **Fig. 25.** Apothecia in their natural habitat; natural size.

MATERIAL EXAMINED: In addition to the type material, I have had in hand: On *Carex aquatilis* Wahl.: — Collection made at Selet, near Lake Gärdjön, prov. Västernorrland, parish of Lövånger, Sweden, June 25, 1932, G. Lohammar, CUPP 21965, (dupl. in Herb. Bot. Inst. Univ. Upsala). On *Carex aquatilis* Wahl. var. *altior* (Rydb.) Fern.: numerous collections (Whetzel & Solheim 1943: 397) made below Nash Fork bridge near Univ. Wyoming Science Camp in the Medicine Bow Mts. (alt. 9,600 ft.), Albany Co., Wyo. during the years 1937, 1939, 1940, 1941, and 1942, W. G. Solheim & C. L. Porter. On *Carex inflata* Huds., Solheim, same locality, June 27, 1942. Duplicates of all these collections are deposited in the herbarium of the University of Wyoming and the Plant Pathology Herbarium, Cornell University. The collection of apothecia made June 26, 1939 on *C. aquatilis* var. *altior* has been distributed by Solheim as 204, Mycoflora Saximontanensis Exsiccata.

SPECIES ON ERIOPHORUM

As far as I have been able to find, there is but one species of *Sclerotinia* reported on *Eriophorum*. This is *Sclerotinia vahliana* described by Rostrup (1891: 607) from specimens collected by J. Vahl, S. Hansen and N. Harz on botanical expeditions at various times on the west coast of Greenland. The earliest collected specimen which Rostrup had before him when he described this species is presumably one collected by J. Vahl for whom he named the species. A specimen preserved in the Rostrup collections in the University Botanical Museum, Copenhagen, bears the label "E. Rostrup's Svampesamling. 1. *Sclerotinia Duriaeana* Tul. (*Carex rigida*). Nonnese 5/1829 by J. Vahl." Through the kindness of the director of the museum, Johs. Grøntved, this specimen was loaned me in September 1927 (Fig. 28). A critical examination satisfied me that this is not *S. duriaeana* and that the suspect is a species of *Eriophorum*. Whether or not this is one of the specimens on which Rostrup based his description it is now impossible to say. Since this is earliest known collection of the species and was collected by J. Vahl, I am designating it the type specimen of *S. vahliana* Rostr.

SCLEROTINIA VAHLIANA

PLATE VII AND TEXT FIG. B

Rostrup gives *Eriophorum scheuchzeri* as the suspect for all the collections he had from Greenland and lists, in addition to Vahl, two other collectors, S. Hansen and N. Harz, who appear to have made their collections during the years 1888 and 1889 (Rostrup 1891: 593). These specimens were presumably deposited in Rostrup's collections in the Botanical Museum in Copenhagen, but I have no record of having seen them when I was there in 1930.

I know of but two other collections identified as *S. vahliana*. One of these is a collection made by J. A. Nannfeldt in northern Sweden in 1927 on *Eriophorum angustifolium* and another collected by Vestergren, *et al.* in the same region in 1903 on the same species and distributed under 730, in Vestergren's *Micromycetes Rariores Selecti*. These agree well in all their characters with the type collection.

During the summer of 1930 I made collections of a *Sclerotinia* attacking *E. angustifolium* (Fig. 26) in Denmark and in southern Sweden. I was able

to study only the early stages of the infection which was developing while I was there during the months of June and July. I obtained the fungus in pure culture (Fig. 27) and also found the sclerotia in early stages of development in culms in the field. Such evidence as I was able to get, indicates that the fungus in these collections is probably *S. vahliana*.

It seems desirable to present here a translation of Rostrup's original description.

"376. *Sclerotinia Vahliana* n. sp.

"Apothecia arising from a sclerotium, stipitate, brown or castaneous. Cup hemispherical, length and height, 4–8 mm. Stipes flexuous, tomentose, striate below, 1–3 cm. long, about 1 mm. thick. Asci cylindrical-clavate, long stipitate, length (including stipe) 150–170 μ x 8–10 μ . Spores ellipsoid, 11–14 x 4–6 μ . Paraphyses numerous. Sclerotia black, oblong, compressed, sulcate, 1 cm. long by 0.5 cm. thick.

"Between the leaf sheaths of *Eriophorum Scheuchzeri* Hoppe, Greenland (Vahl), Umanak (S. Hansen), Egedesminde, Holstenborg, Godthaab (N. Harz).

"Sclerotia assembled, 2–3, between the lower leaf sheaths, with 3–4, deep furrows along the outward turned, free side."

Based upon Rostrup's original description of the apothecia and my studies on the specimens above referred to, the following would appear to be a fairly complete description of this species.

SCLEROTINIA VAHLIANA Rostr. In Tillaeg til "Grønlands Svampe (1888)." Meddel. om Grønland. 3: 607–608. 1891.

Spermodochidia not found.

Sclerotia (Fig. 28 and Text Fig. B) variable in size and shape, shell-like in the form of a short, lobed half-cylinder or hollow hemisphere, up to 2–3 cm. in circumference, about 2–3 mm. thick, black without, white within, surface rough, irregularly and deeply creased, with low ridges, usually 3–4 in each culm, obviously originating within the culm but finally breaking forth to complete its growth. This peculiar morphology of the sclerotia has been recorded by Rostrup (1903: 315) who quotes a note by Ostenfeld, the collector of specimens of this species from Iceland: "Sklerotierne højst uregemaessigt bugtet-foldede" (Sclerotia very irregularly curved and creased). The internal structure is essentially like that of other species of *Sclerotinia*.

Apothecia (Figs. 29, 30) 1–several arising fasciculately from some point on the sclerotium, broadly and deeply cup-shaped, castanean brown, short stipitate; *cup* up to 10 mm. broad by nearly as deep; *stipe* 1–3 cm. long x 1 cm. thick, flexuous, tomentose, darker than cup, black toward base; *asci* cylindrical clavate, long-attenuate below, tip rounded, not thickened, 50 meas. (type) 109–164 x 7.8–10.4 μ , mode 151.7 x 9 μ , av. 144 x 8.6 μ , 8-spored, spores uniseriate; *ascospores* long ellipsoid to fusoid, flat to concave on one side, biguttulate, 50 meas. (type) 10.8–18 x 4.8–6.6 μ , mode 12 x 5.4 μ , av. 13 x 5.6 μ ; paraphyses numerous, slender, simple or branched, 3 μ diam., slightly or not at all enlarged at the tips.

In culture (Fig. 27) on potato dextrose agar forming a sparse white webby aerial mycelium; submerged mycelial mat dark olivaceous brown.



PLATE VII

Sclerotia formed abundantly, irregularly discoid or oblong, flat or low loaf-shaped (from diseased stems collected near Lyngby, Denmark).

HABITAT: In the culms of *Eriophorum scheuchzeri* Hoppe, *E. vaginatum* L., and *E. angustifolium* Roth. in sphagnum bogs, apothecia, May–July; sclerotia, late summer and autumn. An arctic and sub-arctic species.

DISTRIBUTION: Reported from Greenland (Rostrup 1891 and 1906), and Iceland (Rostrup 1903 and Larsen 1932). Known to me from Denmark and Sweden. Should be found in the arctic and sub-arctic zones of continental North America.

TYPE SPECIMEN (Fig. 28): The collection by J. Vahl on *Eriophorum* (*scheuchzeri* ?) Nonnese, Greenland, May 1829. Deposited in the Botanical Museum, Copenhagen, under the name, "*Sclerotinia Duriaeana* Tul." Photograph and microscopic mount deposited in CUPP 16275.

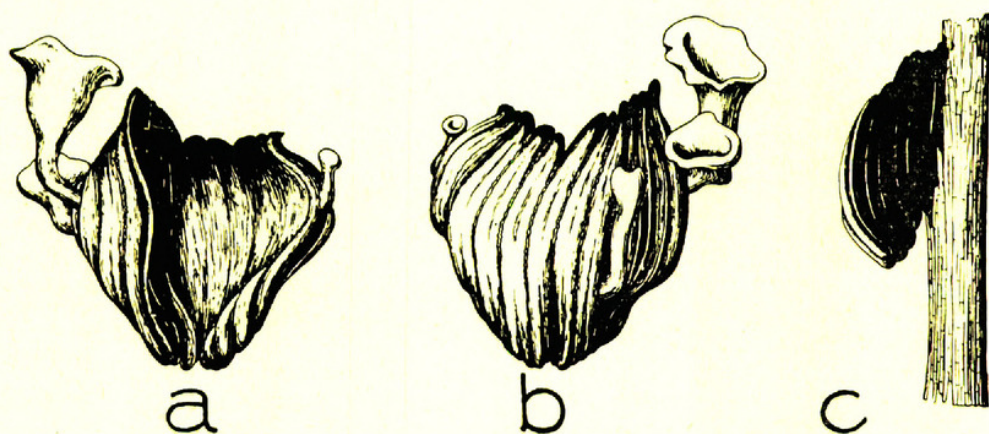
MATERIAL EXAMINED (in addition to the type specimen): On *Eriophorum vaginatum* L.: CUPP 31589, sphagnum bog along north shore of Lyngby Sø, Lyngby, Denmark, June 7, 1930, H. H. Whetzel (early stages of infection); — CUPP 31591, swamp in forest at Nosten, parish of Bondhyrho, near Upsala, Sweden, July 3, 1930, H. H. Whetzel & J. A. Nannfeldt (early stages of infection). On *Eriophorum angustifolium* Roth. (= *E. polystachyon* L.): Vestergren, Micromycetes Rariores Selecti, 730. Lapponica Tornensis, Vassijaure (Sweden), July 1903, A. Roman, N. Sylvén & T. Vestergren (apothecia and sclerotia); — "Fungi Suecici". University Upsala. Dupl. N. Y. Bot. Gard. and CUPP 31606. Collected in Torne, Lappm. Jukkasjarvi. s:n. Abisko, Sweden, June 30–July 5, 1927, J. A. Nannfeldt (apothecia and sclerotia); — CUPP 31590, swamp in forest near Nosten, parish of Bondhyrho, near Upsala, Sweden, July 3, 1930, H. H. Whetzel & J. A. Nannfeldt (early stages of infection).

This species is very distinct from the others in cyperaceous suspects, being especially marked by the unusual form and development of its sclerotia. While I think that the *Sclerotinia* which I found in its early infection activities in the culms of *E. vaginatum* and *E. angustifolium* in Denmark and Sweden is probably *S. vahliana*, it is unfortunate that I was not early enough in the localities to get the apothecia and did not remain late enough in the summer to follow the development to mature sclerotia. I feel quite sure that spermodochidia of some type would have developed during late July or August in the infected culms. Tiny masses of densely protoplasmic, large, thin-walled hyphae, which are present at intervals in the diseased culms which I preserved (CUPP 31589) are characteristic of the initial stages of spermodochidial development in the other species of the cypericolous species of *Sclerotinia*.

The sclerotia of *S. vahliana* appear to have an unusual history of development (see Text Fig. B). They are initiated as in the related species, within the culms of the suspects. I was able to observe only the early stages in

Plate 7. *Sclerotinia vahliana*. Fig. 26. Diseased culms of *Eriophorum vaginatum*; ½ natural size. CUPP 31589. **Fig. 27.** Culture from culms of *E. vaginatum* on potato dextrose agar showing sclerotial formation; natural size. CUPP 31589. **Fig. 28.** Type specimen in Botanical Museum, Copenhagen (revived dry material); natural size. CUPP 16275. **Figs. 29–30.** Apothecia on sclerotia from *E. angustifolium* from Sweden (revived from liquid preservative); natural size. CUPP 31606.

this development. The sclerotia begin as elongate, cottony, white masses at three or four places in the culm. As the young sclerotia begin to solidify they become pink in color as do those of related species. In a few cases I found evidences of the developing rind. I found no mature sclerotia, all being still firmly enclosed within the culms. I observed that the infected culms often appeared to be stouter and apparently to have been more vigorous in their growth than were the healthy ones. This may have been due to stimulation by the fungus during the first days of infection. As far as I was able to discover, these sclerotia were developing only in the upper internode of the culm in *E. vaginatum*. It seems almost certain, however, that sclerotia are formed at intervals throughout the culms even to the base. They apparently do not complete their development within the culm but,



TEXT FIG. B

Text Fig. B. Sclerotium of *Sclerotinia vahliana* from base of culm in crown of *Eriophorum*, (a) front and (b) back view, (c) from one higher up in culm; all x2. Drawn by Miss Charlotte Dill.

bursting out, continue to grow in size. The mature sclerotia I have seen bearing apothecia are obviously too large to have fully matured within the culms.

Rostrup's description of the sclerotia as "assembled between the lower leaf sheaths" suggests that in the dwarfed *Eriophorum* plants of Greenland and Iceland, they may be formed chiefly in the basal region of the culm. However, I have seen specimens of sclerotia bearing apothecia which had clearly developed in the upper reaches of the culm (e.g. Nannfeldt's collection of 1927, Text Fig. Bc). Careful observations in the field may disclose, in the case of sclerotia clustered in the crowns of the susceptibles, that the base of the leaves as well as the culm have been involved in the nourishment of these sclerotia. Larsen (1932), in recording the occurrence of this species in Iceland, cites collections by himself and by Ostenfeld and remarks, "On tufts of *Carex* and *Eriophorum* on swampy ground. The pea-sized sclerotia are often seated in the axils of the leaves, covered by the leaf sheaths". It is very doubtful that *S. vahliana* ever attacks *Carex* species. Larsen is either

in error or has confused some species of *Sclerotinia* actually occurring on *Carex* in Iceland, with *S. vahliana* on *Eriophorum*.

SPECIES ON *SCIRPUS* AND *SCHOENUS*

A species of *Sclerotinia* on *Scirpus lacustris* L., long known to European mycologists, chiefly in its sclerotial stage, was finally described by Rehm (1896) under the name of *Sclerotinia scirpicola*. Although represented in herbaria by but few collections, it is certainly common and widely distributed throughout northwestern Europe. It is not known from North America. No species of *Sclerotinia* is known to occur on other species of *Scirpus*. Ferdinandsen & Winge (1911: 293) report a collection by Ade in Bavaria, Germany, said to be this species on *Scirpus silvaticus* ("the spores finally becoming 2-celled"). Since the spores of *S. scirpicola* are uniformly 1-celled, it is very doubtful that Ade's specimen was correctly determined. There is however a species, pathogenic to the closely related *Schoenus nigricans* L., which appears to have been generally overlooked by mycologists.

SCLEROTINIA SCIRPICOLA

PLATE VIII AND TEXT FIG. C

This species is of peculiar interest because of the nice adaptation it has made to its aquatic habitat. Its suscept is an inhabitant of the shallow waters of lakes and ponds. Not only do the freed sclerotia float like tiny corks upon the water but in the spring the apothecia develop on these where they accumulate in thousands on the low flat shores as the water subsides. Aside from the original description of the apothecial stage by Rehm (based upon dry material) the papers by Ferdinandsen & Winge (1911 and 1913) and Sydow's (1912) appear to be the only contributions of importance dealing with this species. During my stay at Lyngby, Denmark, during June 1930, an exceptional opportunity was afforded for study of *S. scirpicola* as it occurs in Lyngby Sø. As a result of these studies a more complete picture of this species can now be drawn.

SCLEROTINIA SCIRPICOLA Rehm in Rabenh. Krypt. Fl. 1³: 822. 1893.

Sclerotium roseum Moug. in Fries, Syst. Myc. 2 (Suppl.): 43, 1830. (= Elench. Fung. 3: 43. 1828).

Sclerotium roseum Kneiff in Duby, Bot. Gall. 2: 874. 1830.

Sphacelia scirpicola Ferd. & Winge, Biolog. Arbej. Tilegnede, Warming, Nov. 3, p. 290. 1911.

Myrioconium scirpi Syd. Ann. Myc. 10: 449. 1912.

Myrioconium scirpicola V. Höhn. Mitt. Bot. Inst. u. Tech. Hochsch. Wien 3: 50. 1926.⁶

Spermodochidial groups (Figs. 31, 32) more or less oval to elongate, shallow, slightly raised, very variable in size, often minute, irregularly

⁶ Ferdinandsen & Winge (1913: 24) admitted the logic of Sydow's argument (in a letter) for referring the conidial stage of *S. scirpicola* to his genus *Myrioconium* but they did not actually make the combination *M. scirpicola*, as Von Höhnelt seems to imply in this 1926 paper.

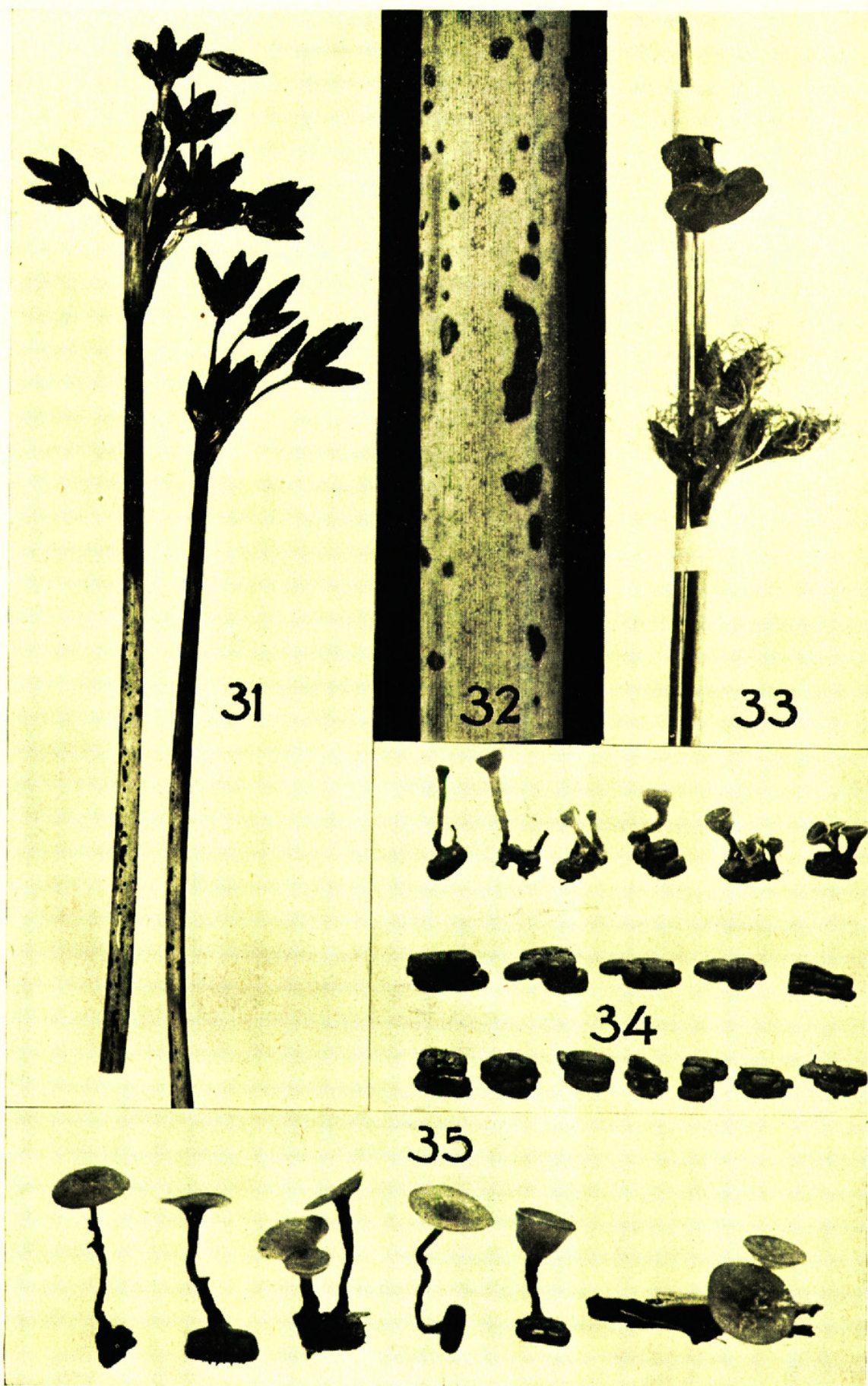


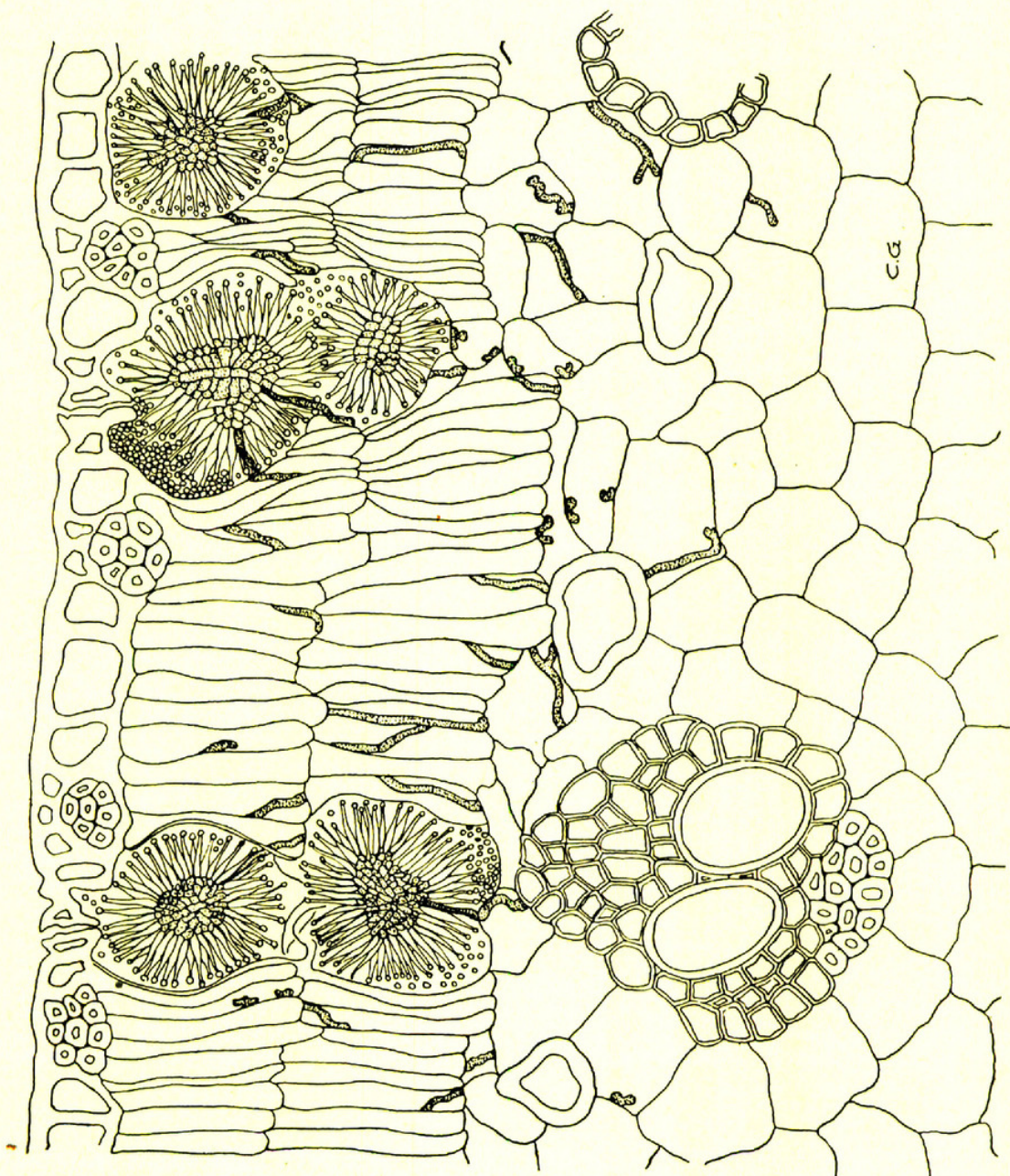
PLATE VIII

disposed along one side of the culm for some distance just below the heads, dull black, rupturing by slits in the epidermis, from which the viscid mass of spermatia are discharged; *spermatia* minute, globose, about $3.3\ \mu$ in diam. The dark color of the spermodochial groups is due to the brownish color of the massed spermodochia, the brown gumbose contents of the epidermal cells, and to brown-walled intercellular hyphae in some of these cells.

Sclerotia (Fig. 34) usually 8–10 per culm, the first one developing with the appearance of the spermodochidia and just below them; successive sclerotia appear a few inches apart as the invading hyphae spread downwards in the culm. The sclerotia originate as soft pinkish mycelial masses in the loose central parenchyma of the culm, at maturity appearing as large, longitudinally lobate, oblong, blunt, black, tuberoid bodies completely enclosed in the culm. The culms, weakened at these points, are easily broken by the wind, discharging the sclerotia into the water, where they float, and drifting with the wind, accumulate, together with broken pieces of the culms, in great patches along the leeward shores of the lake or pond. The sclerotia vary much in shape and size, being usually somewhat longer than broad, ranging from 2–10 mm. by 2–5 mm. in diameter. The form of the sclerotium is striking, being elongately 2–3-lobed, the ends of the lobes blunt and rounded. This compound appearance is more apparent than real, being due to the structure of the culm. A cross section of the sclerotium discloses a narrow outer black rind, one to two cells thick, enclosing a medulla of rather loosely interwoven, relatively thin-walled, large hyphae, distinctly septate and often constricted at the septa. The medulla long retains its bright pink color, even after the formation of the rind, but eventually becomes white. The lobation of the sclerotium is marked out in the cross sections by faint brown lines, the persistent brownish-walled cells which formed the firmer tissues surrounding the cavities originally filled with thin-walled pith cells which have been largely digested by the developing sclerotium.

Apothecia (Figs. 34, 35) appearing in the spring at flowering time of the *Scirpus*; 1–to several from each sclerotium, usually not more than 2, arising at any point on the sclerotium, variable in size, when fully expanded 3–15 mm. in diam., av. 8–10 mm. The size of the apothecium apparently does not depend entirely upon the size of the sclerotium for several, all usually small, or one much larger than the others may arise from a single sclerotium; *cups* deep goblet-shaped becoming nearly flat expanded, light fawn to vinaceous brown, lighter beneath, due to a coating of fine hyphal fuzz; *stipe* usually short, slender, concolorous with under side of the cup, also covered with a hyphal fuzz above, clothed below, especially at the base, with a dense mat of long, dark hyphae which serve to anchor the large apothecia to the

Plate 8. *Sclerotinia scirpicola*. **Fig. 31.** Diseased culms and inflorescence of *Scirpus lacustris* showing spermodochidia; about natural size. **Fig. 32.** Part of culm showing spermodochidia, x6. **Fig. 33.** Showing method of inoculating pistils of *S. lacustris* for study of invasion phenomena; about natural size. **Fig. 34.** Sclerotia and young apothecia; natural size. **Fig. 35.** Sclerotia bearing mature apothecia; natural size. All from specimens in CUPP 31607.



Text Fig. C. Cross section through spermodochidia of *Sclerotinia scirpicola* about x400.

Note that each cavity is directly beneath a stomate, and is formed chiefly by crowding aside the palisade cells rather than by digesting them. Drawn by Carlos Garcés.

surrounding floating debris of broken culms; *asci* long, cylindrical, apex blunt, of about the same diameter throughout, except at the base where they are rather sharply narrowed to about half the diameter of the apical portion, 8-spored, spores uniseriate in the upper third of the ascus, 50 meas. (fresh, in water) $133.3\text{--}181.8 \times 8.1\text{--}10.8 \mu$, mode $157.5 \times 9.5 \mu$, av. $153.2 \times 9.4 \mu$; *ascospores* long oval, 100 meas. (fresh, in water) $11.2\text{--}17.8 \times 5.3\text{--}7.9 \mu$, mode $13.8 \times 6.6 \mu$, av. $14.4 \times 6.6 \mu$ surrounded by a very evident mucilaginous coat; on germination in water often producing spermatophores and spermatia directly; *paraphyses* slender, not appreciably swollen toward the tips, about 3.4μ in diam.

In culture on potato dextrose agar forming a thin, white, aerial, webby coating over the surface of the agar; submerged mycelium feathery as in cultures of *S. longisclerotialis*; no sclerotia formed.

HABITAT: In the culms of *Scirpus lacustris* L. in the shallow waters of lakes and ponds. Apothecia developing on sclerotia stranded along the shore line among sedges, grasses and other plants which afford continuous shade and moisture during their development.

DISTRIBUTION: Throughout western Europe; very abundant in Denmark (Ferdinandson & Winge 1911: 293). Also reported from Finland, Germany, Sweden, and England. Probably to be found in equal abundance when sought in neighboring regions of northern Europe; not known from North America.

TYPE SPECIMEN: The specimen upon which Rehm (1893: 823) based his original description of this species, was found by him in Winter's herbarium. He says it bore the label "*Peziza tuberosa*" with the notation (transl.) "in May, the old culms of *Scirpus lacustris*, in our lakes break up. When these fall into the water, this *Peziza* appears from sclerotia in a few days, from every piece which with us very frequently contains *Sclerotium roseum* (Moug.) Fries." According to Rehm the specimen was probably collected by Winter in Saxony near Zweibrücken in the Rheinpfalz (Germany). I have been unable to discover where this type specimen (if indeed it is still extant) is now deposited.

ILLUSTRATIONS: Ferdinandson & Winge, *Saertryk af Biol. Arbej. Til-gnedede*. Eug. Warming. Nov. 3, fig. 1-7. 1911.

MATERIAL EXAMINED: Exsiccati Specimens: In the Kew Herbarium there is a specimen of three pieces of culm each with an enclosed sclerotium labeled "*Sclerotium roseum*" with a brief written description signed by Persoon. The specimen is unnumbered, undated and locality where collected not indicated; — Mougeot et Nestler, *Stirp. Crypt. Vogeso-Rhen. 884* (1826). "*Sclerotium roseum* Kneiff-Pers.-Fries. in Litt." Specimens of this in the British Museum, in Kew, and at Cornell show sclerotia in culms said to have been collected near "Argenorum", now Strassburg, in Alsace, France. Collected by Kneiff in autumn. No date of collection given; — Kneiff et Hartmann; *Pl. Crypt. Badens, 20*, 1828. "*Sclerotium roseum* Kneiff (nov. sp.)". This specimen in the British Museum consists of pieces of culms containing mature sclerotia collected in canals along the Rhine near Kehl in Germany. Sept.-Oct. No year of collection given and no collector cited; — Klotzsch, *Herb. Mycol. 244* (1842). "*Sclerotium roseum* Moug. Intra culmos *Scirpi lacustris* ad Dresden". This specimen in Kew Herbarium bears only the data above quoted. It consists of a piece of culm containing a sclerotium; — Roumeguère, *Fung. Gallici Exs. 499*, 1879. "*Sclerotium roseum* Kneiff. Pers. Fries. in Litt. Moug." This number was made up from material remaining in Mougeot's herbarium and is of the same origin as his *Stirp. Crypt. Vogeso-Rhen. 884*. Specimens examined in the Kew Herbarium and in CUPP show a single sclerotium in a piece of culm; — Otto Jaap, *Fung. Sel. Exs. 755*. Collected by Jaap in Brandenburg, Triglitz in the Prignitz, Germany. June 15, 1916 (spermodochidia (?), sclerotia and apothecia); — Flora Suecica 4222. Collected by J. A. Nannfeldt on shore of shallow arm of Mälaren. Bondkyrok s:n. Skarholmen, Uppland, Sweden. June 25, 1931 (apothecia). Dupl. CUPP 32615; — In Kew Herbarium a specimen labeled: "*Sclerotinia scirpico*la, Ashgrove Loch, Shevenston, Ayrshire 26.2.21. Coll. D. A. Boyd." Consists of a single culm of *S. lacustris* containing a single sclerotium; — CUPP 31607, along the shore of Lyngby Sø, Lyngby, Denmark, June 3-July 13, 1930, H. H. Whetzel (spermodochidia, sclerotia, apothecia and cultures). Duplicate specimens from this collection have been distributed

to the following herbaria: Kew, England; British Mus., London; Univ. Toronto, Canada; Farlow Herb., Cambridge, Mass.; N. Y. Bot. Gard.; Univ. Mus., Ann Arbor, Mich.; Missouri Bot. Gard., St. Louis, Mo.; Mycol. & Pl. Dis. Survey, Bur. Pl. Ind., Washington, D. C.; Univ. California, Berkeley; Univ. Iowa, Iowa City.

The abundance of apothecia in Lyngby Sö during my stay in Lyngby, and the nearness of laboratory facilities for critical studies and culture work, presented an opportunity not to be neglected. I devoted most of my time to such studies, the results of which are summarized below.

LIFE HISTORY STUDIES

The life history of *S. scirpicola*, while in general quite like that of its near relatives on *Carex* species, presents some unique features largely due to the habits of its suspect *Scirpus lacustris*. This *Scirpus* grows in the shallow waters along the shores of the lake. It is most vigorous and fruits most luxuriantly near the shore, the plants becoming more scattered, shorter and usually producing fewer flowering culms as the plantation spreads out into the deeper water. When we arrived at Lyngby, the first week in June 1930, I found the apothecia already developing in great abundance from the thousands of sclerotia lodged in debris on low-lying projections of the shore, a few minutes' walk from the laboratory of the Phytopathological Experiment Station in which we were kindly afforded working facilities by the Director, Mr. Ernest Gram. The shores of this shallow lake are fringed with great patches of *Scirpus lacustris* and the prevailing southwest winds of the previous fall and winter had deposited the sclerotia in immense numbers along with the broken culms of *Scirpus* just above the receded water level on every flat projection of the northeast shore of the lake and on the water where they were anchored and shaded by a rich growth of grasses and other shore-loving plants and shrubs. The open apothecia reached their maximum abundance about the end of the first week in June. A week later most of the apothecia were shrivelling or decaying, though new ones were still to be found just sprouting from sclerotia here and there. By the 17th of June, only an occasional apothecium was to be found. Many heads of the *Scirpus* were already in bloom on June 2 when we arrived, but blossoming reached its maximum about the time apothecia were to be found in greatest abundance. The weather throughout June was warm, the skies clear, and practically no rain fell. From the abundance of mature apothecia at the beginning of June, we judge that they must have begun to open about the middle of May. This would indicate that the period of apothecial production normally extends over a period of three to four weeks.

The mature apothecia discharge their ascospores in tiny puffs which, caught by gentle air currents among the shading vegetation, are wafted upward, some of them eventually reaching the white extruded pistils of the *Scirpus* inflorescence, where they lodge on the feathery stigmas. By suspending open apothecia over the inflorescence (Fig. 33) of culms (with cut ends in water) placed under an inverted large test tube, I was able to obtain naturally inoculated pistils. These when removed and mounted on glass slides the following morning, afforded excellent material for study of spore

germination and penetration. The spores germinate promptly, sending out from one end a stout simple germ tube. This penetrates the projecting hyaline cells of the stigma, usually forming a swollen globose appressorium where the tip has applied itself to the surface of the stigmatic cells. From this appressorium a penetration tube is sent into the cell from which an invasion hypha passes down into the tissues of the pistil. Infection is promptly indicated by the browning and shrivelling of the pistils. Uninoculated pistils remain white and plump for several days under the same conditions. The fungus having entered the ovary, growth seems to be greatly slowed down. In the open, about two weeks after inoculation, one or more of the peduncles supporting the individual spikes of the inflorescence begin to turn brown, the mycelium having killed the spike and spread downward into the peduncle through which it reaches the main stalk of the culm.

A dark browning just below the point of attachment of the inflorescence announces the invasion and infection of the culm proper. Visible infection of the culm becomes evident about three weeks after inoculation, as Ferdinandsen and Winge had already discovered. Rapid progress of the infection down the culm, however, does not usually occur for another week or so. It is evidenced by a hydrotic discoloration of the culm, with disappearance of the chlorophyll and discoloration in the form of alternating broad bands of a light and dark brown color. When this zonation has extended a foot or so down the culm, the spermodochidial groups begin to appear in an irregular line on one side of the culm in the brown necrotic tissues several inches below the inflorescence (Fig. 31). These spermodochidial areas are very variable in size, ranging from mere specks to elongate or irregularly ovate, black, slightly raised patches just beneath the epidermis. They are usually very numerous and the tissues in which they develop are generally of a distinctly lighter brown color than the adjacent regions. They finally rupture by slits, discharging the viscid masses of spermatia as the first sclerotial initials are to be detected just below. The downward progress of the fungus, indicated by hydrosis and zonate discoloration, now proceeds rapidly with the successive formation of sclerotial initials at intervals of a few inches. As many as ten to fifteen sclerotia may appear in a long vigorous culm, according to Ferdinandsen and Winge. When we left Lyngby on July 15, the first sclerotia were just beginning to appear occasionally in an infected culm.

As the sclerotia mature, they rupture the epidermis over them by several slits. The dead culms, weakened at these points, are gradually broken over by the winds of late summer and autumn. The breaking up of the ice in the spring by storms completes the breaking up of the culms, freeing the sclerotia which float on the surface of the water and are thus transported by the waves to their final resting place among the debris along the shore, ready to germinate and produce apothecia under the favorable conditions of temperature, shade, and moisture prevailing at the blossoming time of the *Scirpus*.

Ascospores discharged onto potato dextrose agar or disinfested segments of infected culm of *Scirpus* planted in the same medium give identical mycelial growths. Growth both from ascospore sowings and from tissue plantings is prompt and vigorous, like that of *S. sulcata*. Aerial mycelium is abundant, usually loose and cottony, at first pure white (never pink) becoming denser with age and faintly brownish, often with large dense masses of a dirty grey color, especially in test tube slants. The submerged mycelium becomes blue black at the center of the colony with radiating dark brown feathery strands. Spermodochia were not observed on this medium. Sclerotia were only tardily developed on test tube slants but were numerous in Petri dish cultures, being globose, black outside, pink where they grow against the glass and more or less completely buried in the dense aerial mycelium.

Although the morphology and life history of *S. scirpicola* are now perhaps more fully known than those of any of the related species on cyperaceous suspects, a number of features require further consideration.

It seems probable that some of the sclerotia may remain dormant through the summer following their formation, as numerous hard, plump, ungerminated sclerotia were found among the debris along the shore of Lyngby Sø long after the last apothecia had disappeared. On the other hand, these sclerotia may not be capable of germination for some unknown reason.

The germinability of the sclerotia may be conditioned in some way by the functioning of the spermatia. The writer's original suggestion (Whetzel 1929: 18) that the microconidia probably function as do the spermatia of the rusts has since been supported by the work of Drayton (1934) in his work on *Sclerotinia gladioli*. Ferdinandsen & Winge (1911: 297) think the microconidia may function as true conidia, causing secondary infections later in the season when primary infections by ascospores are no longer possible. This seems very doubtful though they cite some observations in support of this hypothesis. The writer has had no satisfactory opportunity to attempt a careful study of the germination and role of the spermatia, but believes that *S. scirpicola* is a favorable species for such an investigation. It occurs in great abundance in Lyngby within easy walking distance of excellent laboratory facilities. It is to be hoped that Professor Ferdinandsen or some of his students will undertake intensive investigation on this very interesting and important problem, as they are most favorably situated for such an undertaking.

The suggestion of Ferdinandsen and Winge that invasion by the fungus takes place through the culm at some point just below the inflorescence does not appear tenable. Ascospores shot on to culms at this point, in moist chambers, were observed to germinate poorly or to produce spermatia only. No germ tubes could be found penetrating the epidermis or entering through the stomata, which are numerous all over the culm, while actual invasion of the stigmas was easily demonstrated. The death of the pedicles of infected spikes prior to the first evidences of infection in the culm itself also argues for blossom invasion. While the very limited and preliminary

investigations which we have been able to make all point definitely to the pistils of the *Scirpus* as the infection court, more extensive studies and inoculation experiments should be made.

ORIGIN AND RELATIONSHIPS

Undoubtedly *Sclerotinia scirpicola* is very closely related to the species on *Carex*. It differs from these chiefly in the characters of its spermodochidia and sclerotia. On the whole, it approaches more nearly *S. sulcata* rather than *S. duriaeana*, as suggested by Ferdinandsen and Winge who, however, at that time were not aware of the fact that there were two distinct species confused under the name *S. duriaeana*. Its similarity to *S. sulcata* is most marked in its cultural characters. Its dense cottony growth of aerial mycelium and large tuberoid sclerotia produced on potato dextrose agar are scarcely to be distinguished from those produced by *S. sulcata* in pure cultures. Sclerotial production on potato dextrose agar is, however, much more tardy and less certain, while the growth of aerial mycelium is generally more abundant; the submerged mycelium is also more promptly and extensively darkened. Its spermodochidial patches also simulate those of *S. sulcata* in their irregular distribution on the culm. The form of its sclerotia in nature is quite distinct but may possibly be due entirely to the structure of the *Scirpus* culm. It is probably restricted in its pathogenism to *Scirpus*. Many *Carex* species were common about the shores of Lyngby Sø, but only two or three apothecia arising from sclerotia of the *Carex* type were found among the apothecia of *S. scirpicola* along the lake shore. Cultures from one of these proved to be typical of *S. duriaeana*. Infected culms of *C. disticha* in the same locality yielded typical cultures of *S. sulcata*. Moreover, the period of apothecial development is distinctly later for *S. scirpicola* than for the species on *Carex*. Apothecia of the species on *Carex* were rarely to be found about Lyngby when we arrived at the beginning of June, although infection of the culms of *C. Hudsonii* by *S. sulcata* were discovered in abundance shortly after our arrival. The blossoming period for *Carex* species was also practically past. Since two to three weeks are required for the development of visible infection after inoculation by *S. duriaeana* or *S. sulcata* in their *Carex* suspects, the scarcity of apothecia of these species when those of *S. scirpicola* were at their optimum abundance is significant. In spite of all this evidence as to the specific identity of *S. scirpicola*, careful cross inoculation experiments should be made with this form on species of *Carex* known to be suspects for *S. sulcata* and *S. duriaeana*. Here is another interesting problem for some energetic young pathologist or mycologist who can avail himself of the exceptional opportunity afforded there at Lyngby.

The marked similarity of *S. scirpicola* to *S. sulcata* appears to be of considerable significance in connection with my theory of the origin and evolution of this group of species on cyperaceous suspects. It would seem that *S. scirpicola* has been a relatively recent differentiation derived directly from the European form of *S. sulcata*, which is probably also the mother

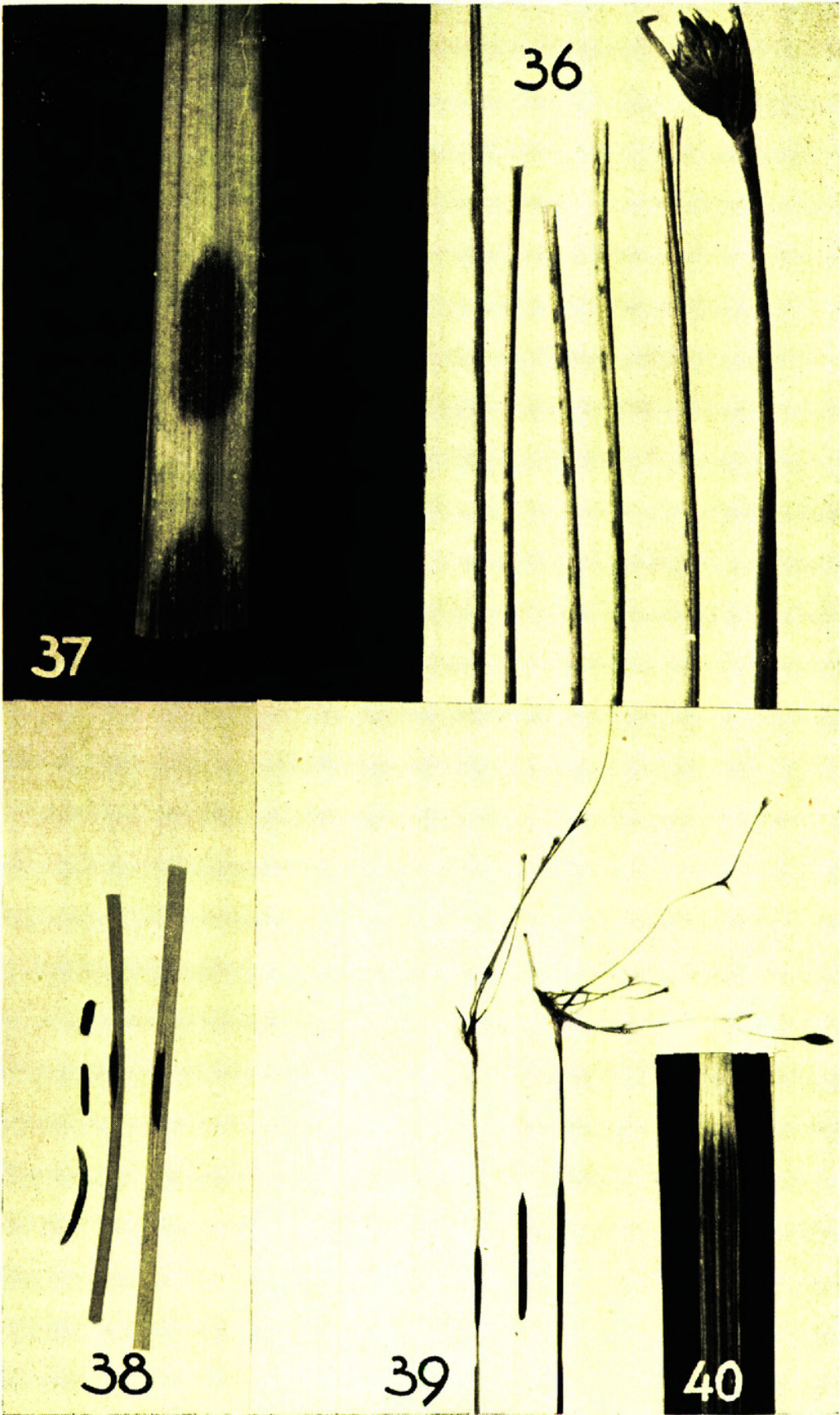


PLATE IX

species of *S. duriaeana*. The characters peculiar to *S. scirpicola* may, in part at least, be due to its adaptations to a different suspect.

While Mougeot is credited by Fries with having first applied the name *Sclerotium roseum* to the original collection made by Kneiff, there is substantial evidence that Kneiff himself is the legitimate author of the name. Not only did Mougeot and Nestler credit Kneiff with this name on the label of their Stirp. Crypt. Vogeso-Rhen. 884 (1826), but also Kneiff and Hartmann, two years later, in distributing this sclerotial stage, in their Pl. Crypt. Badens 20, credit the name to Kneiff. Subsequent writers in referring to this name are divided as to the legitimate author of it. Tulasne and others follow Fries, but most of them credit Kneiff with the name. Saccardo (1899: 1153) notes that the name "*Sclerotium Kneiffi*" is applied to this fungus by others ("Quibusdam"). I have been unable to locate any other reference to the fungus under this name.

Currey's assumption (1857) that "*Sclerotium roseum* Kneiff" is the sclerotial stage of "*Peziza curreyana*" was accepted by all subsequent students of *S. curreyana* until Rehm (1893) pointed out the error in the note to his description of *Sclerotinia scirpicola*. This confusion of the sclerotia in the culms of *Scirpus* with those in the culms of *Juncus* as representing one and the same species had not, however, escaped suspicion in the critical mind of Tulasne (1861: 105) who while admitting that the sclerotium in *Scirpus* "... seems to agree completely with it (in *Juncus*) in its whole structure though no one has yet found it in fruit" remarks "But we are sorry that it has not been possible for us to test it by suitable culture, for we have never seen it alive".

SCLEROTINIA SCHOENICOLA

PLATE IX, FIGS. 36-38

Desmazières appears to have been the only mycologist to refer to specimens of what proves to be a heretofore unrecognized species of *Sclerotinia*. He took the sclerotial and spermatial stages of this fungus on *Schoenus nigricans* (Figs. 36-38) to be the same as those on species of *Carex* which he designated respectively *Sclerotium sulcatum* and *Epidocium affine*, and which were later (1929) recognized by Whetzel as stages in the life cycle of *Sclerotinia sulcata*.

Desmazières⁷ distributed specimens of the culms of *Carex vulpina* and *acuta* and culms of *Schoenus nigricans* all of which contained sclerotia very

⁷ Plantes Cryptogames France, Ed. 1, Ser. I, No. 2029 (1850); Ed. 2, Ser. II, No. 1629 (1853).

Plate 9. *Sclerotinia schoenicola* and *S. luzulae*. **Fig. 36.** Culms of *Schoenus nigricans* showing spermodochidial patches, from Desmazières' Plantes Crypt. France, Ser. II, 21; about natural size. **Fig. 37.** Spermodochidial areas, x6. **Fig. 38.** Sclerotia of *S. schoenicola* from culms of *Schoenus nigricans* from Desmazières' Plantes Crypt. France, Ed. 2, Ser. I, 1629; natural size. **Fig. 39.** Culms of *Luzula pilosa* from Krieger's Fung. Sax. 2073 showing sclerotia of *Sclerotinia luzulae* (revived dry specimens); natural size. **Fig. 40.** Portions of a sclerotium still enclosed in the culm, x6.

similar in character (see Whetzel 1929: 7) and which he collectively labeled "*Sclerotium sulcatum* Rob. in herb." No date or locality is indicated on the packets. Presumably Roberge was the collector. In specimen 2029 the culms were all mixed together. In his formal description of *Sclerotium sulcatum*, Desmazières (1851) does not mention *Schoenus nigricans* specifically, saying only "hab. in culmis siccis Caricum"; but in the note following he says (transl.) "This fungus was found inside triangular stubble of *Carex vulpina* and *C. acuta* and in species with cylindrical culms", the last referring undoubtedly to *S. nigricans* which, in the later distributed specimens (number 1629), were segregated into a separate packet and labeled *Schoenus nigricans*. His description clearly applies primarily to the sclerotia in the *Carex* culms, thus in effect leaving those in *S. nigricans* without a name.

Desmazières⁸ later (1853) distributed the upper portions of the same culms containing the spermatial fruit bodies as those containing the sclerotia (Ed. 1, Ser. I, 2029; Ed. 2, Ser. II, 1629) distributed in 1850. Here, however, he separated the culms of *Schoenus* from those of *Carex* in different packets. In his description of the spermatial fruit bodies (1853) he gives these the name "*Epidocium affine* Desmaz." and gives both *Schoenus nigricans* and *Carex* species as suspects citing his exsiccati specimens Series II, 21. His description, however, clearly applies primarily to the fruit bodies on the *Carex* culms, thus again leaving those on *Schoenus* nameless.

The evidence clearly indicates that the sclerotia and the spermodochidia on *Schoenus nigricans* belong to the same fungus. The spermodochidial patches on the culms of *S. nigricans* are quite distinct in character from those of *E. affine* and from those of the other *Sclerotinia* species on the *Cyperaceae*. (Compare Figs. 36 and 37 with Figs. 11–14.) The sclerotia, while very similar to those of *S. sulcata*, are rather more slender but the spermodochidia are very different. Since the spermodochidia are taxonomically the most distinctive structures of the different species of *Sclerotinia* in this group, I have no hesitation in giving to this species a distinctive name.

It is perhaps remarkable that this species apparently has not been collected by mycologists since the days of Desmazières. It is probably not rare but will be found by one seeking it in the proper localities. I unfortunately encountered *Schoenus nigricans* in but one locality in Europe. That was in late summer on the fens at King's Lynn, England. No trace of the *Sclerotinia* was found.

This species is here presented, chiefly to bring it to the attention of European mycologists in the hope that someone will be stimulated again to discover this very interesting form and make a more complete study of its different stages. Only in this way may it be determined whether I am correct in assuming it to be distinct from other species occurring on members of the *Cyperaceae*. Our present scanty knowledge of this form is summarized in the following technical description.

⁸ *Plantes Cryptogames France*, Ed. 3, Ser. II, No. 21 (1853).

SCLEROTINIA SCHOENICOLA, sp. nov.

Maculis spermodochidialibus majusculis, ovatis vel circularibus, numerosis, magnitudine variabilibus, 2–6 mm. in diametro, sub inflorescentiis infectis irregulariter secundum unum culmi latus dispositis, pallide olivaceo-brunneis coloris atroolivacei massae spermodochidiorum globosorum lurideque brunnei cellularum contextus suscipientis gratia; structura interna spermodochidiorum structurae *S. scirpicolae* subsimili; sclerotiis gracilibus, fusiformibus, apicibus obtusis instructis, strictis, rarius manifeste curvatis vel inaequilateralibus sclerotiorum *S. sulcatae* modo, initio pallide roseis, dein nigrescentibus ad superficiem, intus albis, fortiter arato-sulcatis, 8–10 x 1–2 mm. in statu sicco, per rimam culmi liberatis; apotheciis ignotis.

Spermodochidial patches (Figs. 36, 37) rather large, ovate to circular, numerous, variable in size, 2–6 mm. diam., distributed irregularly along one side of the cylindrical culm, just below the blighted head, pale olivaceous brown, due to the dark olivaceous color of the massed globose spermodochia and dead brown cells of the susceptible tissues; internal structure essentially like that of the spermodochidia of *S. scirpicola*.

Sclerotia (Fig. 38) slender, fusiform, tips blunt, straight, rarely distinctly curved or inequilateral as are the sclerotia of *S. sulcata*, at first pale pink, becoming black externally, white within, strongly furrowed, 8–10 mm. long by 1–2 mm. thick (dry), discharged by a slit in the culm.

Apothecia unknown.

HABITAT: Culms of *Schoenus nigricans* L.

DISTRIBUTION: Apparently known only from France. There is nothing on the labels of Desmazières' specimens (the three cited above) to indicate where, when, and by whom they were collected. All were presumably from material sent him by Roberge.

TYPE SPECIMENS: Desm. Pl. Crypt. France. Ed. 1, Ser. I, 2029 (in part) (1850), and Ed. 2, Ser. II, 1629 (in part) (1853), (sclerotia only); Ed. 3, Ser. II, 21 (in part) (1853) (spermodochidia only).

SPECIMENS EXAMINED: The specimens from Desmazières' Plantes Cryptogames France listed above were examined in the Royal Herbarium at Kew and in the British Museum in London, in the New York Botanical Gardens, in the Farlow Herbarium, Cambridge, Mass., and in the Mycological Collections, Bur. Pl. Ind., U.S.D.A.

The life history of *S. schoenicola* is presumably similar to that of the other species of *Sclerotinia* attacking cyperaceous suspects. Invasion is evidently by way of the flowers. The appearance of the spermodochidia might suggest a near relationship to *S. scirpicola*, while from the shape and size of the sclerotia one would rather infer that *S. schoenicola* is more nearly related to *S. duriaeana* or *S. sulcata*.

SPECIES ON THE JUNCACEAE

There are, as far as I have discovered, but three species of the true *Sclerotinias* attacking members of the Juncaceae. These are *S. curreyana*, very common in culms of *Juncus effusus* in Great Britain and western continental Europe; a species in our Pacific Northwest, described as *Ciboria juncigena*; and an undescribed species on *Luzula pilosa* known only from one collection taken in Saxony, Germany.

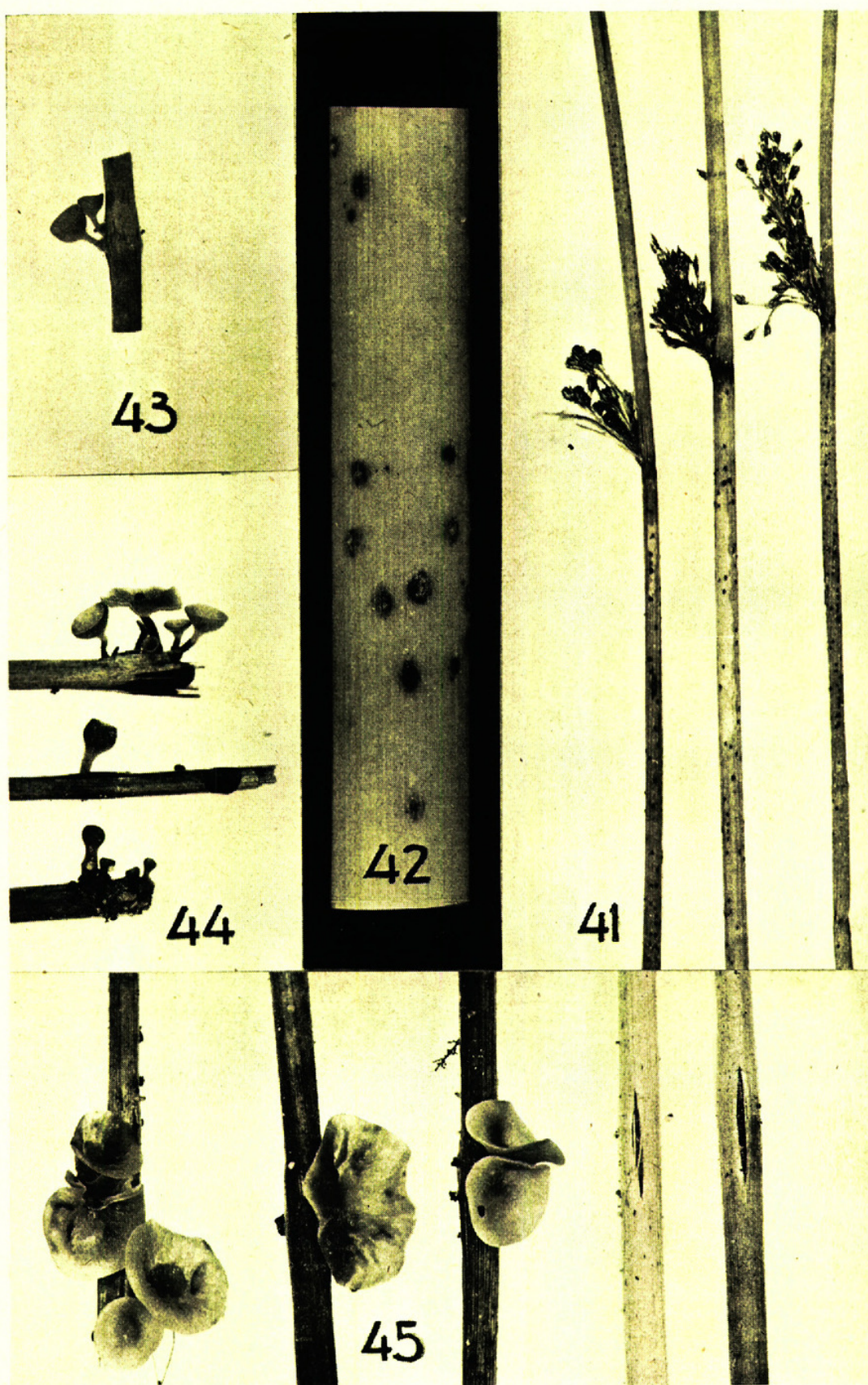


PLATE X

SCLEROTINIA CURREYANA

PLATE X AND TEXT FIG. D

Tulasne in 1861 in his *Selecta Fungorum Carpologia* (1: 104–105) described accurately and in some detail two species of *Sclerotinia* in the group under consideration in this paper, and in 1865 (3: pl. 22) presented beautiful illustrations of both.

Thus *S. curreyana* and *S. duriaeana* may well be regarded as the classical representatives of the species of *Sclerotinia* occurring on sedges and rushes. Of these two, *S. curreyana* has long been the best known to the English and European mycologists since the time of its study by Berkeley and Currey in 1857, because of its very common occurrence and the fact that the apothecia are readily found arising from the sclerotia of the still standing, bleached culms. There is strong circumstantial evidence, however, that it was really first described by Fries in 1818 under the name of *Peziza ciborioides*. Rehm (1893: 822) appears to have been the first to question whether *Peziza ciborioides* of Fries (1824), to which Persoon four years later (1822: 277) gave the new name *Peziza friesii*, may not have been the *Peziza curreyana* which Currey described in 1857. A careful consideration of all the evidence leads me to believe that Fries actually had this species on culms of *Juncus* in view when he named and described *P. ciborioides*. His description fits the species well, inadequate though it is. The fact that his fungus occurred in culms in early spring in marshy places is very suggestive if not confirmatory evidence for my opinion. However, since Fries' specimens are not preserved and since the fungus is so well known under the name suggested by Berkeley, I am not using the Friesian name which current rules of nomenclature might justify. I found this species very abundant in the region about London in the early spring of 1930 and so had an unusual opportunity to observe and study it. I have searched for it diligently since that time on *Juncus effusus* in the Cayuga Lake region of central New York, but have never found it, nor is it recorded from anywhere in North America, unless *S. juncigena* should prove to be conspecific. It should be found throughout the Euro-Asian continent wherever its suscept occurs.

SCLEROTINIA CURREYANA (Berk. in Currey) Karsten, *Revisio Monogr.* p. 123. 1885.

Peziza curreyana Berk. in Currey, *Journ. Linn. Soc.* 1: 147. 1857.

Peziza curreyi Berk. *Outlines Brit. Fung.* p. 370. 1860.

Rutstroemia curreyana Karst. *Myc. Fenn.* 1: 107. 1871.

Phialea curreyana (Bart.) Gillet, *Discom.* p. 211. 1879.

Sphacelia tenella Sacc. *Miscellanea Mycologica in Venezia Ist. Atti*, Ser. 6, 2: 448.

(Reprint 1: 14) 1884. (See Saccardo 1886: 666.)

Plate 10. *Sclerotinia curreyana*. **Fig. 41.** Diseased culms of *Juncus effusus* showing spermodochidia; about natural size. CUPP 31655. **Fig. 42.** Spermodochidia, x6. **Fig. 43.** Apothecia arising from sclerotia within standing culm; natural size. CUPP 15578. **Fig. 44.** Apothecia in various stages of development from sclerotia in culms in moist chamber; natural size. CUPP 20198. **Fig. 45.** Apothecia fully expanded; culms showing rupture slits over enclosed sclerotia, x2. CUPP 20198.

Peziza juncifida Nylander, *Pezizas Fenniae in Sällsk. Fauna et Fl. Fenn. Forhändl. Notiser* (n. s. 7) 10: 39. 1869.

Hymenocypha curreyana Phill. *Manual Brit. Discom.* p. 16. 1887.

Placosphaeria junci Bubák, *Ann. Myc.* 4: 113–114. 1906.

Sphacelia curreyana Grove, *Journ. Bot. Brit. and Foreign* 50: 46. 1912.

Myrioconium tenellum V. Höhnelt, *Mitteil. Bot. Inst. Tech. Hochsch. Wien.* 3: 50. 1926.

Spermodochidia (Figs. 41, 42) numerous, scattered irregularly along and about the upper part of the diseased culms, usually most numerous along one-half of the circumference of the culm, minute, pustulate, ellipsoid, brown, slightly erumpent when fresh and moist, opening by a slit in the epidermis; *spermatia* minute, globose, 2–2.5 μ in diameter, produced from the tips of obclavate spermatophores fasciculately clustered about a centrum to form globose spermodochia as in other species of this group, but also forming an irregular hymenium lining the cavity.

Sclerotia one to several in each culm, short, stout, cylindric with blunt, rounded ends, 4–15 mm. or more long, by 2–4 mm. in diameter, externally black or dark brown, coarsely sulcate, internally white when mature, of a rosy pink color during development, embedded in the pithy interior of the culm, disclosing in section the inclusion here and there of remnants of undigested pith cells. The structure of the rind and medulla is essentially like that of the sclerotia of *S. scirpicola*. The sclerotia are not freed from the culms at maturity but remain embedded, apothecia developing in the spring from the surface exposed by a slit in the epidermis of the culm over the sclerotium.

Apothecia (Figs. 43–45) two to several from each sclerotium, short-stipitate, pale tan to dark avellaneous brown; *cup* thin, deep goblet-shaped to infundibuliform, often umbilicate, 2–12 mm. or more in diameter, margin entire, recurved, smooth without, rugose-fluted within; *stipe* as long as the diameter of the cup, equally cylindrical, flexuous, solid, glabrous or slightly hairy to tomentose at the base, somewhat darker in color than the cup; *asci* long, slender, clavate, apex rounded, 38 meas. gave 47.6–78 x 4–5.4 μ , mode 65 x 5.4 μ , av. 65.2 x 5 μ ; 8-spored, spores uniseriate; *ascospores* slender, allantoid, ends rounded, 99 meas. gave 7.9–14.5 x 1.3–2.9 μ , mode 11 x 2.9 μ , av. 11.5 x 2.5 μ ; *paraphyses* “slender, pale brown at the slightly thickened apex”, according to Massee (1895: 282). I have found it impossible satisfactorily to make out the characters of the paraphyses from dry material.

In culture on potato dextrose agar this fungus makes a dense cottony, felty growth of pinkish aerial mycelium with eventual development therein of more or less globose sclerotia which are at first a bright pink, and finally form a white to pink medulla that is enclosed in an olivaceous brown rind. The olivaceous brown masses of sporodochia form about the margin of the mycelial mat.

HABITAT: In culms of *Juncus*, most common in *Juncus effusus* L. but recorded also on *J. conglomeratus* L., *J. glaucus* Ehrh., and *J. filiformis* L.

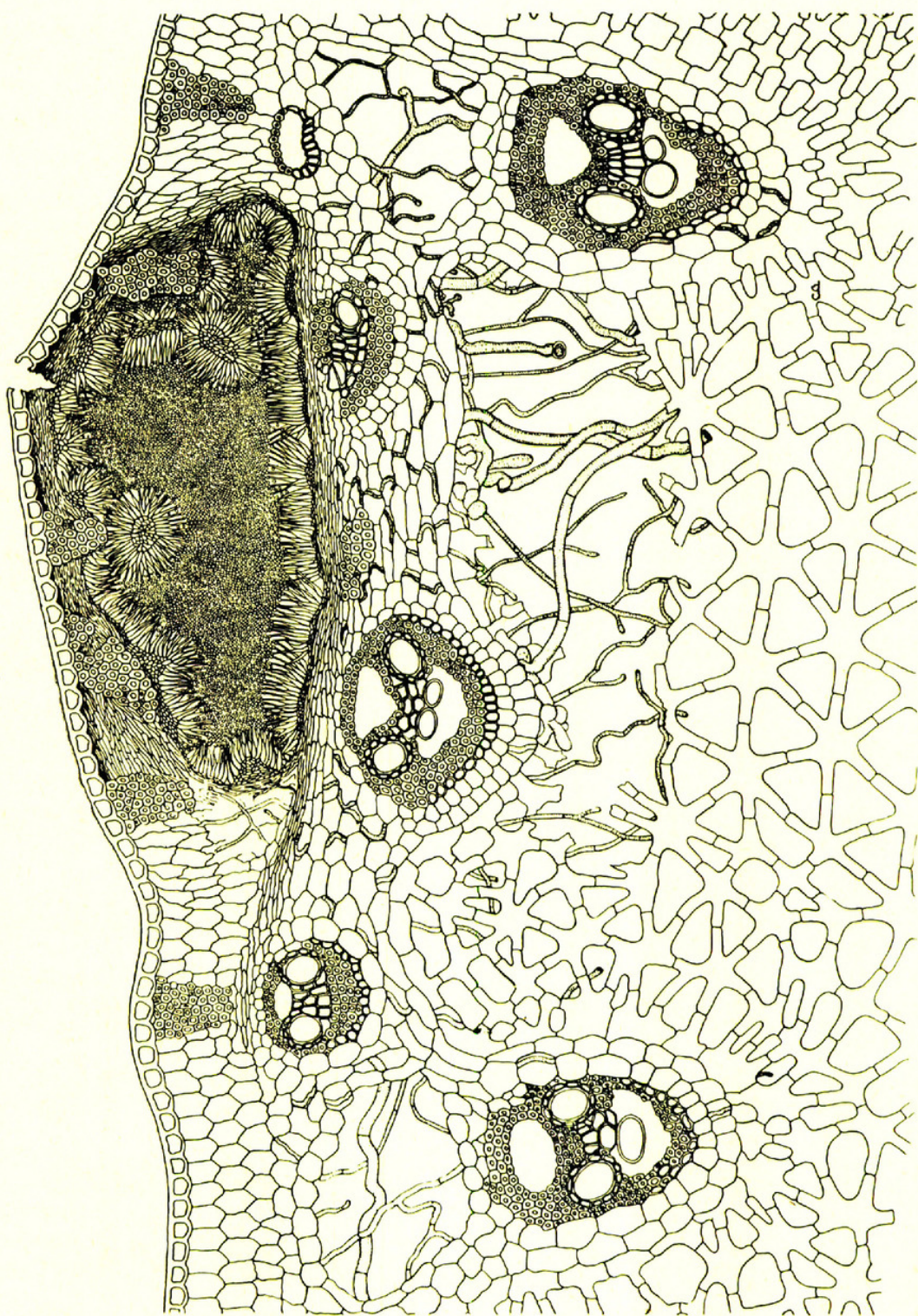
in wet locations, meadows, heaths, moors, and along ditches. The apothecia appear in early spring, followed by infection of the culms in which the spermatia and sclerotia appear during midsummer and early autumn.

DISTRIBUTION: This species appears to be most common in Great Britain judging from my own observations and from the numerous collections in herbaria. Known also from Belgium (Lambotte 1887: 303) and Bommer and Rousseau (1884: 133), France (Boudier 1905: 273-4) and Saccardo (1889: 199), Finland (Nylander 1869: 39), Denmark (Lind 1913: 109), Bohemia (Bubák 1906: 113, spermodochidia). Velenovsky (1934: 223) records this species in Bohemia on *Juncus glaucus* and *J. piscinam*, also in heads of wheat. His description and his figures would indicate that he had some species quite different from *S. curreyana*. The spores as he describes and figures them are certainly not the spores of this species.

TYPE SPECIMEN: There are a number of collections of this species deposited (in 1881) in the Royal Herbarium at Kew of which at least three packets are from Currey's personal herbarium and collected on "Paul's Cray Common, Near Chislehurst in Kent", the locality given by Currey (1857) as the place where, on the 23rd of April 1856, he first discovered the apothecia of *Peziza curreyana*. The label on these specimens says "On *Juncus conglomeratus*" and is dated "May, 1856". These specimens would, therefore, appear to constitute the type material. Massee (1895: 283) says that he had examined the type specimen.

MATERIAL EXAMINED: In addition to Currey's type specimens, I have carefully examined the other twelve specimens in the Kew Herbarium, all of which were apparently collected in England from 1856 to 1884. The labels for most of them are very sketchy. They appear to be mostly specimens collected by (or sent to) Currey and Berkeley. In the herbarium of the British Museum there is a sheet and a half of packets of this species, all originally in the collection of William Phillips. One specimen labeled "conidia" is of special interest, as showing that Phillips recognized the spermatial stage of *S. curreyana*. These all appear to have been collected in England.

In addition to the above, I have had for study the following: On ***Juncus effusus* L.:** CUPP 15578, Worcester, England, October 18, 1926, C. Rea (sclerotia from which I developed apothecia the following April); — CUPP 31648, Wisley, Surrey, England, February 10, 1930, Whetzel, Green & Cotton (apothecia); — CUPP 31654, Goslar am Harz, Germany, Harzerberger Thal, Whetzel & Westcott, April 22, 1930 (apothecia); — CUPP 31655, near Downton in Hampshire, England, August 2, 1930, Whetzel & Brown (spermodochidia); — CUPP 31657, Sandhill bog, Worcestershire, England, August 9, 1930, Whetzel & Rea (spermodochidia and sclerotia). On ***Juncus conglomeratus* L.:** CUPP 31658, shore of Loch Katrine near Stronachlar Pier, Scotland, August 3, 1930, Mrs. Whetzel & Miss Westcott (spermodochidia); — CUPP 31659, near Plowright's old home, not far from King's Lynn, England, Whetzel (spermodochidia); — CUPP 20198, Phytopathological Field Station, Slough, Buckingham, England, December 5, 1931, Mr. and Mrs. E. W. Mason (sclerotia from which I developed apothecia in April at Ithaca, New York); — CUPP 31662, near London, England, May 1934, William Brown (sclerotia); — Otto Jaap, Fungi Selecti Exs. 754 a and b. Prov. Brandenburg, Triglitz in Prignitz, O. Jaap. (a) apothecia, May 30, 1916. (b) spermodochidia, "Placosphaeria junci", Bubák, November 3, 1915; — CUPP 31656, near Downton, Hampshire, England, August 2, 1930, Whetzel & William Brown (spermodochidia); — Sydow, Mycotheca germanica 2358, near Burgholdinghausen, Kreis Siegen, Westfalen, Germany, May 18, 1924, A. Ludwig (apothecia).



TEXT FIG. D

This species is also said to occur on *Juncus glaucus* Ehrh., on *J. filiformis* L. and on *J. communis* E. May. Saccardo (1886: 666) described the spermatial stage under the name *Sphacelia tenella* from a collection on *Juncus glaucus* collected near Rouen, France. Mr. Carleton Rea (in a letter April 24, 1927) says the sclerotia of *S. curreyana* are common in the culms of this species in the vicinity of Worcester, England. Bubák (1906: 113) described what is apparently the spermatial stage of our fungus under the name *Placosphaeria junci* in culms of *Juncus filiformis* and Nylander (1869) has described the apothecial stage under the name *Peziza juncifida* on culms of *Juncus* (*compressi*?) but I have not seen material on any of these suspects.

In numerous records of collections of this fungus, the species of *Juncus* on which it occurred is not given. The evidence available seems to indicate very clearly that *S. curreyana* is most frequently to be found on *Juncus effusus* L. and *Juncus conglomeratus* L.

The erroneous identification of the sclerotial stage of *S. curreyana* with that of *S. scirpicola* by Currey and Berkeley has resulted in the citation of *Sclerotium roseum* in many synonymies of *S. curreyana* (See p. 413). In his transfer of *Peziza curreyana* to the genus *Phialea*, Gillet writes "Bart." for the author of the species. This appears to be an error for "Berk." The inclusion of *Peziza juncifida* Nyl. and *Placosphaeria junci* Bubák in the synonymy of this species might be questioned, since I have not been able to see authentic specimens of either. Nylander's description of *P. juncifida*, while brief, appears to me to justify the conclusion that he had apothecia of *S. curreyana* in hand.

There would appear to be little question of the identity of Bubák's fungus with the spermatial stage of *S. curreyana*, since his sketch of a section through the fruit body is quite in character with the spermodochidium of this Discomycete (See Text Fig. D.) Bubák records his fungus on *Juncus filiformis*, a species on which this Discomycete is not otherwise known to occur.

The slender curved ascospores of *S. curreyana* are strikingly different from the ascospores of any of the other species in the genus. The structure of the spermodochidium is also different from that of the others. The dark color is due in part to the dilute brownish color of the central hyphae of the spermodochidia and brown hyphae in the covering epidermal cells. It is, however, largely the result of the dark brown discoloration of the crushed thin-walled cells of the parenchyma surrounding the spermodochidial cavity giving the appearance of a spermogonial wall. This "wall" is further suggestive of a true hyphal wall, since resting upon it is a spermatophore hymenium, lining the cavity (Text Fig. D). This hymenial lining presents a picture very different from that in the spermodochidia of the species in *Carex* suspects, where it is entirely wanting. However, just as in the *Carex*-

Text Fig. D. Cross section through a spermodochidium of *Sclerotinia curreyana* about x200. Note that the cavity is formed by extensive lysis of the parenchyma between the vascular bundles with collapse and browning of the surrounding cells to form a pseudo-spermogonial wall. Drawn by Carlos Garcés.

invading species, *S. curreyana* also produces globose spermodochidia which lie typically in the central cavity of the hymenium-lined spermodochidium. These peculiarities might be taken to indicate that it is not closely related to the other species in the group here under consideration, but in all its other characters it conforms very closely. Its nearest relationship would seem to be with *S. scirpicola* if one considers the similarity of the sclerotia of these two species.

In culture on potato dextrose agar *S. curreyana* presents a picture strikingly like that of *S. sulcata*, the chief difference being the pinker hue of the mycelial mat of the former. Both form sclerotia on this medium and the medulla of the sclerotium of *S. sulcata* is nearly as pink as that of *S. curreyana* at comparable stages in its development.

It is remarkable in the light of Tulasne's recognition (1861: 104) of the spermatial stage in *S. duriaeanae* that the spermatial stage of *S. curreyana* was not described until 1884 (Saccardo) and not recognized as such until 1912 (Grove). Grove says the spermatia measure 3–5 μ in diameter. Presumably his measurements were made from fresh material. Mine (2–2.5 μ) were made under oil immersion from dry material soaked over night in weak KOH. This difference in size is, however, hard to explain on these grounds.

SCLEROTINIA JUNCIGENA

In May 1883, Suksdorf collected the apothecial stage of a little Discomycete apparently growing on the surface of "dead stems of *Juncus* above the water in Falcon Valley", according to a note on the packets distributed by him in his exsiccati, Flora of Washington. Ellis, who determined the material, gave it the name *Ciboria juncigena* E. & E. Dr. J. R. Keinholz advises me in a letter of June 7, 1942 that the name "Falcon Valley" apparently was abandoned many years ago and the name changed to "Hell Roaring Meadows", which lies at the head of a creek of the same name. No other collections of this form have been preserved as far as I can discover, although Dr. S. M. Zeller of the Oregon Experiment Station writes me that he has once come upon this fungus in the field. The species of *Juncus* is not given by Suksdorf but it is probably *J. effusus* var. *pacificus* Fern. & Wiegand. Dr. Keinholz who kindly undertook to locate fresh material of this fungus has thus far been unsuccessful. Its close resemblance to *S. curreyana* of Europe makes a critical study of living specimens highly desirable. Pending such a study it seems wisest to retain its present specific standing.

SCLEROTINIA JUNCIGENA (E. & E.) n. comb.

Ciboria juncigena E. & E., Proc. Acad. Nat. Sci. Phila., Nov. 30, 1894, p. 348.

Spermodochidia not seen.

Sclerotia one, possibly more, within a diseased culm, slender, cylindric, with truncate, slightly rounded ends, up to 15 mm. long by 2 mm. in diameter, externally black, finely sulcate, internally white when mature; apparently lying free in a lysigenous cavity in the pith region of the culm; structure essentially like that of *S. curreyana*. The sclerotia are not freed from

the culm at maturity, nor are they apparently exposed by a slit on emergence of the apothecia as in *S. curreyana*.

Apothecia usually but one from each sclerotium, long-stipitate, avellaneous (?); *cup* thin, membranous, shallow cup-shaped, sub-umbilicate, 4–5 mm. in diameter; *hymenium* "wine colored"; *stipe* arising from the sclerotium within and penetrating the wall of the culm, relatively long, about 1 cm. by 1 mm. thick, lower half or more black, longitudinally wrinkled, fibrillose, anchored at point of emergence to the surface of the culm by a spreading dark hyphal mat, concolorous above with the cup; *asci* clavate-cylindrical, (Ellis meas.) about $60 \times 4\text{--}5\ \mu$, 8-spored, spores sub-biseriate; *ascospores* allantoid, slender, distinctly curved, hyaline, (Ellis meas.) $7\text{--}8 \times 1.25\ \mu$, (Whetzel, 50 meas. in KOH) $7.2\text{--}10.8 \times 1.2\text{--}2.4\ \mu$, mode $8.4 \times 2.4\ \mu$, average $8.86 \times 1.83\ \mu$; *paraphyses* not distinguishable in mounts from dried material.

HABITAT: In culms of *Juncus* (probably *J. effusus* L. var. *californicus* Fern. & Wiegand) in wet marshes. The apothecia appear in May on standing dead culms.

DISTRIBUTION: Known only from the type locality. Falcon Valley (now Hell Roaring Meadows), Washington State.

TYPE SPECIMEN: Exsiccata specimens distributed as 371 Flora of Washington. Collected by W. N. Saksdorf, May 31, 1883. I have seen two packets, one deposited from the Ellis Collection in the N. Y. Bot. Gard. herbarium and another in the Mycol. Coll. Bur. Pl. Ind., Washington, D. C.

It is with some hesitation that I treat *Ciboria juncigena* E. & E. as a species distinct from *S. curreyana*. It is undoubtedly a *Sclerotinia* rather than a *Ciboria*. Ellis entirely overlooked the presence of the sclerotia, which was perhaps due to the absence of a slit in the culm over the sclerotium and the unusual anchorage of the stipe to the surface of the culm. As far as the characters of the cup are concerned, it could hardly be distinguished from *S. curreyana*, but the long, slender stipe, its black color, and the basal, dark hyphal mat anchoring it to the culm at the point of emergence, together with the slender character of the sclerotium, may well prove to be dependable evidence of its specific character. It is unquestionably very closely related to *S. curreyana* and may indeed be more properly regarded as an American form or variety of that species. However, my experience with the closely related *S. duriaeana* and *S. sulcata*, together with the fact of its long geographical isolation from the ancestral *S. curreyana*, inclines me to believe that a fuller study of *S. juncigena* in fresh condition and in its spermatial stage will prove it to be a distinct species.

SPECIES ON LUZULA

SCLEROTINIA LUZULAE

PLATE IX, FIGS. 39 AND 40

W. Krieger distributed in his *Fungi Saxonici 2073* culms of *Luzula pilosa* L. in which are embedded slender black sclerotia of a fungus which he

labeled provisionally "*?Sclerotinia Curreyana* (Berk.) Karst." The label bears a brief description of the sclerotia with the remark that unfortunately he had been unable to develop the fruit body of the Ascomycete, hence the question mark before the name he was giving the specimen. He apparently collected the specimens he distributed under this number in two different localities and in different years, in Polenztales, Utterwaldergrunde, late May 1896, and near Königstein, June 1897. In Rehm's collections at Stockholm, Sweden, there is in addition to Krieger's exsiccati specimen 2073, another packet labeled in Krieger's handwriting bearing the same data, evidently duplicate material.

I have been able to locate but one other collection which is in the herbarium of the Mycological Collections, Bur. Pl. Ind., U. S. D. A., Washington, D. C. This bears the label "Herbarium G. Bresadola, 221 *Sclerotium roseum* Moug. en feo oritur Scler. Curreyana Berk. *Sclerotium Luzulae* Krieg. n. sp.? In den dürren Halmen von *Luzula pilosa* Willd. bei Königstein, 19. Juli, 1897. Lg. W. Krieger". The name "*Sclerotium luzulae* Krieg." appears never to have been published. The specimen is apparently a part of the 1897 collection distributed by Krieger in his *Fungi Saxonici* 2073. Krieger's collections of a sclerotial form on *Luzula pilosa* would seem, for the present, best regarded as a distinct species.

SCLEROTINIA LUZULAE sp. nov.

Spermodochidiis apparenter nullis; sclerotiis 1-3 vel pluribus, intra culmos natis et maturitate ad superficiem soli ruptionis culmorum causa liberatis, 5-30 x 1 mm., fusiformibus, acute abrupteque acuminatis unum ad latus, aqua imbutis obscure castaneis, siccis nigris, indistincte arato-sulcatis, cortice uno e strato cellularum atro-tunicatarum consistente, medulla alba, ex hyphis dense compactis, multo minoribus diametro ordinario specierum stirpis huius composita; apotheciis ignotis.

Spermodochidia apparently wanting.

Sclerotia one to three or more formed within the culms which are ruptured at maturity, discharging the sclerotia onto the soil, 5-30 mm. long by 1 mm. in diameter, fusiform, sharply and abruptly pointed at either end, dark mahogany brown when soaked in water, black when dry, indistinctly furrowed, not sulcate as in other species in this group, rind one layer of dark-walled cells, medulla white, composed of densely packed hyphae which are much smaller in diameter than those of the sclerotia of other species in this group.

Apothecia unknown.

HABITAT: In culms of *Luzula pilosa* Willd. in Saxony, Germany.

DISTRIBUTION: Known only from the type locality and very rare, according to the collector.

TYPE SPECIMEN: Krieger's *Fungi Saxonici* 2073, in culms of *Luzula pilosa* Willd. in Polenztales, Utterwaldergrunde, May 1896 and near Königstein, June 1897, *W. Krieger*.

MATERIAL EXAMINED: I have carefully examined the specimens of the type collections in the British Museum and in the CUPP Herbarium; also the specimen from the herbarium of the Bur. Pl. Ind., U.S.D.A.

Krieger, on the label of his *Fungi Saxonici* 2073, refers the specimen provisionally to *Sclerotinia cureyana* and cites *Sclerotium roseum* Fr. as a synonym, obviously two errors. This species is probably more common than Krieger surmises and should be sought wherever the suspect occurs.

The apparently complete absence of spermatial fruit bodies is puzzling. I have scrutinized carefully all the culms which I find in Krieger's collections but without finding any trace of spermodochidia. Their absence is most unusual, this being the only species in this group, except *S. vahliana* and *S. juncigena*, in which I have not found them. That I should have found them in these two species is almost certain had I had specimens of diseased culms collected during the summer.

EXCLUDED SPECIES

Several species of stromatic Discomycetes other than those described above occurring on species of the *Cyperaceae* and *Juncaceae* have been put in the genus *Sclerotinia* by various authors. None of these species with which I am acquainted are, however, congeneric with the true species of *Sclerotinia* as I interpret that genus. I list them here with some observations and comments which may prove useful to my mycological colleagues until such time as I may treat them more fully.

Sclerotinia aschersoniana P. Henn. & Plötn. Verh. Bot. Vereins, Prov. Brandenburg 41: IX, 1899.

This species is pathogenic in the ovaries of certain species of *Carex*, notably in *C. hudsonii* A. Bennet (= *C. stricta* Good.) in Europe and on *C. stricta* Lam. in North America. I have collected and cultured it frequently from the latter species in swamps in central New York and once from *C. prairea* Dewey in the same region. It is certainly not a *Sclerotinia*. It infects the suspect by ascospore invasion through the stigma, converting the ovary into a black stromatized mummy. It might be referred to the genus *Ciboria* but its proper taxonomic relationships require further consideration.

Sclerotinia utriculorum Boud. Bull. Soc. Myc. France 19: 196-197, pl. 8, fig. 6. 1903.

This is described as growing on the hard seeds of *Carex davalliana* in May, in the Jura in France. Boudier says it differs from other species of *Sclerotinia* on *Carex* in that the apothecia do not arise from sclerotia but from the sclerified achenes of the *Carex*. As he makes no reference to *S. aschersoniana* it is probable he was unaware of that species. As far as I can judge, *S. utriculorum* Boud. is specifically the same as *S. aschersoniana* P. Henn. & Plötn. Velenovsky (1934: 224) apparently regards this species as identical with *S. aschersoniana*, citing the latter as a synonym of *S. utriculorum*, but his reason for this is not clear.

Sclerotinia vesicariae Giesenhagen, Ber. Bayer. Gesell. Erforsch. der Heim. Flora **11**: 167-169. 1907.

This species is said to occur among ("inter") fallen dead seed of *Carex vesicariae* in autumn, collected by Stechsee near Seehaupt, Bavaria. The sclerotia are said to be irregularly cylindrical, rough, black, white within, 5-8 mm. long by 2 mm. in diameter. This would seem to indicate that this species does not occur in the ovaries of the *Carex*, but there is little else to indicate that it is distinct from *S. aschersoniana*. The asci are said to be 180-190 μ , considerably longer than those of *S. aschersoniana* which are given as 90-110 μ in the original description; the width is about the same. Ascus measurements, however, are so very variable in the stromatic Discomycetes, especially the length, as to be of little specific significance. The size and shape of the spores approximates those of *S. aschersoniana*. I am inclined to regard *S. vesicariae* as specifically distinct.

Sclerotinia caricina Velenovsky, Monog. Discom. Bohemiae **1**: 224; **2**: pl. 22, fig. 40. 1934.

This species is said to occur on the roots of *Carex muricata* among *Juncus communis*. It is not possible to tell from Velenovsky's description and figure whether this is a true *Sclerotinia* or not.

Sclerotinia paludosa Davidson & Cash, Mycologia **25**: 271. 1933.

A critical examination of all the specimens on which this species is based, discloses that the sclerotia shown in their fig. 7 are those of a *Typhula*. The apothecia in the other specimens do not arise from sclerotia but from stromatized leaf tissues. This fungus is undoubtedly a *Rutstroemia*. It is a common species of wide distribution occurring on leaves and culms of various species of sedges, grasses, etc. The proper species name remains to be determined. It is probably conspecific with the following species.

Sclerotinia heterocarpa Bennett, Ann. Appl. Biol. **24**: 254. 1937.

While this species is described as occurring on grasses as the cause of the "dollar-spot" of turf, what is without doubt the same species has been discovered by the writer on leaves of *Carex* and several other plants. It was earlier described under the name *Ciboria armeriae* by Von Höhnelt (Frag. Myk. **22**, Mitt. No. 1122, p. 43. 1918). This fungus is clearly not a *Sclerotinia*. It is without doubt a species of *Rutstroemia*.

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