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THE SECOTIOID SYNDROME

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I would like to begin this lecture by complimenting the Officers and Council of The Mycological Society of America for their high degree of cooperation and support during my term of office and for their obvious dedication to the welfare of the Society. In addition, I welcome the privilege of expressing my sincere appreciation to the membership of The Mycological Society of America for allowing me to serve them as President and Secretary-Treasurer of the Society. It has been a long and rewarding association. Finally, it is with great pleasure and gratitude that I dedicate this lecture to Dr. Alexander H. Smith, Emeritus Professor of Botany at the University of Michigan, who, over thirty years ago in a moment of weakness, agreed to accept me as a graduate student and who has spent a good portion of the ensuing years patiently explaining to me the intricacies, inconsistencies and attributes of the higher fungi. Thank you, Alex, for the invaluable experience and privilege of spending so many delightful and profitable hours with you.

The purpose of this lecture is to explore the possible relationships between the gill fungi and the secotioid fungi, both epigeous and hypogeous, and to present a hypothesis regarding the direction of their evolution. Earlier studies on the secotioid fungi have been made by Harkness (**1**), Zeller (**13**), Zeller and Dodge (**14**, **15**), Singer (**2**), Smith (**5**, **6**, **7**), Singer and Smith (**3**, **4**), Trappe (**11**, **12**) and Thiers (**9**). Unfortunately, there is not complete agreement regarding the phylogeny and evolution of this group of fungi. The major problem does not seem to involve so much the determination of their affinities as it does their origin and the direction of the evolutionary sequences. In other words, is the typical gilled fungus the ancestral type from which the various types of secotioid fungi, either epigeous or hypogeous, arose or was the evolutionary pathway in the opposite direction? My justification for addressing this question stems from observations made on the secotioid fungi as they occur in the western United States. I should like to emphasize that my concepts are largely conjectural due to the lack of substantiation from fossil material and to the paucity of cultural or other peripheral studies within the group.

Whereas it is obviously not necessary to review the nature of the basidiocarp of a typical gilled fungus with you, I would like, however, to point out some of the ways in which the secotioid basidiocarp differs. The typical epigeous or subepigeous secotioid basidiocarp closely approaches that of the gilled fungus in appearance and structure. There is usually a well differentiated stipe and pileus. The pileal margin, however, may not break free from the stipe, or, if it does, the

Mycologia, 76(1), 1984, pp. 1–8.

Harry D. Thiers

pileus rarely, if ever, becomes fully expanded. The lamellae, because of the constrictions resulting from the unexpanded pileus, never become parallel in their orientation; instead, they appear convoluted and anastomosed. Thus the typical stipitate secotioid fungus somewhat resembles an unopened agaric. There is another significant difference between the two types of basidiocarps: the basidia in none of the secotioid fungi forcibly discharge their basidiospores. The hypogeous secotioid basidiocarp more closely resembles a typical gastrocarp. A stipe is no longer present although sterile tissue in the form of a columella may be percurrent or interspersed throughout the enclosed gleba. The gleba has become finely lacunose and is not powdery at maturity as in the Lycoperdales and other true puffballs. When referring to hypogeous or epigeous secotioid forms of boletes and discomycetes the characters enumerated above are modified to greater or lesser degrees to accommodate the differences in the hymenophore and hymenium.

As intimated above, most of the observations on the secotioid fungi included in this paper have been made from specimens collected in the mountain ranges of the western United States, especially in the Sierra Nevada Range in California, but other geographical areas in the world with similar climates have not been disregarded. Published accounts of the mycota in such regions have been consulted, and it has been possible to visit some of these habitats. The secotioid fungi appear more abundantly and in greater variety in the mountain ranges of western North America than in any of the other areas where the mycota is known. More than thirty genera, for example, have been reported from the Sierra Nevada.

It seems quite apparent that the climate of these montane regions must have played a major role in establishing the diversity and in giving rise to many of these organisms. The typical climate of the western mountain ranges, particularly the Sierra Nevada, consists of winters that are cold and harsh and in which there is an abundance of precipitation, mostly in the form of snow. The late spring and summer seasons, on the other hand, are relatively warm and rainfall may be either absent or in the form of erratic, scattered thunderstorms. During the late fall and early spring there is usually an abundance of fleshy fungi, but they rarely occur, as would be expected, during the dry summer and early fall seasons. The thunderstorms may supply a sufficient amount of moisture to initiate basidiocarp formation; however, these sporocarps often dry out and become arrested in their development before reaching maturity. The lack of sufficient moisture during this part of the growing season has had a profound effect not only upon the rich and highly diverse mycota of the Sierra Nevada, but also has supported the origin and diversity of the secotioid fungi. Furthermore, as an adaptation to the aridity of the area there is clearly a trend toward a hypogeous habitat and a reduced, gastroid type of basidiocarp. In other words, there has been a natural selection for that type of basidiocarp which offers protection against the dry, warm environment which prevails during the summer and early fall seasons. It follows, therefore, that from an agaric or apothecial type of sporocarp with a fully exposed hymenium there has arisen an epigeous to subepigeous secotioid type which has at least a partially protected hymenium which has, in turn, given rise to the truly hypogeous type of sporocarp in which the hymenium or gleba is fully protected.

A few select examples of the different evolutionary series of secotioid fungi as they occur in the Sierra Nevada of California are given below.

RUSSULALES

Russulaceae

Russula Series

The well known genus of gilled fungi, *Russula,* is easily recognized by the heteromerous trama of the context and lamellae, by the formation of basidiospores with walls having strongly amyloid ornamentations in the form of spines, warts, or reticulations and by the absence of a latex. This large genus is represented by numerous species in the Sierra Nevada and there is frequently an abundance of basidiocarps. Also abundant in the same area are the secotioid genera *Elasmomyces* and *Macowanites,* which produce epigeous basidiocarps similar in appearance to *Russula.* However, their pilei either fail to expand or only partially do so, and the lamellae are highly convoluted, anastomosed and irregular in orientation. The basidiospores are typically ballistosporic but are not forcibly discharged from the basidium. These two genera are obviously closely related to *Russula* as evidenced by the presence of sphaerocysts in the trama, the russuloid basidiospores and the absence of a latex. The absence of sphaerocysts in the lamellar trama of *Elasmomyces* distinguishes it from *Macowanites.* Occurring in the same habitat and sometimes in abundance are two strictly hypogeous, secotioid genera, *Martellia* and *Gymnomyces,* which produce typically appearing gastroid basidiocarps. There is no stipe although a columella may be present. The gleba is enclosed by the peridium and is compact and finely lacunose. The basidiospores are typically statismosporic. These genera, like *Elasmomyces* and *Macowanites,* show an affinity with *Russula* by having sphaerocysts in some part of the trama, by the production of russuloid basidiospores and in the absence of a latex. *Gymnomyces* has sphaerocysts in the tramal plates while they occur only in the peridium of *Martellia.* Thus in the *Russula* series the basidiocarps range from a typical agaricoid type as seen in *Russula* to an intermediate epigeous, secotioid type exemplified by *Elasmomyces* and *Macowanites,* and terminate with a truly hypogeous type as seen in *Martellia* and *Gymnomyces.* All of these are closely related, so much so, that they are frequently all placed in the family Russulaceae.

RUSSULALES
Russulaceae
Lactarius Series

The genus *Lactarius* has a heteromerous type of trama similar to that in *Russula* except that the sphaerocysts do not commonly occur in the lamellar trama. *Lactarius* produces typical russuloid spores and differs from *Russula* chiefly by the production of a latex. The genus also occurs abundantly throughout the Sierra Nevada and is represented by a relatively large number of species. It is interesting to note that several species of both *Lactarius* and *Russula* which fruit in the early fall season often produce basidiocarps that reach full maturity before breaking through the soil. This is, perhaps, an adaptation to the arid conditions which prevail during that part of the year. The stipitate secotioid fungus in the lactarioid series which parallels *Elasmomyces* and *Macowanites* in structure and appearance is *Arcangeliella,* which is perhaps more abundantly represented in the western mountain ranges than elsewhere. In *Arcangeliella* the pileus expands either partially or not at all, the lamellae are anastomosed and labyrinthiform and the basidiospores are not forcibly discharged. It is noteworthy that two recently discovered species of this genus, *A. parva* (ined.) and *A. saylorii* (ined.) produced basidiocarps which were located several inches deep in the soil and both had a well developed stipe, but the peridium remained permanently attached to the stipe. They perhaps represent an advanced intermediate stage between the epigeous species such as *A. variegatus* Thiers or *A. desjardinii* (ined.) and the truly hypogeous forms which completely lack a stipe. The genus *Zelleromyces* is the only representative of a hypogeous, lactarioid form in which the stipe has disappeared but which typically retains a columella. Sphaerocysts are found only in the peridium, the basidiospores are russuloid and a latex is present indicating its close relationship to both *Lactarius* and *Arcangeliella.* These lactarioid fungi closely parallel the *Russula* Series and show the same apparent relationships and evolutionary tendencies.

AGARICALES

Cortinariaceae

Cortinarius Series

This very well known genus of gilled fungi is very common and diverse in the western regions of the United States. It is recognized by the rusty brown basidiospores which have roughened walls, the presence of a typically thin, cortinoid veil, a filamentous epicutis and a terrestrial habitat. What appears to be another example of adaptation to the dry environment is seen in the development, in some species, of a very heavy, resistant veil which is of sufficient tensile strength to prevent the expanding pileus from rupturing it. These velate species, as reported by Thiers and Smith (**10**) are usually partially hypogeous. Their lamellae are, however, parallel in orientation and the basidiospores are forcibly discharged. The typical secotioid fungus apparently derived from *Cortinarius* is *Thaxterogaster*. There is only a single species, *T. pingue* (Zeller) Singer & Smith, commonly found in the United States, but in other areas of the world with similar climatic conditions, such as parts of South America and Australia, several additional species are known to occur. In *Thaxterogaster* the stipe is well developed, and the pileus is well differentiated. The pileal margin, however, rarely breaks free from the stipe and the lamellae never become parallel in their arrangement, but, instead, are highly convoluted and anastomosed. The basidiospores are of the same color as those of *Cortinarius*, have similarly roughened walls and are not forcibly discharged. The hypogeous fungus appearing most closely related to *Cortinarius* is *Hymenogaster*. Species of this genus are widespread but rarely abundant. They have lost all traces of a stipe, but there is a columella which varies in its elaboration from a highly branched and complex structure to nothing more than small, inconspicuous veins of sterile tissue. The gleba is finely lacunose. The spores are rusty brown or darker brown and the walls are roughened as in *Cortinarius*. The *Cortinarius* series seems to offer considerable support to the tenet that there is a trend toward establishing a hypogeous habitat from an epigeous ancestor as evidenced by the velate forms and by the various types of secotioid forms.

BOLETALES

Boletaceae

Bolete Series

The boletes are characterized by the presence of a tubular hymenophore. Otherwise the basidiocarps are morphologically and anatomically similar to those produced by members of the Agaricales. The number of bolete genera is relatively small and they are usually easily determined by macroscopic features. Most genera, except those producing rough-walled basidiospores, are represented in the western United States and are often found in abundance. It is interesting to note that in two genera, *Suillus* and *Tylopilus*, there are species [*S. riparius* Thiers, *S. tomentosus* (Kauff.) Singer, Snell & Dick and *T. humilis* Thiers] that occur in this region which demonstrate a definite trend toward gastromycetization. In these taxa the pileus rarely fully expands, and the margin is often highly irregular with some portions only slightly pulling free from the stipe. The tubes are, however, more or less vertical in their orientation and a spore deposit can be obtained.

There is a relatively rich and varied flora of the secotioid genus *Gastroboletus* in the western mountains. The basidiocarps of *Gastroboletus* resemble closely those of the true bolete except that the tubes are frequently enclosed, are not vertically oriented and the basidiospores are not forcibly discharged. In the Sierra Nevada, several species occur, including *G. subalpinus* Trappe & Thiers which shows obvious affinities with Subsection *Boleti* of Section *Boleti*, *G. turbinatus*

(Snell) Smith & Singer which appears to be related to members of Subsection *Luridi* of Section *Boleti*, and *G. xerocomoides* Trappe & Thiers and *G. amyloideus* Thiers which seem closely related to members of Section *Subtomentosi*. In addition, *G. suilloides* Thiers shows close relationship with species of the genus *Suillus* as evidenced by the presence of fascicled cystidia which stain dark brown in dilute solutions of potassium hydroxide.

There appear to be several examples of hypogeous fungi which were possibly derived from a boletoid ancestor. Perhaps most closely related to the true boletes is the genus *Truncocolumella* which has spores more or less similar in shape and size to those of some of the boletes, and some pigments are common to both groups. Perhaps more distantly related is the genus *Rhizopogon*, the most abundant of hypogeous fungi in the west. It is readily admitted that the evidence of any degree of relationship with the boletes is not overwhelming; however, there is some similarity in the shape of the spores. The genus *Chamonixia*, very rare in the United States, has grooved or striate basidiospores which are somewhat similar to those produced by some species of the rough-spored boletes. In addition, the context turns blue when exposed. Steglich *et al.* (**8**) have shown that the same pigment, gyroporin, occurs in *Chamonixia* and in some species of boletes. It is also possible that a similar relationship might exist between species of the genus *Gautieria* and some of the rough-spored boletes. Even though there are no rough-spored boletes known from western North America, it is quite possible that they might have been here at some earlier period and might have been the ancestral form of *Gautieria* which is abundant in this area.

ASCOMYCETES

Discomycetes

Pezizoid Series

The inclusion of discomycetous fungi in this series is done with some reluctance. Part of this reluctance is derived from a lack of sufficient expertise to treat the group adequately. In addition, I have not been able to establish well defined phylogenetic sequences as has been done with the Homobasidiomycetes. The only purpose, therefore, in presenting this series is to demonstrate that ascocarps similar to the sporocarps discussed in the Homobasidiomycetes also occur in the Ascomycetes, and, at least superficially, the same type of evolutionary pattern seems to have prevailed. As would be expected, there are numerous genera of apothecial-forming fungi throughout the western mountain ranges. Since there are relatively few large pezizoid apothecia which are truly stipitate, it is not surprising that no stipitate secotioid ascocarps have been found in the region. There are, however, several genera and numerous species of hypogeous Ascomycetes. These ascocarps vary from those in which the initial development is underground but later break free to the surface, such as in *Sarcosphaera*, to those which remain underground during their entire development. One of the most interesting of the hypogeous Ascomycetes is *Geopora*. This fungus produces a relatively large ascocarp in which the hymenium is highly convoluted and labyrinthiform and is more or less enclosed by a sterile peridial covering. Although the ascocarps develop underground, the asci forcibly discharge the ascospores, suggesting that it is only slightly removed from the epigeous series having an exposed hymenium. *Hydnotrya*, like *Geopora*, is also completely hypogeous and likewise has a sterile layer of cells which surrounds the highly convoluted hymenium. It differs from *Geopora*, however, in that the ascospores are not forcibly discharged. In addition, in many of the ascocarps the asci show a tendency to become somewhat irregular in outline. By citing the two genera above it is not meant to infer that they may be closely related. In view of the fact that *Geopora* has hyaline, ellipsoid, smooth-walled ascospores while *Hydnotrya* (at least the common species) has globose spores which are yellow brown and have roughened walls, it is quite possible that they are only distantly related. They do, however, clearly represent different stages in the evolutionary progression toward a hypogeous habitat. The genus *Tuber,* also common in the west, represents perhaps the most advanced type of ascocarp produced by a hypogeous ascomycete. There are no air spaces in the fertile portion. The hymenium no longer exists as a definite organized entity, the asci are nearly globose to variable in shape, and the number of ascospores varies from one to eight per ascus. Thus it seems apparent that a similar sequence of events resulting in similar modifications of the sporocarp has occurred in the "fleshy" Ascomycetes as in the Homobasidiomycetes.

In the foregoing discussion five different evolutionary series have been presented. These were selected because they show significant stages in the evolution of different types of sporocarps and seem to offer some indication of the pathway along which the hypogeous sporocarp might have evolved from an epigeous ancestor. There are additional evolutionary series but in most cases they are not as complete as those given above. Perhaps the missing stages have either not yet appeared or they no longer exist. In the list below are examples of the incompletely known series.

Genus and family of gilled fungi	Genus of stipitate, secotioid fungi	Genus of sessile, hypogeous fungi
Agaricus	Endoptychum Longula	Melanogaster (?) Sedecula (?)
Amanita	Torrendia	
Bolbitiaceae	Galeropsis Setchelliogaster	
Bolbitius	Gastrocybe	
Chroogomphus	Brauniellula	
Coprinaceae	Montagnea	
Gomphidius	Gomphigaster	
Laccaria		Hydnangium
Lepiotaceae	Neosecotium (?)	
Pholiota	Nivatogastrium	
Stropharia	Weraroa	

As would be expected, there are several genera of secotioid or secotioid-like fungi for which no connection with the gilled or other groups of fungi has been determined. Some of these may well have had a different origin and are not members of any series. Below is a partial list of those genera of secotioid fungi for which no convincing connection has yet been established.

Alpova
Balsamea
Battarraea
Chlamydopus
Chondrogaster
Cystangium
Genabea
Genea
Hysterangium
Leucogaster
Leucophlebs
Mycolevis
Octavianina
Phellorinia
Podaxis
Richoniella

In conclusion I would like to give an explanation of why I believe the progression went from an epigeous to a hypogeous habitat and why the sequence went from a typical agaric type of basidiocarp with an exposed hymenium and a ballistosporic type of spore to an enclosed, gastroid type of basidiocarp with statismospores. At the outset it must be kept in mind that I am speaking only of areas with climates similar to the western mountain ranges of the United States where there are extended periods of drought.

1. Initially there was a natural selective process favoring those basidiocarps which offered some protection against the loss of moisture from the hymenium. Perhaps this protection arose from the permanent establishment of arrested stages in sporocarp formation. Such protection would, therefore, be derived from the failure of the pileus to expand and expose the hymenium. Furthermore, constrictions placed upon the hymenophore due to the failure of the pileus to expand would result in the formation of pockets or spaces in the hymenophore which would be effective in maintaining a higher humidity and enhancing spore production.

2. The forcible discharge of the spore could have been lost during any of the various arrested stages; however, it seems to me that this character must have disappeared early in the sequence. If the hymenophore is no longer exposed there is no selective advantage in the forcible discharge of basidiospores. Perhaps when the hymenophore became enclosed the basidia for some reason, unknown at this point, might have lost this dispersal mechanism. At least at the present time there are no Homobasidiomycetes known to me which have retained the forcible discharge of spores when the hymenium is enclosed.

3. With the disappearance of forcibly discharged basidiospores it is apparent that the stipe offered no selective advantage for the survival of the species. Thus perhaps by attrition, if in no other way, it slowly disappeared. Again, it should be pointed out that truly stipitate hypogeous species are very rare. A continuation of the stipe in the form of a columella within the gleba has persisted much longer and many of the hypogeous species possess such a structure.

4. The disappearance of the stipe removed any means by which the sporocarp could be elevated from the soil, thus it became hypogeous.

5. The absence of a differentiated stipe allowed the peridium (epicutis) to enclose the hymenophore and hymenium thereby resulting in the formation of a gastroid type of basidiocarp.

6. The restrictions placed upon the development and elaboration of the hymenophore by the enclosure by the peridium eventually resulted in the formation of a finely lacunose type of gleba.

7. In the case of boletes or Discomycetes the process was essentially the same with allowances being made for differences in hymenium, hymenophore and carpophore.

8. The principal disseminating agent for the spores of secotioid fungi is, obviously, no longer air currents but dissemination is now dependent largely upon animal dispersal. The two most important agents are small rodents (**12**) and insects. Water perhaps plays a minor role, particularly run-off and percolating waters which may carry spores for some distance.

The major basis for the belief that the evolutionary process proceeded in the manner elaborated upon above is the forcible discharge of the spores. It seems to be the most logical and simplest assumption that this character was acquired by an early ancestral type which in turn transmitted it to the various groups of present-day Homobasidiomycetes. Otherwise it would have been necessary for this character to have arisen *de novo* in each of the different evolutionary series. It seems unrealistic to believe that this same character would have been independently acquired in so many different groups of fungi and in so many different series of organisms.

Finally I should like to say that I fully realize that the contributions of this paper will not resolve the controversy regarding the origin and phylogeny of the secotioid fungi. I sincerely hope, on the other hand, that I might have been able to stimulate your interest and curiosity regarding these fungi and to make you more aware of their presence and significance and to alert you to their value as potential research organisms in studies on the evolution of the fleshy fungi.

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