Delimitation of the Economically Important Plant Pathogenic *Sclerotinia* Species

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Despite the continued interest of mycologists and plant pathologists, the taxonomic position of the economically important, plant pathogenic species of *Sclerotinia* has remained unresolved. Over 250 species of diverse relationships, both pathogenic and nonpathogenic, have been assigned to the genus *Sclerotinia*, with consequent controversy and confusion over generic limits. Attempts to delimit the pathogenic species assigned to the genus using a few traditional taxonomic characters have resulted in recognition of too many or too few species in relation to what is now known about the biology and microanatomy of this group to satisfy the practical need of the plant pathologist to name the pathogen in hand. Examination of type specimens of preserved material as well as observation of living isolates in the light of microanatomical and cultural characters employed by contemporary discomycete taxonomists has resulted in the delimitation of plant pathogenic species of *Sclerotinia* in the revised and more limited circumscription of the genus presented here.

DELIMITATION OF *SCLEROTINIA*

Generic characters. The family Sclerotiniaceae was erected in 1945 by Whetzel (22) to accomodate inoperculate discomycetes that produce stromata, stipitate apothecia, ellipsoidal ascospores, and globose spermatia. He provided keys and diagnoses to the genera assigned to the Sclerotiniaceae and used stroma type, ascospore color, the presence of functional conidial state, and type of conidia as major characters in delimiting new and revised genera. The genus *Sclerotinia* was designated type genus of the Sclerotiniaceae.

Whetzel recognized two basic types of stroma: one is the substratal stroma, an indeterminate type of stroma with a medulla consisting of a portion of the host substrate permeated by hyphae and with a thin black rind covering at least a portion of the stromatal surface. Genera placed in the Sclerotiniaceae by Whetzel and subsequent authors with this type of stroma include *Lambertella, Ciboria, Ciboriopsis* [= *Moellerodiscus*], *Lanzia, Poculum, Rutstroemia,* and several apparently unnamed genera. The other type of stroma, a distinct sclerotium, either may develop within host tissues with remnants of these tissues remaining within the sclerotial medulla, as in *Ciborinia, Verpatinia, Monilinia, Myriosclerotinia, Phaeosclerotinia, Scleromitrula, Seaverinia, Botryotinia,* and *Streptotinia,* or may develop free from the tissues of the suscept as in *Sclerotinia* and *Martininia,* in which suscept tissues are not embedded in the sclerotial medulla. In *Stromatinia,* two types of sclerotium are formed; a thin, effuse manteling stroma (with medulla and rind) and small, black "sclerotules" produced above the manteling stroma on aerial mycelium. A simple laboratory technique for determining whether suscept tissues are incorporated in the sclerotial medulla has been reported by Noviello and Korf (16).

Another valuable character used by Whetzel and subsequent authors is the presence of a functional conidial state. Sclerotium-forming genera with known anamorphic (conidial) states include *Phaeosclerotinia* (*Monilia*), *Monilinia* (*Monilia*), *Pycnopeziza* (*Acarosporium*), *Scleromitrula* (unnamed), *Ovulina* (*Ovulitis*), *Botryotinia* (*Botrytis* and *Amphobotrys*), *Streptotinia* (*Streptobotrys*), *Seaverinia* (*Verrucobotrys*), *Gloeotinia* (unnamed), and *Septotinia* (*Septotis*). The remaining genera, including *Sclerotinia,* have no known functional conidial state.

Within the Sclerotiniaceae, only three genera produce brown ascospores: *Lambertella, Martininia,* and *Phaeosclerotinia*; the remaining described genera produce hyaline ascospores.

Although virtually ignored by Whetzel, characters of the sterile tissues of the apothecium and sclerotium have been considered by Buchwald (1), Dumont (5), and Korf (11,12) in delimitation of genera within the Sclerotiniaceae. In addition to the development of a free, discrete sclerotium, absence of a functional conidial state, and production of hyaline ascopsores, I delimit the genus *Sclerotinia* in an even more restricted sense to include only those species in which the ectal excipulum, or outermost layer of the apothecium, is composed of globose cells in chains oriented perpendicularly to the receptacle surface. *Myriosclerotinia,* a genus segreated from *Sclerotinia,* produces sclerotia within the culms of sedges, rushes, and grasses and produces a *Myrioconium* state (probably spermatial) in locules within host tissues. In contrast, superficial development of both the sclerotia and the *Myrioconium* state occurs in *Sclerotinia* sensu Kohn. The two genera also show anatomical differences in tissue structure of the apothecium.

The Correct Name for *Sclerotinia.* Althouth I accept *Sclerotinia* in the restricted sense outlined above, many workers, including Dennis (4), circumscribe *Sclerotinia* in the broad sense to include *Monilinia, Ovulinia, Ciborinia, Botryotinia, Myriosclerotinia,* and *Sclerotinia*; this is a taxonomic decision and, therefore, open to opinion. The genus *Sclerotinia* was erected by Fuckel to accomodate *Sclerotinia candolleana, S. fuckeliana, S. libertiana* (an obligate synonym of *S. sclerotiorum* erected by Fuckel to avoid a supposed tautonym), *S. tuberosa,* and *S. baccata.* Of these original species, *S. baccata* has been transferred to the Pezizales and is of no further interest in relation to *Sclerotinia*; Whetzel (22) transferred *S. fuckeliana* to *Botryotinia* and *S. candolleana* to *Ciborinia* on taxonomic grounds. Clearly if Whetzel's taxonomic decision is not accepted (many plant pathologists and a few taxonomists do not) *Sclerotinia* may be treated in the broad sense of Fuckel to include a large and diverse group of plant pathogenic species.

Though taxonomic considerations afford some choice among the broad circumscription of Fuckel, the more restricted concept of Whetzel, and my still more restricted concept, there is no room for choice in considering the nomenclaturally correct name for *Sclerotinia sclerotiorum*. The genus *Sclerotinia* was lectotypified in 1928 by Honey (7) with *S. candolleana*. In 1945 Whetzel (22) transferred *S. candolleana* to his new genus, *Ciborinia*, and ignoring Honey's lectotypification, retypified his redelimited genus *Sclerotinia* with *S. sclerotiorum*. If one accepts Whetzel's restricted circumscription of genera (a taxonomic decision) *Sclerotinia*, lectotypified by *S. candolleana*, becomes the oldest available name for *Ciborinia*. This was the position taken by Korf and Dumont (13) in erecting *Whetzelinia*, typified by *S. sclerotiorum.* Because many workers, especially plant pathologists, accept both Whetzel's circumscription and his typification of *Sclerotinia* with *S. sclerotiorum*, a proposal to conserve *S. sclerotiorum* as the lectotype of *Sclerotinia* has been presented and accepted by the Special Committee for Fungi and Lichens of the International Association of Plant Taxonomists (IAPT) and by the IAPT General Committee, with only routine action by the International Botanical Congress in 1981 still pending. It is now correct to refer to *Sclerotinia sclerotiorum*, and to ignore the generic name *Whetzelinia* henceforth.

Species characters in *Sclerotinia.* Taxonomic decisions are based upon observation and evaluation of characters falling into

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four principal categories: macroscopic, cultural, biological, and microscopic. The publication in 1932 of Nannfeldt's *Studien über die Morphologie und Systematik der nicht-lichenisierten inoperculaten Discomyceten* (14) revolutionized the description and classification of discomycetes by introducing microanatomical studies of sterile tissues as a source of additional taxonomic characters. Using pre-Nannfeldt characters, as employed by many workers who described species of *Sclerotinia*, a description of a species was limited to the following range of characters:

(i) Macroscopic characters, such as color, size, and shape of the apothecium, stipe, and sclerotium.
(ii) Cultural characters, often the size and distribution of sclerotia on agar plates.
(iii) Biological characters, such as host, season, and part of substrate invaded.
(iv) Microscopic characters, usually limited to the size, shape, and color of the ascospores, asci, and paraphyses.

While it must be noted that these characters are useful ones, and indeed several have been heavily weighted in making the taxonomic decisions reported here, the microanatomical characters introduced by Nannfeldt in his classification offer further information on zones of the apothecium, stipe, and sclerotium in addition to the hymenium, which has long been the center of attention. The sterile zones of the apothecium and sclerotium show diverse and distinctive tissue types (for an explanation of tissue types the reader is referred to Korf [11]). These zones include the subhymenium, the medullary excipulum, and the ectal excipulum subdivided into three component zones; the margin, the flank, and the stipe, and including any hairs, or as in the Sclerotiniaceae, tomentum hyphae.

The tissue types of the apothecial and sclerotial zones are characteristic within the genus *Sclerotinia*. The subhymenium, a compact zone of interwoven prosenchyma, is usually brown-walled and bound in gel. The medullary excipulum is composed of loosely interwoven textura intricata oriented more or less parallel to the surface of the apothecium. The most characteristic zone, the ectal excipulum, is composed of textura prismatica which turns out at the apothecial margin perpendicular to the apothecial surface and, further down the flank, develops into textura globulosa as cells become inflated, round off, and become somewhat disarticulated. Globose cells and often tomentum hyphae occurring as processes growing from globose cells, comprise the ectal excipulum of the stipe and are often brown-walled. The sclerotial medulla in *Sclerotinia* does not include suscept tissues, but is composed of hyaline textura oblita with heavily gelatinized hyphal walls (composed of β-1,3-glucans and proteins according to Saito [18]). The sclerotial rind is composed of the apices of these medullary cells which turn out perpendicularly to the sclerotial surface and develop into textura prismatica, again with cells that become globose and somewhat disarticulated. Pigmentation of these rind cells may occur in the walls of a two- to six-deep layer of the outermost cells.

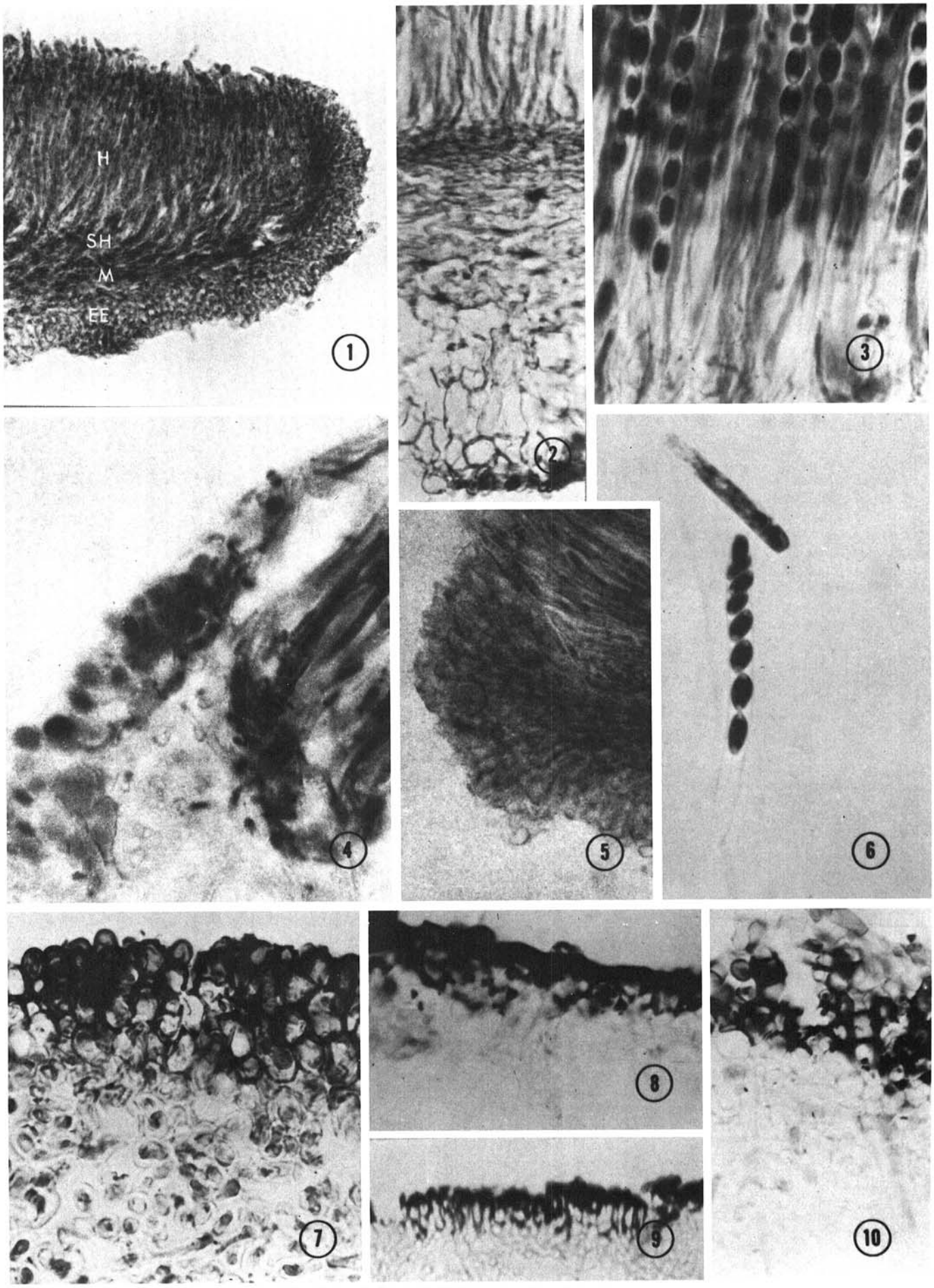
All species retained in *Sclerotinia* show a positive reaction of the ascus pore channel wall in Melzer's Reagent (0.5 gm iodine, 1.5 gm KI, 20 g chloral hydrate, 20 ml distilled water). Dimorphism in spore size has been observed by the author in one species, as it has for some species of *Monilinia* (25) and in *Sclerotinia allii* (19), which is a species of *Ciborinia*.

Variability in species characters in *Sclerotinia*. The question of reliability of taxonomic characters has long been a disturbing one. Purdy (17) studied variation in ascus, ascospore, and sclerotium sizes in isolates tentatively identified as *S. sclerotiorum, S. trifoliorum, and S. minor.* Comparing averages and ranges of ascus and ascospore measurements from two to three generations with those given in species diagnoses and elsewhere in the literature, Purdy found no line of demarcation between species and concluded that "it was impractical, if not impossible to distinguish the asci or the ascospores of one species from those of another." Purdy obtained a variety of cultural variants within species ranging from those which produced no sclerotia to those which produced very large sclerotium-like masses. He found a continuous intergradation in sclerotium size from the small sclerotia of *S. minor* to the large ones of *S. sclerotiorum*. Consequently, he could not distinguish species on the basis of sclerotial size. On the strength of this evidence, without examining any type specimens and without examining apothecial tissue structure, Purdy synonymized not only *S. minor* and *S. trifoliorum* under *S. sclerotiorum,* but also *S. trifoliorum* var. *fabae, S. intermedia,* and *S. sativa* maintaining that it is "impossible to identify these species in practice because of the variability of the characters that have been used." Purdy's data may demonstrate the variability of the characters studied, but many more characters are available for consideration in species delineation. By reducing the number of species recognized it first appeared that the task of identifying plant pathogenic species of *Sclerotinia* would be simplified. As more was learned about the biology of this group, however, it became apparent that this broad definition of *S. sclerotiorum* seemed to submerge several taxa under one species. In this paper additional taxonomic characters are used to circumscribe several species, taking into consideration consistency with biological data.

Although certain cultural characteristics have been studied extensively by plant pathologists and taxonomists, in only a few cases have apothecial structures been examined for variation between apothecia produced in nature and those produced in vitro. Working with a collection of approximately 65 isolates of species of *Sclerotinia, Myriosclerotinia, Ciborinia,* and *Botryotinia* from Europe, Australia and New Zealand, Asia, and North America, I have observed cultural characteristics and, for 26% of these isolates, apothecial production. Apothecia produced in vitro were obtained only for isolates finally identified as *Sclerotinia sclerotiorum* (10 of 18 isolates), *S. minor* (five of seven isolates), and *S. trifoliorum* (two of five isolates). Most isolates were derived from diseased tissue, although some were made from single ascospores or ascospore masses. Cultures, grown and maintained on Difco potato dextrose agar (PDA), were transferred to PDA in 9 cm diameter glass petri plates, incubated for 3–4 days at room temperature, then transferred with a 5-mm diameter cork borer from the growing margin of the colony to 500-ml Erlenmeyer flasks containing autoclaved carrot disks and 25 ml of distilled water. The flasks were incubated for 4 wk without light at 15 C. Sclerotia were harvested, rinsed in sterile distilled water, and transferred to sterile preparation dishes containing glass wool saturated with distilled water. The sclerotia then were "cold conditioned" for 4 wk at 0 C. The dishes were removed to a growth chamber set at 15 C, with fluorescent and incandescent light at approximately 21,520 lx (2,000 ft-c) and a 14-hr photoperiod. Apothecial initials appeared 4-12 wk after introduction to the growth chamber. The subject of apothecial initiation in *Sclerotinia* has been studied by many workers; for a review, the reader is referred to Saito (18).

In the studies reported here, the only environmental factor modified was the amount of light supplied to incubating sclerotia in

Fig. 1-10. Microscopic details of apothecia and sclerotia of *Sclerotinia* spp. **1)** *Sclerotinia sclerotiorum*, CUP 58252. Cross section of apothecium. H = hymenium, SH = subhymenium, M = medullary excipulum, EE = ectal excipulum. ×211. **2)** *S. sclerotiorum*, CUP 58252. Subhymenium, medullary excipulum, and ectal excipulum. Note cells of the ectal excipulum oriented perpendicularly to the apothecial surface. ×528. **3)** *S. trifoliorum*, CUP 58244. Dimorphism in ascospore size. ×528. **4)** *S. minor*, CUP 58232. Ectal excipulum at margin of apothecium, composed of globose cells. ×528. **5)** *S. sclerotiorum*, CUP 58252. Ectal excipulum at margin of apothecium, composed of prosenchyma "turning out" perpendicularly to the apothecial surface. ×528. **6)** *S. trifoliorum*, CUP 58244. Dimorphism in ascospore size, 4:4 segregation of small and large ascospores. ×528. **7)** *S. sclerotiorum*, CUP 58246. Sclerotial rind and medulla. Rind composed of dark-walled textura prismatica with cells becoming globose. × 528. **8)** *Myriosclerotinia borealis*, CUP 58222. Sclerotial rind composed of globose cells with outermost cell walls forming a thick, carbonaceous, melanized layer. × 528. **9)** *"Sclerotinia" tuberosa,* CUP 58253. Sclerotial rind and medulla. Rind composed of a single layer of dark-walled, clavate cells. × 211. **10)** *Sclerotinia trifoliorum,* CUP 58244. Sclerotial rind and medulla. Medulla composed of textura oblita intergrading to textura prismatica of rind cells, with some cells becoming globose, continuing beyond rind as erect tomentum hyphae, × 528.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the growth chamber. Fertile apothecia were produced only at 4,304 lx (400 ft-c) or above. At levels significantly below 4,304 lx only stipes were produced, and just below this threshold level, apothecia developed only a pallisade layer of tomentum hyphae in place of a fertile hymenium.

Sclerotia and apothecia produced in nature by *S. sclerotiorum, S. minor,* and *S. trifoliorum* were compared with apothecia and sclerotia produced in vitro. One isolate of *S. trifoliorum* was obtained from a European collection of fresh apothecia from which a mass ascospore shoot was made, as were several isolates of *S. tuberosa.* Apothecia and sclerotia were sectioned at 20 μm and 5 μm, respectively. Sectioned apothecia were examined in Melzer's Reagent, cotton blue in lactophenol, and KOH/phloxine; sectioned sclerotia were examined in KOH/phloxine only.

In studying the cultural behavior of *S. borealis*, Groves and Bowerman (6) reported that "the apothecia in the Swedish specimen [topotype] were smaller and more delicate than those developed in our cultures, but we have observed in other species of Sclerotiniaceae that apothecia produced in culture are usually more robust than those formed in nature." Until Christiansen's (3) studies of variability in apothecial structure of several species of *Ciboria, Ciborinia, Lambertella,* and *Rutstroemia,* this observation had not been followed up by examination of sectioned apothecia to determine the histological relationship to this macroscopic variation. Variability in gross size of sclerotia and apothecia as well as in color and external mealiness of apothecia has long been observed in both cultures and field collections of pathogenic species of *Sclerotinia*. On examining sectioned apothecia I found that this variation in size was not due to differences in cell size or in tissue types but, as Christiansen noted in her studies, "basically the tissue types of the different layers of the apothecia were stable, varying only in the compactness and in the admixtures present." Variation in gross size of apothecia of *Sclerotinia* appears to be due to the proliferation and compactness of cells.

Only in the subhymenium are cells consistently bound in gel; in other zones of the apothecium, gel is present or not, with variation between isolates as well as among them. Since gel may be a factor in the conservation of moisture within apothecial tissues, presence or absence of gel is probably influenced by varying amounts of moisture in the microenvironment of the developing apothecium and should be approached with caution as a taxonomic character in this group of species.

The bluing of the ascus pore channel in Melzer's Reagent has long been accorded importance as a consistent taxonomic character by discomycete taxonomists. Enhancement or initiation of this reaction after pretreatment with KOH has been reported (10,15). Though all species retained in *Sclerotinia* have ascus pore channels which turn blue in Melzer's Reagent, without KOH pretreatment most collections of *S. minor* showed a weak reaction or none at all; all reactions were enhanced or (in *S. minor*) occurred only after KOH pretreatment. No mention of the reaction is found in Jagger's original species diagnosis (8). Bluing of sterile zones of the apothecium in Melzer's Reagent was observed in all species with variation in whether or not bluing occurred among isolates; variability was not observed between field-collected apothecia and apothecia derived from isolates obtained from the same collection but developed in vitro. The apothecial zone that most often turned blue in Melzer's Reagent was the subhymenium, and this reaction is probably due to the presence of gel in this layer, although not all apothecia with tissues bound in gel displayed this reaction.

Variation in macroscopic color of apothecia, including mottling, is reflected in corresponding variation in pigmentation of cell walls in all zones of the apothecium. The ectal excipulum of the apothecium and stipe is the most frequently pigmented zone but cell walls in this zone may be hyaline, light brown, or dark brown with no consistency between or among isolates.

External mealiness on the receptacle and stipe may be due to the presence of abundant tomentum hyphae to which soil particles may adhere. Occurrence and abundance of tomentum hyphae are extremely variable on the ectal excipulum of both the apothecium and the stipe, but tomentum hyphae are most frequently present on the stipe. While presence of tomentum in these areas cannot be relied upon as a taxonomic character in species retained in *Sclerotinia,* it does appear to be a more stable character of the sclerotial rind.

In comparing measurements of ascospores with those given in species diagnoses, variations of as much as 3 μm in range and average measurements made from a single apothecium were observed in different mounting media. Dilute solutions of chloral hydrate and potassium hydroxide often are used to rehydrate and inflate dried specimens with collapsed cells and both also inflate ascospores. Since most authors do not indicate the mounting medium in which measurements have been taken, workers should be aware of the effect of mounting media on ascospore and ascus size, both of which are already subject to variability within a certain range in nature.

Cultures grown on PDA or autoclaved carrot disks at 15-20 C consistently produced either small sclerotia scattered throughout the colony or large sclerotia arranged radially at the periphery of the growing margin of the colony, consistent with whether original isolates were small sclerotial forms (*S. minor*) or large sclerotial forms (*S. trifoliorum,* and *S. sclerotiorum*), respectively. Studies of sclerotial ontogeny by Willets and Wong (23) confirm this observation as reflecting a difference in the mode and location of sclerotial initiation among these species. Degeneration in the ability to produce sclerotia in isolates of these three species as well as in size and quantity of sclerotia produced has been observed, with the eventual loss of the ability to produce sclerotia occurring in some cultures. Although the failure of an isolate to produce sclerotia is often permanent, in some cases formation of sclerotia may be induced by transferring the isolate to autoclaved carrot disks. Subcultures from the sclerotia produced on these carrot disks appear normal.

Keys to The Plant Pathogenic Species of *Sclerotinia*

I. KEY LEADING TO THE PLANT PATHOGENIC SPECIES OF *SCLEROTINIA*. BASED ON SCLEROTIA-PRODUCING CULTURES GROWN ON PDA AT 15-20 C *AND* ON FIELD-COLLECTED SCLEROTIA.

1. Sclerotia and mycelium with one or both of the following characters: a) clamp connections; b) dolipore septa (use phase microscopy or mounts in aniline blue/glycerine; see Tu & Kimbrough [21] ..... Basidiomycetes
1. Sclerotia and mycelium with neither of the above characters 2
2. Conidia present ..... Not *Sclerotinia* cfr. *Verticillium, Phaeosclerotinia, Monilinia, Pycnopeziza, Sclero-mitrula, Botryotinia, Gloeotinia, Septotinia, Cristulariella,* etc.
2. Conidia absent, except for phialidic "spermatia" (*Myrioconium*) 3
3. A mantling sclerotial stroma of indefinite dimensions present, and smaller sclerotia ("sclerotiules") formed on aerial mycelium above the mantle ..... *Stromatinia*
3. Not as above 4
4. Sclerotial medulla containing host cells (n.b. vessel elements with spiral cell-wall thickenings), or, in culture, sclerotia at least partially immersed in the agar ..... *Ciborinia, Myriosclerotinia, "Sclerotinia" kerneri.*
4. Sclerotial medulla free of suscept tissues, or, in culture, sclerotia formed above the agar surface 5
5. Sclerotial rind a single layer of dark-walled, clavate cells ..... *"Sclerotinia" tuberosa*
5. Sclerotial rind composed of a 2-6 deep layer of dark-walled, globose cells 6
6. Sclerotia formed abundantly, scattered throughout colony, sometimes adhering to form an aggregate crust in culture; individual sclerotia 0.5-2 mm long ..... *S. minor*
6. Sclerotia produced at growing margins of colony only, forming concentric rings, radial lines, and other patterns; individual sclerotia 2-20 mm long 7
7. Sclerotial rind composed of textura prismatica with cells becoming globose, continuing beyond the rind as erect tomentum hyphae ..... *S. trifoliorum*

7. Sclerotial rind composed of textura prismatica with cells becoming globose, no tomentum present ..... *S. sclerotiorum*

II. KEY LEADING TO THE SCLEROTIUM-FORMING, PLANT PATHOGENIC SPECIES OF *SCLEROTINIA* BASED ON APOTHECIA WITH SCLEROTIA, PRODUCED IN VITRO OR IN NATURE.

1. Apothecia cupulate, stipitate, on a distinct sclerotium with a well-differentiated rind and medulla; conidia present ..... Not *Sclerotinia*
1. Apothecia cupulate, stipitate, on a distinct sclerotium with a well-differentiated rind and medulla; conidia absent, except for phialidic spermatia (*Myrioconium*) 2
2. Sclerotial medulla containing host cells, or, in culture, sclerotia at least partially immersed in the agar ..... *Ciborinia, Myriosclerotinia, "Sclerotinia" kerneri.*
2. Sclerotial medulla free of host cells, or, in culture, sclerotia formed above the agar surface 3
3. Stroma consisting of a mantling stroma of indefinite dimensions, and smaller sclerotia formed on aerial mycelium above the mantle; apothecia occurring on the mantling sclerotial stroma only ..... *Stromatinia*
3. Not as above 4
4. Outer layer of ectal excipulum of apothecia composed of prosenchymatous cells usually embedded in gel ..... *"Sclerotinia" tuberosa*
4. Ectal excipulum composed of globose cells, gel present or absent ..... *Sclerotinia* (5)
5. Ascospores dimorphic in size, showing segregation in ascus, tetranucleate, length/width ratio of ascospores $\leqslant$ 2.0 ..*S. trifoliorum*
5. Ascospores uniform in size, no segregation in ascus 6
6. Ectal excipulum at margin of apothecium composed of globose cells, ascospores tetranucleate ..... *S. minor*
6. Ectal excipulum at margin of apothecium composed of prosenchyma "turning out" perpendicularly to the apothecial surface; ascospores binucleate, length/width ratio of ascospores > 2.0 .... *S. sclerotiorum*

Plant pathogenic species included in *Sclerotinia*. Of approximately 250 epithets considered, three species of economic importance are retained in *Sclerotinia*. Materials in culture were compared with available type and authentic specimens, with many names placed in synonymy or transferred to other genera. Complete species diagnoses and synonymies will not be provided here, but appear in the author's thesis publication (9). A brief discussion of the plant pathogenic species included in *Sclerotinia* and some plant pathogenic species synonymized under them is provided.

S. sclerotiorum is a cosmopolitan species with a host range of over 350 species in 60 families (20). In comparing the type specimen of Libert with contemporary material collected in nature and with that developed in vitro, the ectal excipulum of the apothecium and stipe emerges as characteristic for the species, marked by prosenchymatous cells at the apothecial margin parallel to the asci that gradually "turn out" perpendicular to the outer surface of the apothecium and develop shorter cells toward the flank (textura prismatica) which inflate to form the globose cells in chains oriented perpendicularly to the apothecial surface of the flanks and stipe. The sclerotial rind is also composed of globose cells, a layer of dark-walled cells two to six cells thick. The length/width ratio of the slender, ellipsoid ascospores is greater than 2.0 (2.1–2.4). *Sclerotinia libertiana* is an obligate synonym (based on the same type specimen) of *S. sclerotiorum*, erected by Fuckel to avoid a supposed tautonym (an epithet that repeats the generic name). Since *S. sclerotiorum* is the earlier name and does not constitute a tautonym, *S. libertiana* is a superfluous name.

Sclerotinia trifoliorum appears to be a cosmopolitan species with a host range limited to forage legumes. While *S. sclerotiorum* and *S. minor* occur on a wide range of host plants, including forage legumes, *S. trifoliorum* is known only on forage legumes. Dimorphism in spore size, usually with 4:4 segregation of small and large ascospores, has been observed in material from Europe and North America and in isolates made from European collections. Eriksson's original collections of this species and the type collection of the synonymous *Peziza ciborioides* Hoffm. all display spore dimorphism. In addition, the ascospores of *S. trifoliorum* are broader than those of *S. sclerotiorum*, with length/width ratios of 2.0 and lower (1.9–2.0).

Apothecia of *S. trifoliorum* are produced in nature during late summer and autumn, contrasting with *S. sclerotiorum*, which produces apothecia in spring and early summer. Apothecia are produced simultaneously by both species under identical conditions in vitro.

Since no type specimen of *S. trifoliorum* var. *fabae* Keay exists or is available, it is impossible to determine whether this is actually a variety of *S. trifoliorum*, or is *S. sclerotiorum* as suggested by electrophoretic assays of isolates of *Sclerotinia* from forage and crop legumes (24).

Sclerotinia minor is accepted here for small sclerotial forms with a characteristic apothecial ectal excipulum composed of globose cells in chains oriented perpendicularly to the apothecial surface from the margin of the apothecium down the flanks. When grown at temperatures between 15–20 C, small sclerotia (0.5–2 mm long) are produced throughout the colony, contrasting with the terminal development of sclerotia at the growing margins of the colony observed in other species of *Sclerotinia* that produce large sclerotia (2–20 mm long). On carrot disks incubated at 15 C, this species produced aggregations of small sclerotia easily distinguished from the large sclerotia produced by other species. *Sclerotinia sativa* Drayton & Groves occurring on bulbs of *Tulipa* and *Narcissus* and on roots of *Melilotus* and *Medicago* is considered a synonym. *Sclerotinia intermedia* Ramsey, on the basis of my type studies and despite the cultural differences observed by Chivers (2), is also considered a synonym of *S. minor*.

Economically important or often cited species excluded from *Sclerotinia*. *Sclerotinia allii* is transferred to *Ciborinia* as ***Ciborinia allii*** (Saw.) Kohn, *comb. nov.* (basionym: *Sclerotinia allii* Sawada, Govt. Formosa Agric. Exp. Stn., Spec. Bull. 19:206. 1919). Yamamoto (26) by error thought that Sawada's species produces a *Botrytis* state, which he identified as *B. byssoidea* Walker, calling the species *Botryotinia allii* (Saw.) Yamam. Unpublished cultural studies by R. P. Korf and G. L. Hennebert show that Sawada's species has no conidial state. The combination in *Botryotinia* is now unfortunately well-established in the literature.

Sclerotinia borealis, occurring on graminaceous hosts, is related to those juncicolous and cypericolous species assigned to *Myriosclerotinia* and is transferred here as ***Myriosclerotinia borealis*** (Bub & Vleug.) Kohn, *comb. nov.* (basionym: *Sclerotinia borealis* Bubák & Vleugel *in* Vleugel, Svensk Bot. Tidskr. 11:308. 1918). As with other species of *Myriosclerotinia*, development of sclerotia is within the culms of the host plant.

Sclerotinia camelliae Hara *non* Hansen & Thomas belongs either in an unnamed new genus or may be a species of *Moellerodiscus*.

Sclerotinia camelliae Hansen & Thomas *non* Hara is a *Ciborinia*. This epithet was published after 1935 without a Latin diagnosis and is, therefore, not validly published. I have provided a Latin diagnosis for it in my thesis publication (9).

Sclerotinia fructicola (Wint.) Rehm is *Monilinia fructicola* (Wint.) Honey.

Sclerotinia fructigena Aderh. & Ruhl. is *Monilinia fructigena* Honey.

Sclerotinia fuckeliana (d By.) Fckl. is *Botryotinia fuckeliana* (d By.) Whetz.

Sclerotinia gladioli Drayton is *Stromatinia gladioli* (Drayt.) Whetz.

Sclerotinia homeocarpa Bennett has no existing type specimen and is not a *Sclerotinia*. The epithet has been applied to species with apothecia identified as belonging to *Lanzia* and to *Moellerodiscus*. The symptoms attributed to "dollar spot" probably are caused by more than one species.

Sclerotinia kerneri Wettstein belongs in a new genus, described elsewhere (9).

Sclerotinia laxa Aderh. & Ruhl. is *Monilinia laxa* (Aderh. & Ruhl.) Honey.

Sclerotinia narcissicola Gregory is *Botryotinia narcissicola*

(Greg.) Buchw.

Sclerotinia panacis Rankin is transferred to *Stromatinia* as ***Stromatinia panacis*** (Rank.) Kohn, *comb. nov.* (basionym: *Sclerotinia panacis* Rankin, Phytopathology 2:30. 1912).

Sclerotinia perplexa Lawrence is *Ovulinia perplexa* (Lawr.) Seav.

Sclerotinia ricini Godfrey is *Botryotinia ricini* (Godfr.) Whetz.

Sclerotinia serica is transferred to *Stromatinia* as ***Stromatinia serica*** (Keay) Kohn, *comb. nov.* (basionym: *Sclerotinia serica* Keay, J. Bot. 75:132. 1937).

Sclerotinia tuberosa (Hedw. *ex* Mérat) Fckl. belongs in a new genus described elsewhere (9).

SOME CONCLUSIONS

Work must continue on species delimitation in the genus *Sclerotinia* even in its most restricted sense. Delimited here are three readily recognizable, closely related species, of major economic significance in plant pathology, which have been confused in the literature. Anyone should be able to distinguish apothecia and/or sclerotia on the basis of morpholgical characters. Many so-called "species of *Sclerotinia*" belong in other genera, however. Closely related genera in the Sclerotiniaceae such as *Ciborinia, Monilinia, Myriosclerotinia,* and *Stromatinia* are badly in need of monographic work. Phytopathologists working with Sclerotiniaceous species are concerned about the need to reconcile cultural and epidemiological variation with the taxonomy of the genus. Questions about the taxonomic significance of mycelial germination of sclerotia and cultural differences between dimorphic ascospores from a single ascus remain to be answered. The framework for comparing specimens offered here is meant to simplify examination of isolates with a set of standardized conditions under which isolates can be compared. Continued exchange of isolates and accessioning of voucher specimens in herbaria, particularly those including apothecia, are the only ways to insure that variation will be taken into consideration in the future delimitation of species in *Sclerotinia*.

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