THE LIFE HISTORY AND IDENTITY OF "PATELLINA FRAGARIAE," "LEPTOTHYRIUM MACROTHECIUM," AND "PEZIZA OENOTHERAE"

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(With Plates 8–10 and 5 Text-figures)

During our studies of the causes of decay and spoilage of small fruits in picking, shipping and marketing a number of fungi have been found which have been only recently or not heretofore reported on fruit. The pathological and economic aspects of these organisms will be treated in a separate paper. We would direct attention here to only one point of distinct pathological significance brought out by this study and that is the importance of a full knowledge of the life history, identity, and synonymy of pathogenic fungi. The conidial form of the organism under consideration here was recently recognized as the cause of disease and decay in strawberries in this country, referred to the form genus *Patellina* and described as a new species, *P. fragariae* Stevens and Peterson (1916). Obviously, if this pathogen were really an undescribed species new to this country and restricted to the strawberry, its pathological and economic aspects would be quite different from those of an old and widely distributed organism known to occur on a variety of hosts in three forms, not only in this country, but in Europe and South America, as now proves to be the case.

The present paper treats of the life history, morphology and taxonomy of this particular fungus which has been found frequently by the writers on strawberries and other small fruits and is now shown to occur on a great variety of plants and plant parts. Besides the new information brought out in connection with the interesting life history, morphology and host relations of this organism, there are other facts strikingly illustrated by

the list of synonyms given. Though this list is probably incomplete it shows that the fungus has not only been described under various generic names but that the conidial form has been referred to such widely separated genera as *Dacryomyces*, among the Basidiomycetes and *Sphaeronema* and *Tubercularia* among the Imperfecti. This is an excellent example of the confusion which prevails in the present nomenclature and taxonomy of the ascomycetes. This deplorable condition must be remedied before much permanent progress can be made in systematic mycology.

It has been found that three distinct types of fructification are developed in the life cycle of this fungus. The oldest name which we have yet proved to belong to the first or conidial stage is *Hainesia lythri* (Desm.) v. Höhnel (see *pl. 8*). The second or pycnidial stage, will be referred to as *Sclerotiopsis concava* (Desm.) (see *pl. 9*), and the third or ascogenous stage as *Pezizella lythri* (Desm.) (see *pl. 10, figs. 19–22*).

The first record we have of the conidial form of the fungus in our laboratory is by the late Dr. W. Ralph Jones who secured cultures from *Rubus* in May, 1912, which were referred tentatively to *Patellina*. The fungus was next found on decaying strawberries sent by Mr. G. M. Darrow of the Bureau of Plant Industry from Tennessee. It produced shallow cup-shaped, pinkish-yellow bodies and was doubtfully referred to the genus *Excipula*. In 1915 specimens of decaying strawberries bearing the same fungus were received from Hammond, Louisiana. Several other collections were also received from the same locality the same season. This conidial stage on strawberry was described and figured by F. L. Stevens and A. Peterson (1916) as *Patellina fragariae* n. sp.

During the spring of 1918 the writers found the rot caused by this fungus to be very common on strawberries in the markets of New York City and Washington and a thorough study of the organism was undertaken. The same year what appeared to be the same fungus was found frequently on rotting dewberries at Hamlet, Cameron and other points in North Carolina and at Hammonton, New Jersey. It has also been found on red and black raspberries in the New York markets and is not uncommon

on blackberries in New Jersey. A few sporodochia of the same fungus were found in April, 1920, on old dewberry vines from Cameron, North Carolina, and cultures were readily obtained from this material, showing that the fungus had survived the winter on the old vines.

The material from North Carolina was also found to bear conspicuous brown or black sclerotium-like pycnidia which proved to be *Leptothyrium macrothecium* Fckl. This was reported by Fuckel to occur on a variety of hosts, one of which was *Rubus*. On account of the close association of the *Hainesia* sporodochia and the *Leptothyrium* pycnidia and the great similarity of the spores of the two forms a possible genetic relation was suspected. If this was true the *Leptothyrium* stage, being evidently of a more persistent and resistant character than the other, might be the means of carrying the fungus over the winter. It may be noted here that cultures from these pycnospores produced typical conidial sporodochia. The pycnidial stage was also produced at will on leaves and stems of *Rubus* and other plants by spraying with a suspension of conidia.

Assuming that this fungus had but two lower spore forms it now remained to find the ascogenous stage. If any similarity in form was to be expected between the pycnidium and the ascocarp, *Hypoderma* might perhaps be suggested on account of its slight superficial resemblance to the pycnidia and its occurrence on some of the dewberry canes. On the other hand the sporodochia suggest in form a possible small discomycete of similar appearance. The discovery a little later of a small amber-colored discomycete on old leaves of raspberry at Arlington Farm, Virginia, July 24, closely associated with both sporodochia and pycnidia was immediately followed by pure cultures from ascospores which proved the genetic relation of the three forms. A search of literature and herbaria showed that a discomycete apparently agreeing in all respects with the one found on raspberry leaves, had been described as *Peziza* (Mollisia) *oenotherae* C. & E. (1878) and distributed as No. 846, Ellis and Everhart, N. A. F. and 244 Fun. Col. All three forms were found occurring together on stems of *Oenothera biennis* on the same herbarium specimen of No. 244

in the New York Botanical Graden and several other herbaria. The conidial stage was named *Sphaeronema corneum* C. & E. (1878) and distributed as No. 2074, E. & E., N. A. F. and the pycnidial stage was distributed as *Leptothyrium protuberans* Sacc. No. 733, E. & E., N. A. F.

CULTURES AND INOCULATIONS

The small, curved, hyaline spores of both conidial and pycnidial stages are produced abundantly and are easily recognized. As they germinate readily on all ordinary nutrient media, it is not difficult to obtain pure cultures by the poured plate method. On two per cent cornmeal agar the young colonies show a white mycelium, the branches of which unite in fascicles projecting above the surface of the agar. The sporodochia appear on poured plates about the third day and in test tube cultures about the fifth or sixth day. In both tubes and petri dishes they are frequently arranged concentrically. In old cultures on potato agar the sporodochia become brownish or almost black. On four per cent potato dextrose agar there is much greater aërial growth of mycelium and very small white sporodochia are formed in the water of guttation while those below on the agar are brown, especially when old.

Cultures of the conidial stage were obtained from strawberries in the market and inoculation experiments were carried out to determine whether the rot could be readily produced by artificial inoculations. As it is impracticable to thoroughly sterilize the surface of berries, clean, fresh fruit was chosen, the berries set on the calyx end in damp chambers and inoculated at the tip. A drop of water containing conidia was simply placed on the end of the berry or the epidermis punctured with a needle, or rubbed lightly. The controls sometimes developed sporodochia, especially those which had been punctured. The sporodochia originate subcuticularly or intraepidermally. Berries that are inoculated by puncturing will always develop sporodochia unless *Rhizopus* appears at once and prevents. The results of a large number of experiments show that only a slight injury to the epidermis is necessary to bring about infection but we have no proof

that the germ tubes are able to penetrate the uninjured, normal cuticle of the strawberry.

As the skin of many berries is usually injured and insects probably carry spores from berry to berry, it is frequently only necessary to provide moisture to insure development of sporodochia. It was found to be much more satisfactory to carry on this work with blackberries and dewberries as individual carpels could be carefully inspected before inoculation. The same experiments were carried out on these berries with strains of the fungus found on the berries in nature. The fungus spreads to carpels adjoining the one inoculated but slowly. Over-ripening brings about a softening or breaking of the cuticle so that such carpels become infected following surface inoculation. Berries in boxes were sprayed with a suspension of conidia, shipped from North Carolina to New York City and then placed in damp chambers. They developed large numbers of sporodochia. Boxes of berries similarly treated except that hulls were left on in picking, arrived in excellent condition and very few sporodochia could be found even after the berries had been left several days in damp chambers. The injury to the fruit caused by pulling off the hull apparently provides opportunity for the entrance of the fungus as berries picked with the hulls on are certainly not so susceptible to this and other fruit rot fungi which are not able to penetrate the unbroken cuticular layer.

It is also a question whether this fungus is able to penetrate the cuticle and epidermis of a normal living leaf. It is likely in most cases where sporodochia are found on living leaves that some injury has occurred to the epidermis. There is frequently evidence of insect injury in such cases. Under favorable conditions the fungus having gained entrance to the tissue appears to be able to spread to the adjoining tissue so that the spots become larger and quite characteristic as noted by Halsted (1893) on *Rhus* and Massalongo (1908) on leaves of *Rubus,* also by Stevens and Peterson (1916) on fruit of strawberry. The pycnidial stage is seldom found on living leaves but Massalongo noted that it sometimes occurs on spots on *Rubus* leaves. Both stages occurred very abundantly here during August and September,

1920, on decaying leaves of host plants cut earlier in the season. On such old leaves sporodochia are apt to be overlooked because of their very minute size. In some cases none is present though the pycnidia are very abundant.

There appear to be no morphological differences between the strains of the conidial form found in nature on fruits of species of *Fragaria* and *Rubus*. Many cross-inoculation experiments from one to the other have shown conclusively that the fungus can be readily transferred from the fruit of one of these hosts to the other.

Strains from dead spots on living leaves of *Fragaria, Rubus, Oenothera, Acer, Epilobium, Cornus, Smilax,* five species of *Rhus* and dead leaves of *Vitis,* and from the fruits of *Fragaria* and several species of *Rubus* show practically identical characters in culture.

The pycnidium is frequently one millimeter in diameter and as the wall is thick and composed of thick-walled cells it can be easily handled and thoroughly sterilized before being crushed out to obtain spores for cultures. When plated out and grown on the ordinary culture media sporodochia in no way distinguishable from those of *Hainesia* appear on the surface of the medium in three or four days. Such cultures have been isolated many times from the dark, heavy-walled pycnidial form on dewberry, strawberry, sumac, evening primrose, and other hosts and there can be no question of their being the pycnidial form of the same fungus that first appears as sporodochia of the *Hainesia* type.

The various agar media upon which the fungus has been grown do not appear to be favorable for the development of the pycnidia although they are occasionally produced in agar. The fungus grows well on the cut surface of apples and produces sporodochia, some of which resemble a broadly ostiolate pycnidium (*pl. 8, fig. 6*).

Strains of the *Hainesia* form isolated from a number of different hosts were grown on sterilized stems and leaves of blackberry in large test tubes. These cultures produced vast numbers of sporodochia within a week or two and then began to produce large, brown pycnidia of the *Sclerotiopsis* type.

So far as observed none of the cultures carried through under sterile conditions in petri dishes or test tubes has produced the perfect (*Pezizella*) stage. However, inoculation of wild blackberry leaves and stems under natural conditions in the woods produced all three forms. On May 20, 1920, living leaves and stems were punctured, then sprayed with a spore suspension of a strain of *Hainesia* originally obtained from dewberry. The tissue soon began to die about the points of inoculation and by the middle of June sporodochia were very plentiful on the spots. As the leaves died during July and August typical pycnidia and discocarps of *Pezizella oenotherae* began to appear in abundance on the dead leaves, petioles, fruit stalks and small branches. The perfect and pycnidial stage continued to develop slowly down to the larger branches and stems during September. While it is not claimed that the perfect stage might not have arisen from natural infections in this case, the experiment shows that it develops on leaves and branches of the season's growth and that it is unnecessary for the vines to lie over winter in order that, as is supposed with many ascomycetes, the ascocarps may mature in the spring and spread new infection. The ascospores of this *Pezizella* are set free or dispersed as soon as mature and germinate readily. The problem of over-wintering seems to have been provided for to a large extent by the thick-walled closed pycnidium. It is certain that many of these pycnidia pass through the winter unopened although filled with spores which will readily germinate in April.

Leaves petioles and runners of cultivated strawberry in a garden were inoculated in the manner described above with similar strains of *Hainesia,* May 20. Brown spots formed about the injured places and sporodochia began to appear within three weeks. By July 25 both sporodochia and pycnidia were abundant on the dead leaves of these and other plants in the same plot. No ascocarps of *Pezizella* were found.

Several leaflets of *Rhus glabra* were treated in the same manner August 5. On August 20 it was noted that many inoculated leaflets on this plant showed dead areas with typical amber-colored sporodochia. Leaf hoppers had by this time injured

many leaves on this plant and infection had spread naturally also. As the leaves died and fell to the ground they began to develop pycnidia. The perfect stage has not yet been found on *Rhus*.

Sclerotiopsis pelargonii Scalia has been reported on *Pelargonium* leaves. As it was impossible to obtain a specimen of this species to compare with the pycnidial stage of *Pezizella* which according to the description it appears to resemble closely, several leaves of rose geranium (*Pelargonium capitatum*) were inoculated by puncturing and spraying with conidia obtained originally from a single ascus culture from *Pezizella oenotherae*. The plant was kept under a bell-jar for four days and well aired and sprayed with water. Blackish streaks soon began to spread along the veins of several of the leaves where punctured. On September 11 sporodochia of *Haniesia* appeared and on September 14 most of the infected leaves bore typical pycnidia of *Sclerotiopsis*. A comparison of these pycnidia with *Sclerotiopsis pelargoni* Scalia will be made later. Scalia drew his description from specimens which developed on leaves kept in a damp chamber and does not mention finding any other form of fungus on the leaves.

On September 5, Dr. Neil E. Stevens found at North Livermore, Maine, on living leaves of *Epilobium spicatum* spots bearing sporodochia of *Pezizella*. Cultures made from this form differed in no way from those from other hosts. The leaves bearing conidia were placed in damp chambers from September 9 to 14 when they showed an abundance of the pycnidial form of the fungus. If leaves of any one of the host species upon which sporodochia are found are placed in a damp chamber for a week or two and kept fairly moist, pycnidia usually develop.

A hill of dewberries at Cameron, N. C., sprayed with conidia from dewberry, May, 1919, showed no signs of sporodochia on leaves or stems during the next two weeks, although berries picked from this hill developed many sporodochia. These vines were cut in July, kept in a warm, dry laboratory until April, 1920, and then placed on the ground in the woods. On July 25 they were examined. The leaves, fruit stalks and many of the

small branches bore an abundance of discocarps of *Pezizella oenotherae* and also typical pycnidia and sporodochia of the same. During the latter part of August pycnidia began to appear on the larger stems and in September these pycnidia could be found even at the base of the vines. It is not unlikely that the fungus winters over in this condition as many unruptured pycnidia can be found on vines collected in the field in April, too early for them to have developed during the spring. Spores taken form these overwintered pycnidia germinated readily.

It is rather difficult to obtain large quantities of ascospores of *Pezizella oenotherae*. Noting that spores still within the ascus germinated readily, apothecia were crushed in water and the young asci separated so that when small drops were placed on the surface of agar media the spread of the water was sufficient to separate the asci, care being taken to secure the proper dilution. By marking a number of spots on the petri dishes the separate asci could be located after germination had begun. The ascospores are so nearly the size of the conidia that they might otherwise be easily confused. In order to avoid this, only asci with germinating spores clearly distinguishable were transferred. Several dozen single ascus cultures were made at this time and in all about two hundred pure cultures in plates and tubes were obtained from asci. Without exception all produced sporodochia agreeing with *Hainesia*. Twenty-five single ascus cultures were made from two apothecia on raspberry leaves from Arlington Farm, Virginia, July 23, and 110 tube cultures from ascospores on the dewberry vines first sprayed with conidia at Cameron, N. C., May 26, 1919, and kept on the ground in the woods at Radnor, Virginia, from April 15 to July 26, 1920. The culture work here summarized proves conclusively the genetic connection between the three forms of fruit bodies described.

MORPHOLOGY

The morphological features of the *Hainesia* stage of this fungus have been fairly well described by the authors of the various specific names which have been applied to it. Stevens and Peterson (1916) have noted the variation in form, color and size of

the conidial fructifications as they appear on rotting strawberries and figured some of the essential features. Saccardo (1881) figures conidia and branched conidiophores.

I. CONIDIAL STAGE, HAINESIA LYTHRI (Desm.) v. Höhn.

By some writers these conidial fructifications are called pycnidia, by others acervuli and by still others sporodochia. There is great need of a thorough comparative study of the development and morphology of the various forms before a terminology can be applied which will indicate the true nature and relationships of different sporocarps that occur. Such studies made in connection with the life histories of the organisms should prove very helpful in determining the phylogeny and classification of the ascomycetes. For the purposes of this paper the conidial fructification of this fungus will be called a sporodochium. The fructification of *Hainesia* is a small disc-shaped body with a distinct excipulum-like base similar to that found in the apothecium of many discomycetes. It seems to the writers that this stage might well be placed among the excipulaceous fungi in the system of Saccardo. Considering only the variations of this one stage it will be shown that the fruit body assumes a variety of forms, some of which might be considered sporodochia of the *Tubercularia* type, while others approach true pycnidia with more or less clearly defined, broad ostioles.

In size the structures vary from a few conidiophores united in a fascicle with a minute globule of spores at the top, to a disc-shaped body 1 mm. in diameter which is readily visible to the unaided eye. The color may be brown, white, black, pink, yellow, amber, or golden depending upon the host or medium upon which the fungus is growing, the age of the culture, or other conditions of environment. The most common color when dry is some shade of amber. When wet they appear white from the mass of hyaline spores that gathers in a droplet of water and covers the disc. Though ordinarily disc-shaped or patellate the sporodochia may be elongate and slender or even cylindrical. Such forms when dried and capped with a pointed mass of spores were mistaken by Cooke and Ellis for a *Sphaeronema* and described as

S. corneum (1878). When the spores of the flat types spread out so that the spore masses coalesce a *Hymenula* is suggested, as *Hymenula rhoina* (1893) (Ell. & Sacc.), Bub. & Kab. (1912), or a *Tubercularia* as interpreted by Halsted (1893) (*T. rhoina* Halsted). Ordinarily nothing which might be called a stipe is present, yet forms are met in nature and in cultures on twigs of *Rubus* in which there is a distinct stipe-like base surmounted by a flaring disk (*pl. 8, fig. 7*).

The outer wall of the sporocarp is but a few cells thick. These cells are thin-walled and nearly isodiametric. Toward the margin the cells are arranged in more or less parallel rows and become considerably elongated and branched. Very long, branched slender paraphyses-like hyphae line the cup portion and extend even beyond the margin, sometimes producing a fimbriated edge (*pl. 8, fig. 10*). These structures appear in no way to differ from the conidiophores in their morphology, as they are found among the sporophores in young fruit bodies. The spores are borne terminally and become quickly detached, but cohere in a mass which becomes elongated and cone-shaped in case the spores are not washed away or there is not enough moisture present to lead to the formation of the trembling drop on the sporodochium which no doubt suggested the name *Glocosporium tremellinum* to Saccardo. In nature very small sporodochia may develop on old, dead plant parts and in culture they form in the water of guttation where there is an abundance of aërial mycelium formed. These fruiting bodies, consisting of a few conidiophores united together, are clearly gymnocarpous and of the *Tubercularia* type, being open from the very beginning. They scarcely resemble the large patellate, urceolate or flack-shaped structures commonly collected (*pl. 8, figs. 1–4*). The amount of margin or the depth of the cup may become so great as to form a globose or pear-shaped structure which in no way differs from a true pycnidium with a large ostiole through which the spores ooze in a broad cirrhus (*pl. 8, figs. 6, 9*). In normal forms in nature most of the dark color is confined to the basal portion. The margin is at first inrolled (*pl. 8, fig. 5*), later becoming expanded and frequently revolute and lobed (*pl. 8, fig. 2*).

The conidia borne on simple or sparsely branched sporophores (*text-fig. 1*) are hyaline or only very slightly colored as seen under the microscope. In mass, however, the color is as variable as that of the sporodochium—white, pink, yellow, amber, brown, or blackish, depending upon the nature of the host, medium, moisture, age or other conditions. The usual color when dry is a

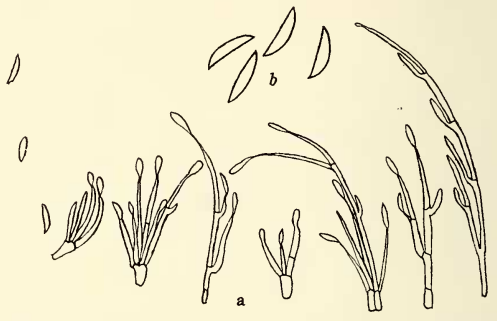

FIG. 1. a. Various types of sporophores of *Hainesia lythri*. × 700. b. Spores more highly magnified. × 1200.

light amber. The terms lunate, allantoid, curved and navicular have been used to describe their shape. Stevens & Peterson (1916) say they are straight or slightly convex on one side and concave on the other. Massalongo (1889) calls the pycnospores, which are the same shape as the conidia, navicular, and his drawings (l.c., *pl. 10, figs. 19–21*) suggest a boat or canoe viewed from the side as it floats on the water. Others describe them as straight with the ends sharply and obliquely angled. None has mentioned the small oil droplet frequently attached to one or both of the sharply pointed ends.

The conidia are remarkably uniform in size and shape. The average size is about 6–9 × 1.5–2 μ. Saccardo's record (1881) of 10–12 μ long for the spores of *Gloeosporium? rhoinum* is evidently an error judging from the magnification indicated and also from the spore measurements of *Hainesia rhoina* (Sacc.) Ell. & Sacc., No. 2278, E. & E., N. A. F., the spores of which are 7–8 × 1.5–2 μ.

II. Pycnidial Stage, Sclerotiopsis concava (Desm.) n. comb.

The pycnidial form has been most frequently referred to *Leptothyrium macrothecium* Fckl. A study of the type of the genus *L. lunariae* Kze., however, shows that this species is not congeneric with it. In further search for a generic name it was found that the genus *Sclerotiopsis* of Spegazzini was based on the same species as ours. His type *S. australasica* proves indistinguishable from *Leptothyrium macrothecium*. *Sclerotiopsis* is the oldest unquestionable generic name we have found for the pycnidial form. The pycnidium is a large, closed, shield-shaped or depressed, pulvinate body which is packed with an enormous number of spores. Like the sporodochial stage this fruit body arises intra-epidermally so that as growth continues the cuticle together with the upper wall of the epidermal cells is stretched and pushed up until a shield-shaped or pulvinate body is formed, entirely covered by the upper part of the epidermal layer. On dewberry canes the epidermis may split at the center or in a line along the center. On leaves and large stems these pycnidia are nearly circular in outline often collapsing at the center on drying. This is the condition which suggested the specific name "*concava*" to Desmazieres.

The color varies with the age of the pycnidium, being at first gray to argillaceous, then light brown. Mature specimens are shining chestnut brown or almost black. These changes of color are well shown on leaves of *Epilobium*. As carbonization of the cell walls progresses the color approaches more nearly chestnut brown. On a substratum such as the blackberry cane the pycnidium is very smooth and shining, a feature not noticeable where the epidermis, such as that of a young *Oenothera* or *Quercus* leaf, is rough or covered with fine hairs. The pycnidium, being intra-epidermal, is long covered by the cuticle and cuticularized layer of the epidermis (*pl. 9, fig. 17*). The outer wall of the pycnidium is composed of small polyhedral thick-walled brown cells, the outer ones being somewhat flattened and brick-shaped. The inner ones have much thinner walls and are more angular, forming a rather broken or jagged border line. The basal or lower wall is made up of at least three distinct tissues. The first lying next to

the host cells below is composed of small thin-walled cells. Above this is to be found a dark layer composed of rather larger, polyhedral cells. This becomes thinner toward the margin which would appear to offer a favorable place for the pycnidium to rupture, but so far as observed marginal dehiscence does not occur. Above the middle layer lies that from which the conidiophores originate. It is composed of small, thin-walled, colorless cells (*pl. 9, fig. 16*).

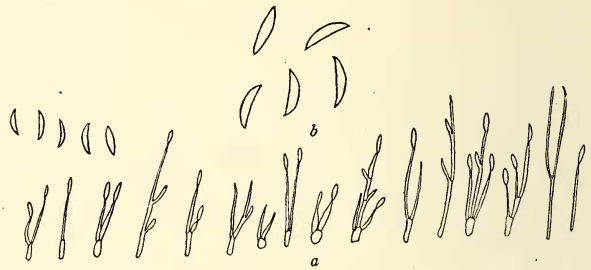

FIG. 2. a. Sporophores of *Sclerotiopsis concava*. × 700. b. Spores more highly magnified. × 1200.

In mature pycnidia the sporophores form a palisade-like layer covering the base of the pycnidium. They are 10–20 × 1 μ, frequently with short lateral branches (*text-fig. 2*). The spores are hyaline or faintly chlorine colored 6–9 × 1.5–2 μ. In old ruptured pycnidia the spores in mass may approach olivaceous. They are borne apically on the terminal and lateral branches, sometimes slightly adhering in chains as noted by Massalongo; but not ordinarily found in that condition as the spores usually separate as fast as they mature. They are boat-shaped, curved, acute, oblique-angled, convex on one side, slightly concave on the other. In keel view they are fusoid.

No ostiole is formed and the dehiscence of the pycnidium is often delayed until spring. It may occur, however, within a few weeks after maturity if the weather is very moist. The rupture of the epidermis should not be confused with the splitting of the wall of the pycnidium. In oblong forms on small branches, the rupture may extend in a single line from end to end (*pl. 9, figs. 14, 15*). In the circular types there are usually three or four cracks extending from the center toward the margin. The an-

gular segments thus formed (*text-fig. 3*) turn up or fold over exposing the spores which are quickly dispersed when wet, as they are surrounded by a mucilaginous substance which swells very quickly on addition of water and causes the spores to be pushed out and spread just as they are from the sporodochia.

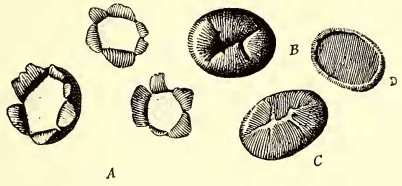

Fig. 3. Pycnidia of *Sclerotiopsis concava*. a. Three pycnidia showing characteristic dehiscence. b. Pycnidium after having discharged all of its spores and dried. c. A pycnidium just previous to spore discharge. d. Pycnidium after spore discharge and the breaking away of the segments of the wall.

III. Ascogenous Stage, Pezizella lythri (Desm.) n. comb.

The ascogenous stage has been found from the latter part of July to October. So far as known at present the discocarps were first described by Cooke & Ellis (1878). Ellis collected the specimens on *Oenothera* in August. They occur frequently associated with the other stages on dead leaves, petioles, fruit stalks and small branches of *Rubus,* and are especially abundant on the "bark" at the base of stems of living *Oenothera* and on the midrib and petioles of *Steironema.* They are most easily seen in the morning when the dew is on or after a rain when all the plant parts are wet. The disc then appears white, about ½–1 mm. in diameter and flat. The sides and short stalk-like basal portion are light-brown or amber colored. When dry they may retain the flat disc-shape, or the margin may become somewhat involute. In the latter condition they closely resemble the amber colored, hard resin-like dried sporodochia which are frequently found side by side with the discocarps. The pycnidia are not uncommonly found on the same specimens with the other two forms. Ellis evidently sometimes mistook the large dried sporodochia for the *Pezizella* stage on stems of *Oenothera* which he distributed as No. 846, N. A. F. On the specimens of this number in the herbarium of the U. S. Department of Agriculture there

are several large amber colored sporodochia of *Hainesia* and not a single ascocarp of the *Pezizella*. The white appearance of the apothecia when moist is due mostly to the presence of a mucilaginous substance including large quantities of small globules. Addition of water produces a sort of emulsion which spreads in a white layer over the flat disc. This epithecial substance may occur as the result of the disorganization of the upper ends of the paraphyses which in young ascocarps extend somewhat above the ends of the asci. The photograph (*pl. 10, figs. 19, 21*) shows some of this substance that persisted through the imbedding and sectioning processes.

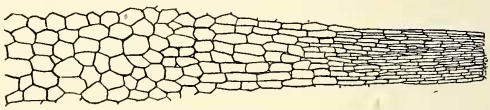

FIG. 4. Semi-diagrammatic view of a portion of the margin of the discocarps.

The stipe-like basal portion and the side walls of the apothecium are composed of a pseudoparenchymatous (plectenchymatous) tissue of light brown cells. At the margin the cells elongate forming a border of narrow cells arranged side by side (*text-fig. 4*). In view of this peculiar border or margin it is very likely that the apothecium is not "at first closed," strictly speaking, but from the appearance of the young fruit bodies as they break through the upper wall and cuticle of the epidermis they would commonly be said to be "closed at first then opening irregularly." Whether the apothecium has a true stalk may be questioned. Sections show the base to be variable, in some cases at least stalk-like (*pl. 10, fig. 22*), and at others simply tapering downward and funnel-shaped. Perhaps the shape of the apothecia of those species placed by Boudier (1910) in the genus *Micropodia* best represents the condition found here.

The asci are cylindrical, about 55–70 × 7–8 μ (*text-fig. 5*). The apex is not colored blue by iodine. Sections show that the ascus is truncate at the apex and would probably be called marginate by Boudier, although this does not show at all in specimens crushed out on a slide.

The ascospores are straight or slightly curved, occasionally

somewhat enlarged at one end, $8 \times 2\,\mu$, uniseriate when young becoming biseriate when mature especially toward the apex (*pl. 10, fig. 21*). Spore dispersal is certainly not by "puffing" and air currents. The walls of the asci appear to deliquesce rapidly and it may be that insects and water are the chief agencies for the distribution of the ascospores. The paraphyses are narrow

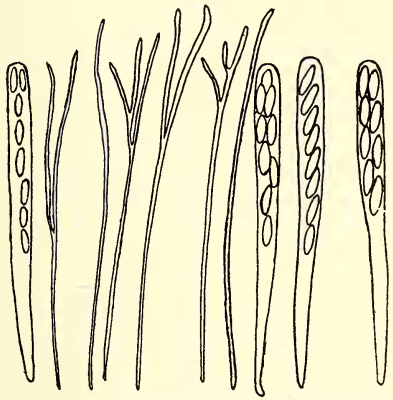

Fig. 5. Asci and paraphyses. *Pezizella lythri.* × 920.

linear 60–70 × 1–1½ μ, simple or branched, at first extending above the level of fully developed asci. The tips spread out and disorganize, giving rise to the "epithecium" which is composed in part of the mucilaginous products of this disorganization (*pl. 10, fig. 21*).

A comparison of the fruit forms of this species of fungus shows that the sporodochia and discocarps are so similar in their texture, size, color and general appearance as to be easily confused when dry. Even in this condition, however, they can be distinguished with a fair degree of certainty with a good lens as the mass of conidia usually forms a heap giving a pulvinate or conical shape to the top of the sporodochium; whereas the discocarp does not retain such a spore mass and is nearly plane or somewhat concave. They are readily distinguished in wet weather or when a drop of water is put on the surface of the fruit body. Under such conditions the conidia collect in a large droplet which maintains its form in whatever position the sporodochium be placed. Such a drop never collects on the surface

of the discocarp when wet. All three forms of fruit bodies ordinarily arise intra-epidermally. With the growth of the apothecium the basal portion may extend downward so that the lower portions of the epidermis become surrounded by cells of the fungus and are lifted up as the point of attachment elongates (*pl. 10, fig. 22*). The intra-epidermal habit is apparently quite fixed even when the leaf is covered with hairs. Sections through pycnidia on leaves of *Pelargonium* show that while the coarse, pointed hairs as well as the short, glandular hairs are raised so as to stand out like bristles on the wall of the pycnidium, yet the fungus is found to have invaded the lumen of the lower part of the hairs to a remarkable extent.

SYNONYMY

In view of the occurrence of three distinct types of fructifications in the life history of the fungus under discussion and considering that one or all of these forms may be found on a large number of host plants, either living or dead, some of which are distantly related; it is likely that the synonymy given here is not complete. This synonymy is based primarily upon a careful study of type or authentic specimens of most of the species discussed and on an abundance of fresh and herbarium material from various localities and hosts. A few probable synonyms based upon comparison of original descriptions only have been given. These are indicated in the list.

I. CONIDIAL STAGE, HAINESIA LYTHRI (Desm.) v. Höhn.

DACRYOMYCES LYTHRI Desm. The oldest name we have positively identified as belonging to any stage of this fungus is *Dacryomyces lythri* Desm. In 1846 Desmazières described this species on the label accompanying No. 1545 of his Pl. Crypt. France Ser. I. A careful study of the fungus distributed under this number from three sets, two in the herbarium of the Department of Agriculture and one in the New York Botanical Garden herbarium, shows that it is identical with the conidial stage of the *Pezizella* described here. Von Höhnel (1906 and 1918) had already pointed out that Desmazières' plant is a true *Hainesia*. It may

seem remarkable that this form should have been referred to *Dacryomyces,* which is now well understood to be a genus of Basidiomycetes. It must be remembered, however, that at the time this species was described, careful microscopic studies of these organisms had not been made and the reference to this genus was probably based upon the slight superficial resemblance which large sporodochia of this fungus have to the fructifications of certain small species of *Dacryomyces.*

Sphaeronema corneum C. & E. The next description of the conidial stage which we have positively identified is under the name *Sphaeronema corneum* C. & E. (1878). The original description is brief and one would scarcely think from reading it that it applied to our fungus. It was said to have "cylindrical perithecia." A study of authentic specimens on stems of *Oenothera,* however, issued by Ellis & Everhart in N. A. F. No. 2074, shows that there is no fungus on these specimens, either the one in the herbarium of the Department of Agriculture or in the New York Botanical Garden habarium, agreeing with the usual generic characters attributed to *Sphaeronema.* There are, however, small sporodochia of *Hainesia* present with typical spores of this form. There is also found with the specimen of *Peziza oenotherae* E. & E., N. A. F. No. 846, a note on the label stating that this species is accompanied by *Sphaeronema corneum,* E. & E. on the same specimens. Here we also find well developed sporodochia of *Hainesia* but no trace of a true *Sphaeronema.* It seems certain, therefore, that the fungus to which Cooke & Ellis applied the name *Sphaeronema corneum* is none other than the conidial stage of *Pezizella lythri* and its reference to *Sphaeronema* was evidently due to the superficial resemblance of the sporodochia to the pycnidia of *Sphaeronema;* as has been already referred to in describing the morphology of this stage (p. 144).

Gleoesporium ? tremellinum Sacc. This was found on leaves of *Acer campestris* in Europe and first described by Saccardo (1880). The long branched sporophores lead him to insert the question as to its belonging to *Gloeosporium.* Later (1884) he referred it to *Hainesia* as *H. tremellina.* His figures (1881) and his description agree so well with the conidial form

of *Pezizella lythri,* as found on *Acer* in America, that there can be little doubt of its identity. We have, however, seen no authentic specimens of Saccardo's species.

GLOEOSPORIUM? RHOINUM Sacc. This species found on leaves of *Rhus glabra* in Italy and figured by Saccardo in 1881, was later (1882) described by him. Still later (1884) this was made the type of a new genus *Hainesia* by Ellis and Saccardo. Specimens collected by Ellis on *Rhus* in New Jersey are also cited by Ellis & Saccardo in the description of the species. The spore measurements given with the original figures and descriptions are 10–12 × 3 μ. This may be an error. There is a possibility, however, that Saccardo had another species of *Hainesia* with larger spores, as we suspect that one of this character does occur on *Rhus,* from the fact that there is on *Rhus cotinus* a *Sclerotiopsis* having larger spores, which has been described as *Leptothyrium rhois* West. by Fuckel (1870) but is not Westendorp's species. Saccardo has proposed the name *Gloeosporium rhois β fuckelii* for Fuckel's plant. This, according to Fuckel's specimen, which we have examined, is a true *Sclerotiopsis* closely related to *S. concava.* The conidia in Ellis' specimens on *Rhus copallina* in his herbarium and *Rhus aromatica* in N. A. F. No. 2278 are only 6–8 × 1.5–2μ. Von Höhnel (1918) also found the spores from European specimens on *Rhus* to 7–9 × 1.6–1.8 μ. Except for the measurements given, the figure and description of *Gloeosporium*? (*Hainesia*) *rhoinum* Sacc. agree perfectly with *Hainesia rhoina* Ellis & Sacc. Authentic specimens in Ellis' herbarium show that this is the same conidial form that is commonly found on several species of *Rhus* and other hosts in this country. In a later paper (1918) von Höhnel states that *Hymenula rhoina* (Ellis & Sacc.) Kab. & Bub. on *Rhus cotinus* is identical with specimens of *Hainesia rhoina* on *Rhus glabra* from Italy and North America. Von Höhnel finds the spores in Kabat's specimens Fun. Imp. 749, to be 7–9 × 1.6–8 μ and not as given by Saccardo (1882) and by Bubák and Kabát (1912). The latter authors state that the spores are 6–10 × 2.5–4 μ but in a later paragraph in the same paper the measurements are given as 6–16 × 2.5–4 μ. It appears clear that this is a typographical error, the "6" in "16" being used by mistake instead of "0."

Tubercularia rhois Halsted. This species collected by F. L. Stevens on *Rhus radicans* at New Brunswick, N. J., and issued and described in Seymour & Earle, Economic Fungi No. 273, May, 1893, is the same fungus that was later described by Stevens & Peterson as *Patellina fragariae* on fruit of cultivated strawberry and is identical with *Hainesia lythri* (Desm.) v. Höhn.

Hainesia epilobii Eliasson. We have seen no specimens of this species but the description (1897) agrees with *Hainesia lythri* as found on *Epilobium* in this country.

Hainesia castaneae Oud. This species on *Castanea vesca* and *H. rostrupii* Oud. (1902) on *Quercus rubra* according to the original descriptions agree very closely with *H. lythri* except for slightly thicker conidia, and are probably identical. Authentic specimens, however, should be examined in order to verify this.

Tubercularia zythioides C. Massal. (1908). No authentic specimen of this species has been seen but judging from the original description and its association with a pycnidial form, *Sclerotiopsis rubi* C. Massal. which is apparently identical with *Sclerotiopsis concava,* this conidial form is the same as *Hainesia lythri.* The fungus was found on leaves of *Rubus caesius* in Italy and the author suggested that the fungus might be the conidial stage and the accompanying *Sclerotiopsis* the pycnidial stage of some unknown ascomycete. The present investigations have verified this prophesy in every particular.

Patellina fragariae Stev. & Pet. (1916). Authentic specimens of this species kindly supplied by Dr. Stevens and carefully compared and grown in culture leave no doubt that it is identical with *Hainesia lythri* (Desm.) v. Höhn. The form from strawberry is shown (*pl. 8, figs. 3, 4*).

II. Pycnidial Stage, Sclerotiopsis concava (Desm.) n. comb.

This is the earliest name as yet positively connected with the pycnidial stage of *Pezizella lythri.* During the winter following the discovery of his "*Dacryomyces*" on *Lythrum,* Desmazières found on dêcaying leaves of *Rosa,* the branches of which had been cut the preceding summer, a fungus which he described as *Ceuthospora concava* (1847). An examination of his specimens

of this fungus in Pl. Crypt. France Ser. I, No. 1625 shows that there is a single cavity in the pycnidium as he stated and that there is no stroma, hence it could not be correctly referred to *Ceuthospora* whose type is *C. phacidioides*, which has a clypeate stroma enclosing several distinct pycnidia. However, like so many genera this was poorly defined and contained a group of very diverse species not congeneric. Desmazières' fungus proves to be identical with the pycnidial form of *Pezizella lythri* found on *Rosa, Rubus* and other hosts. Since this is the oldest specific name yet known to have been applied to the pycnidial form, it may be called *Sclerotiopsis concava* (Desm.) n. comb. The pycnidial form of *Pezizella lythri* is referred to the form genus *Sclerotiopsis* of Spegazzini (1882) because it is identical with his monotype of the genus, *S. australasica*, as shown by careful study of an authentic specimen of Spegazzini's species preserved in the herbarium of the New York Botanical Garden. Diedicke (1911) basing his interpretation of this genus apparently on that of Allescher (1901) and on *S. cheiri* described by Oudemans, and other forms previously referred to Phoma, revises the original diagnosis and includes several species with multilocular stromata clearly not congeneric with Spegazzini's type. V. Höhnel (1914) has already pointed out Diedicke's error in the interpretation of *Sclerotiopsis*. The latter's mistake might perhaps have been avoided if the type method of applying generic names had been followed and the application of Spegazzini's genus restricted to species congeneric with his monotype, *S. australasica*. Of course even then one might have such broad views of generic limits as to include forms having large multilocular stromata; but it seems best to the writers to keep such forms separate until more is known about the constancy and taxonomic value of such characters and the life histories of the organisms. On a basis of a comparison of morphological characters, one might be justified in regarding *Pilidium* Kunze (1823) as a synonym of *Sclerotiopsis* and in substituting Kunze's name for this pycnidial form. The monotype of Kunze's genus, *P. acerinum* Kze. (not *Leptothyrium acerinum* attributed to (Kunze) Cda. as found in some exsiccati, *e.g.*, D. Sacc. Myc. Ital. Nos. 762 and 974) is almost if not quite

identical in the structure of the pycnidium and scarcely differs from *S. concava* in any way except in the shape and size of the spores.

Leptothyrium macrothecium Fckl. Fuckel (1870) described this species from leaves of *Rosa, Potentilla, Quercus,* and *Rubus* in Germany. Specimens in his exsiccati, Fun. Rhen. Nos. 551, 553 and 1714 on leaves of the first three hosts respectively and others on leaves and stems of *Rubus* from Fuckel's herbarium have been examined. The specimens are identical with *Sclerotiopsis concava* (Desm.), the pycnidial form of *Pezizella lythri* found in America on a great variety of hosts. *Leptothyrium macrothecium* has been figured by Saccardo (1881) and by Laibach (1908). The latter has an excellent figure of a section of a pycnidium showing the character of the thick wall and a palisade-like layer of conidiophores extending across the base of the pycnidium. Laibach makes no mention of finding a conidial fungus corresponding to the *Hainesia* stage associated with the pycnidia.

No. 552, Fun. Rhen. was originally labeled *Leptothyrium macrothecium* f. *rhois* in Fuckel's herbarium. This form resembles the species superficially except that the surface of the pycnidium is somewhat rugose. The spores are 14–15 μ long. Noting these differences Fuckel later (1870) referred the fungus to *L. rhois* West. Westendorp's plant, however, as already pointed out (p. 154) is quite different from Fuckel's. Fuckel's form *Rhois* is not a *Gloeosporium* as stated by Saccardo (1884). The fungus agrees in all morphological characters except spore measurements with *L. macrothecium* and seems undoubtedly congeneric with it. Typical *L. macrothecium* has been frequently found on both native and introduced species of *Rhus* about Washington, but we have never found the form with large spores described by Fuckel. The occurrence of this second species of pycnidial fungus on *Rhus* seems to justify the belief that it belongs to a discomycete congeneric with *Pezizella lythri* and probably has a conidial form similar to *Hainesia lythri.* A pycnidial fungus very similar, if not identical, with this is *Pilidium acerinum* Kze. which occurs in Europe on *Acer* and *Carpinus* leaves. It has not

yet been reported in this country so far as we can learn. If this is found to be congeneric with *Sclerotiopsis,* as suggested above, the name *Pilidium* Kunze (1823) would displace *Sclerotiopsis* of Spegazzini (1882). A thorough search for the ascogenous and conidial stages of this fungus should be made where this *Pilidium* occurs.

The first report of the pycnidial form of *Pezizella lythri* on strawberry in this country was that of Saccardo (1913). The specimens were collected by Dearness, No. 3507 b, in Canada. A portion of this material kindly contributed by Professor Dearness is interesting, as it shows that besides the typical *L. macrothecium* pycnidia there are also present several sporodochia of the *Hainesia* stage. These seem to have been overlooked by Saccardo if they were on the specimens sent him.

LEPTOTHYRIUM PROTUBERANS Sacc. This specific name was first attributed by Saccardo (1882) to Lévéillé, as Saccardo thought at that time it was the *Phoma protuberans* of that author (1846). Saccardo was apparently misled by Roumeguere's application of Lévéillé's name to his No. 516 Fun. Sel. Gal. on *Coronaria myrtifolia,* which was the first specimen Saccardo referred to this species (1882). Later (1884), he recognized the mistake, dropped the citation of Lévéillé and used the name as his own. Saccardo mentions (1882, 351) that his *Leptothyrium protuberans* is closely related to *L. macrothecium.* An examination of Roumeguere's No. 516 in Ellis' herbarium shows that it is identical with *L. macrothecium* Fckl. and *Sclerotiopsis concava* (Desm.).

SPORONEMA DUBIUM C. Massal. Massalongo (1889 *a*) described this species from Italy on *Castanea.* A little later the same year (1889 *b*) the same species is described and illustrated with colored figures. Through the kindness of Dr. Massalongo we have been able to examine and compare part of the type collection of this species as well as two others described and figured at the same time. A study of these specimens shows that this species is identical with *Sclerotiopsis concava,* the pycnidial form of *Pezizella lythri.* Massalongo described the spores as catenulate. Whether they are slightly catenulate just before or

at maturity is very difficult to determine positively. When packed in the pycnidium before it ruptures the spores sometimes appear to be catenulate. If so it is an evanescent character and of little or no diagnostic value.

Sporonema quercicolum C. Massal. This was described (1889 *a*) and figured (1889 *b*) at the same time as *Sporonema dubium*. Examination of type material of this also shows that it is identical with our plant. This was said to differ from *S. dubium* in being argillaceous in color and dehiscing somewhat differently. Our study of many specimens of different age and condition shows that the color is variable, ranging from clay color through light brown and chestnut brown to black. Old specimens are usually darker than younger ones. The dehiscence of the pycnidia at maturity also varies greatly. *S. castaneae* C. Massal. (1889 *b*), which it was thought might also be a form of the same species, proves upon examination of part of the type to be specifically distinct, having considerably larger and differently shaped spores. This species appears to be identical with *Pilidium acerinum* Kze. (1823).

Leptothyrium borzianum F. Tassi (1896). This was found on *Jambosa* (*Eugenia*) *vulgaris* in the Botanical Garden at Siena, Italy. Tassi's figures show clearly the form of the pycnidia which he says are concave or collapsed when dry. The characteristic navicular spores borne upon branched conidiophores are also shown. We have seen no authentic specimens of Tassi's plant but we have found typical *Sclerotiopsis concava* on the same species of Jambosa in the greenhouses of the New York Botanical Garden which agree in all respects with Tassi's description and figure and which when cultured gave the typical sporodochia of *Hainesia lythri*. There seems scarcely any doubt, therefore, that Tassi's species is the pycnidial stage of *Pezizella lythri*.

Sclerotiopsis potentillae Oud. (1900). This was found on *Potentilla* in Holland. Oudemans says this differs but little from S. *australasica* Speg. except that the spores are 1.5 μ longer. This slight variation in the length of spores is very common even in Spegazzini's own specimens. As the original description of Oudemans' agrees in every respect with *Sclerotiopsis concava* as

found on *Potentilla* in this country, we have no hesitation in regarding it as a synonym.

SCLEROTIOPSIS PELARGONII Scalia (1903). This was based on specimens that developed on leaves of *Pelargonium capitatum* in damp chamber in Italy. We have seen no authentic specimens of this species but the description applies in all particulars to specimens of *Sclerotiopsis concava* which developed on leaves of the same host in a damp chamber in our laboratory and also in nature on *P. zonale* in New Jersey. Sporodochia of *Pezizella lythri* have been found also in September on old leaves of *Geranium maculatum,* in the drug garden at Arlington Farm, Virginia.

SCLEROTIOPSIS RUBI C. Massal. (1906). This was found on dead spots on old leaves of *Rubus caesius* in Italy. The author compares the species with his *Sporonema dubium* and *Sclerotiopsis potentilla* Oud. The original description agrees entirely with that of pycnidia of *Pezizella lythri* as found on various species of *Rubus* from different localities in this country. Though we have seen no authentic specimens of Massalongo's species there seems to be no doubt that it is the same as *Sclerotiopsis concava* (Desm.).

SPORONEMA PULVINATUM Shear (1907). Comparison of the type specimen of this species, which was found on cranberry leaves kept in a moist chamber, shows that it is identical with the pycnidial form, *Sclerotiopsis concava.* We also find, upon examining the original material, other leaves in the same collection bearing amber-colored spore masses which had been referred provisionally to *Gloeosporium*; but which upon careful comparison now prove to be typical *Hainesia lythri.* Other specimens of the pycnidial form on *Vaccinium macrocarpum* have been collected in New Jersey and at Olympia, Washington. Judging from the character of the monotype of the genus *Sporonema* Desm. (1847) which is *S. phacidioides,* and also by study of its ascogenous stage, *Pyrenopeziza medicaginis* Fckl., which was demonstrated by Jones (1918), this is very closely related to *Sclerotiopsis* and *Pezizella oenotherae,* but it is apparently generically distinct.

Ceuthospora rubi Petrak (1911). This is apparently a *nomen nudum*, as we have been unable to find any description of it. The name is used on specimens distributed by Petrak in his exsiccati, Fl. Bohem. et Morav. No. 512 and was found on canes of *Rubus thrysoideus*. A specimen of this number which we have examined is identical with *Sclerotiopsis concava*.

III. Ascogenous Stage, Pezizella lythri (Desm.) n. comb.

Peziza (Mollisia) oenotherae C. & E. Cooke and Ellis (1878) described this discomycete which Ellis collected upon old stems of *Oenothera*. An examination of a part of the original material from Ellis' herbarium and also of the specimens distributed in North American Fungi Exsiccati No. 846 and Fungi Columb. No. 244 shows that this is identical with the discomycete which we have found on this same host and on various other hosts associated with the conidial and pycnidial form, and which has been demonstrated by single ascus cultures and inoculation to be identical. If the ascogenous form has ever been described or reported from Europe we have been unable thus far to find it. The discocarps have been found abundantly on old leaves of *Oenothera, Rubus, Gaura, Steironema, Prunus, Salix* and other hosts. They are generally accompanied by the pycnidial form and also usually by the conidial form as well.

Pezizella oenotherae (C. & E.) Sacc. Saccardo (1889) referred Cooke and Ellis' species to *Pezizella*. This was merely a transfer of the species to this genus and was not based on any new material or information.

Until we have much more knowledge of the life histories, comparative morphology and taxonomic value of the various characters and also can agree as to the generic types, it will be impossible to make any satisfactory disposition of the numerous genera and species of the discomycetes. In the meantime all attempts at classification must be regarded as tentative and of little value. The treatment of genera of discomycetes by the various systematists such as Phillips, Rehm, Boudier, Saccardo, von Höhnel and others is so diverse that one is left in a quandary as to what course to pursue in dealing with members of this group.

Mollisia, to which Cooke and Ellis referred this plant, seems to have been first used as a generic name by Karsten (1871), who includes 28 species, a considerable number of which he regarded as new. *Peziza cinerea* Batsch might perhaps be chosen as the type of *Mollisia,* as it is one of the common species included by Fries in his subgenus of the same name and is included in the first section by Karsten and Rehm. It is very doubtful, however, whether *M. cinerea* is congeneric with *Pezizella lythri.* Some idea of the confusion which exists in these genera may be derived from Von Höhnel's statement (1919) in regard to *Pezizella.* He says that his investigation of over 50 species, which have been referred to this genus, shows that they represent 23 different genera! As he does not specify to which of these 23 genera our species, *P. oenotherae,* belongs, we shall leave it for the present where Saccardo placed it, only adopting as the specific name the oldest one applied to any stage of the species so far as at present known.

SYNONYMS

The synonymy of each stage of the fungus is given below, also the exsiccati which have been cited and examined, the various illustrations which have been published and the distribution and hosts so far as at present known.

In connection with distribution and hosts it seems somewhat remarkable that so few collections of any of the three stages of this fungus should have been made or reported heretofore in this country; and especially in view of the variety of hosts upon which it occurs and its abundance the past season in several widely separated localities. This indicates quite forcibly the scantiness of our knowledge of our mycological flora and the great need of more systematic collection and study before we can hope to know what species occur or their distribution as to localities or host plants.

PEZIZELLA LYTHRI (Desm.) n. comb.

I. CONIDIAL STAGE, HAINESIA LYTHRI (Desm.) v. Höhn.

1. *Dacryomyces lythri* Desm. Pl. Crypt. France No. 1545. 1846.
2. *Sphaeronema corneum* C. & E. Grev. **6**: 84. 1878.
*3. *Gloeosporium? tremellinum* Sacc. Michelia **2**: 168. 1880.
4. *Gloesporium? rhoinum* Sacc. Fungi Italici, Pl. 1035. Jl. 1881.

*5. *Hainesia rhoina* (Sacc.) Ell. & Sacc. Syll. Fun. **3**: 699. 1884.
6. *Tubercularia rhois* Halsted. Seymour & Earl. Economic Fungi No. 273. 1893. Also Bull. Torr. Bot. Club **20**: 251. 1893.
*7. *Hainesia epilobii* Eliasson. Bih. K. Sv. Vet. Akad. Handl. III, **22**: 16. 1896.
*8. *Hainesia castaneae* Oud. Ned. Kruid. Archief Ver. Med. Ned. Bot. Ver. III, **2**: 755. 1902.
*9. *Hainesia rostrupii* Oud. Ned. Kruid. Archief Ver. Med. Ned. Bot. Ver. III, **2**: 756. 1902.
10. *Hainesia lythri* (Desm.) v. Höhn. Frag. Myc. (in Sitz. Akad. Wiss. Wien. **115**: 687. 1906).
*11. *Tubercularia zythioides* C. Massal. Madonna Verona **2**: 39. 1908.
12. *Hymenula rhoina* (Sacc.) Bub. & Kab. Kabát & Bubák, Fungi Imp. Exs. No. 749. 1910.
13. *Patellina fragariae* Stevens & Peterson. Phytopathology **6**: 264. 1916.

II. PYCNIDIAL STAGE, SCLEROTIOPSIS CONCAVA (Desm.) n. comb.

1. *Ceuthospora concava* Desm. Ann. Sci. Nat. Bot. Ser. III. **8**: 17. 1847.
2. *Leptothyrium macrothecium* Fckl. Symb. Myc. 383. 1870.
3. *Leptothyrium protuberans* Sacc. Michelia **2**: 351. Mr. 1881. Syll. Fun. **3**: 635. 1884.
4. *Sclerotiopsis australasica* Speg. Ann. Soc. cien. Arg. **13**: 14. 1882.
5. *Sporonema dubium* C. Massal. Nuovo Giorn. Bot. Ital. **21**: 166. Apr. 1889.
6. *Sporonema quercicolum* C. Massal. Nuovo Giorn. Bot. Ital. **21**: 166. Apr. 1889.
*7. *Leptothyrium borzianum* F. Tassi. Rev. Myc. **18**: 171. pl. 173 F. 1896.
*8. *Sclerotiopsis potentillae* Oud. Ned. Kruid. Archief III Ver. Med. Ned. Bot. Ver. **2**: 248. 1900.
*9. *Sclerotiopsis pelargonii* Scalia. Mycetes Siculi Novi. II. 2. 1903.
*10. *Sclerotiopsis rubi* C. Massal. Malpighia. **20**: 166. 1906.
11. *Sporonema pulvinatum* Shear. Bull. Torr. Bot. Club **34**: 308, 309. 1907.
12. *Ceuthospora rubi* Petrak. nomen nudum. Flora Bohem. et Morav. Exs. No. 512 II Ser. 1 Abt. Lfg. 11. 1912.

II. ASCOGENOUS STAGE, PEZIZELLA LYTHRI (Desm.) n. comb.

1. *Peziza* (Mollisia) *oenotherae* C. & E. Grev. **6**: 90. Mr. 1878.
2. *Pezizella oenotherae* (C. & E.) Sacc. Syll. **8**: 278. Dec. 20, 1889.

* No authentic specimens seen.

EXSICCATI EXAMINED

HAINESIA LYTHRI.

Desmazières, J. B. H. J. Pl. Crypt. France 1545 as *Dacryomyces lythri* Desm. 1846.

Ellis & Everhart. N. A. Fun. 846. *Peziza oenotherae* C. & E. with sporodochia (*Sphaeronema corneum*, C. & E.). 1881 or 1882.

Seymour & Earle. Econ. Fun. 273. *Tubercularia rhois* Halsted. 1893.

Ellis & Everhart. Fun. Col. 244. *Peziza oenotherae* C. & E. with sporodochia also in the four sets examined. 1894.

Ellis & Everhart. N. A. Fun. 2074. *Sphaeronema corneum* C. & E.

Ellis & Everhart. N. A. Fun. 2278. *Hainesia rhoina* (Sacc.) Ell. & Sacc.

Kabát & Bubák. Fun. Imp. Exs. 749. *Hymenula rhoina* (Sacc.) Bub. & Kab. 1910.

SCLEROTIOPSIS CONCAVA.

Desmazières. Pl. Crypt. France 1625. *Ceuthospora concava* Desm. 1847.

Fuckel. Fun. Rhen. 551, 553, 1714. *Leptothyrium macrothecium* Fckl. 1870.

Roumeguère, C. Fun. Sel. Gal. 516. *Phoma protuberans* Lév. 1879.

Vestergren, T. Mic. Rar. Sel. 61. *Leptothyrium protuberans* Sacc. 1882.

Ellis & Everhart. N. A. Fun. 733. *Leptothyrium protuberans* Sacc. 1881.

Ellis & Everhart. Fun. Col. 287. *Leptothyrium protuberans* Sacc. 1894.

Ellis & Everhart. Fun. Col. 244. *Peziza oenotherae* C. & E. with pycnidia and sporodochia. 1894.

Petrak. Fl. Boh. & Morav. Exs. Ser. II, 1 Abt. 512. "*Ceuthospora rubi* n. sp." 1912.

PEZIZELLA LYTHRI.

Ellis & Everhart. N. A. Fun. 846. *Peziza oenotherae* C. & E. 1881 and 1882. Only the conidial stage, *Hainesia lythri,* on specimens of this number in Herb. U. S. Dept. Agr. and N. Y. Bot. Garden.

Ellis & Everhart. Fun. Col. 244. *Peziza oenotherae* C. & E. 1894.

Ellis & Everhart. Fun. Col. 287. *Leptothyrium protuberans* Sacc. 1894. The discocarps are also found with this in the specimens of one set of this number in the Herb. N. Y. Bot. Garden.

ILLUSTRATIONS

CONIDIAL STAGE.

Saccardo. Fungi Ital. pl. 1035. 1881.

Saccardo. Fungi Ital. pl. 1039. 1881.

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PYCNIDIAL STAGE.

Fuckel. Symb. Myc. pl. 3, fig. 28. 1870.

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Distribution

Americas. The fungus has been found in one or more of its three fruiting conditions in Ontario (Canada), Maine, Massachusetts, New York, New Jersey, Maryland, District of Columbia, Virginia, North Carolina, Georgia, Florida, Wisconsin, Minnesota, Ohio, Tennessee, Louisiana, Texas, Washington (United States), and Argentina (South America).

Europe. Sweden, Holland, France, Germany, Bohemia, Italy.

Hosts

In the Americas the conidial stage has been found on dead spots on living leaves, or on mature fruit, dead leaves, petioles or stems of the following plants: *Acer rubrum, Ampelopsis quinquefolia, Castanea dentata, Castanea* (*dentata* × ?), *Cercis canadensis, Cornus canadensis, Duchesnia indica, Epilobium angustifolium, Eucalyptus globulus, Fragaria virginiana, F. virginiana chiloensis, F. mexicana, Gaultheria procumbens, Gaura biennis, Hicoria glabra, Jambosa* (*Eugenia*) *vulgaris, Lythrium salicaria, Nyssa sylvatica, Oenothera biennis, Vaccinium macrocarpum, Pelargonium capitatum, Pelargonium zonale, Populus nigra italica, Potentilla canadensis, Prunus serotina, Quercus alba, Q. rubra, Q. velutina, Rhus copallina, R. glabra, R. cotinus, R. toxicodendrum, R. typhina, Ribes prostrata, Rosa rugosa prostrata, Rubus occidentalis* var. (cult. black raspberry), *R. strigosus* var. (cult. red raspberry), *R. idaeus, R. setosus, Rubus* spp. (wild blackberry), *Rubus villosus* var. (Lucretia dewberry), *Salix humilis, Smilax rotundifolia, Ulmus* sp., *Vitis cordifolia.*

The pycnidial stage has been found on all of the above hosts with the exception of *Ampelopsis, Cercis, Cornus, Duchesnia, Geranium* and *Ribes.*

The ascogenous stage has been found on *Castanea* (*dentata* × ?), *Gaura biennis, Oenothera biennis, Prunus serotina, Steironema ciliata, Rubus strigosus idaeus* (cult. var.), *R. villosus* var. (Lucretia dewberry) and *Rubus* sp. (wild blackberry).

All hosts from the United States and Canada except the following are here reported for the first time: *Fragaria, Oenothera, Rhus, Rubus,* and *Vaccinium.*

CONCLUSION

Too much emphasis cannot be placed upon the great need for serious and concentrated effort in improving the conditions in mycology, which are so strikingly illustrated by the results of the present study. With such confusion prevailing in the taxonomy and such lack of knowledge of the morphology of the fungi as is here indicated, it is imperative that all mycologists and pathologists should unite in trying to remedy these conditions and to establish a fairly stable system of nomenclature and terminology for the fungi. The most practical and effective plan yet suggested for establishing generic names is to fix a type species for each genus, which shall furnish a basis for a definite application and interpretation of the genus. We cannot hope for complete agreement as to the exact limitations of genera, but the application of the generic type method would at least insure that a certain species or small group of species would always be inseparable from the generic name. This would certainly be a great improvement over the present practice so frequently followed of shifting the generic name from one species or group of species to another group with little or no consideration for the original species of the genus.

This work also emphasizes the need of more careful study and comparison of all the morphological characters of the different forms or stages of the pleomorphic fungi. The various conidial and pycnidial fructifications when thoroughly studied and compared in detail will, we believe, show points of resemblance or difference which can be coördinated with their relationships to each other and to their perfect stages. Such knowledge combined with that derived from life history studies will probably provide the best foundation for determining the natural relationships of genera and species as well as the higher groups. The failure to appreciate the significance of the confusion and lack of knowledge of various genera involved in the present taxonomic practice has apparently lead some to think that the conidial and pycnidial stages of ascomycetes show no consistent resemblances or differences of taxonomic value, and are therefore of little or no use in determining the relationships of genera and

species. It is said, for example, that species of *Gloeosporium* are conidial forms of such diverse and distantly related ascomycetes as *Glomerella* and *Pseudopeziza*. When, however, one studies and compares carefully the so-called species of *Gloeosporium* involved, it is found that they are very different, and could not on a purely morphological basis be considered congeneric. The present genus *Gloeosporium* as treated by Saccardo, for example, contains a heterogeneous collection of many imperfectly known and poorly described forms, really belonging to various and sometimes widely separated genera having in some cases only very slight superficial resemblances. The same is true of most of the large genera of the so-called fungi imperfecti.

Summary

This paper contains an account of the life history, morphology and taxonomy of a discomycete, *Pezizella lythri* (Desm.) Shear and Dodge, which is found on a great variety of plants and plant parts and has three stages in its life cycle: sporodochia, pycnidia and apothecia.

The conidial stage has received at least seven generic and ten specific names. It belongs to the form genus *Hainesia* and was described as the monotype of that genus. Its first specific name so far as at present known is *lythri,* it having been described as *Dacryomyces lythri* by Desmazières in 1846. The new combination *Hainesia lythri* (Desm.) was proposed by von Höhnel in 1906.

The pycnidial stage has also been described under various generic and specific names. It has been referred to at least four different genera and has had at least twelve specific names. It is the type of the genus *Sclerotiopsis* and its oldest specific name at present known is *concava,* it having been described at *Ceuthospora concava* by Desmazières in 1847. The new combination, *Sclerotiopsis concava* (Desm.) Shear and Dodge is therefore proposed for it.

The ascogenous or perfect stage has been described but once so far as known. Cooke & Ellis described it as *Peziza* (Mollisia) *oenotherae* in 1878 from stems of *Oenotherae biennis* collected

in New Jersey. Later Saccardo transferred it to the genus *Pezizella* as *P. oenotherae* (C. & E.) Sacc. It is left for the present in this genus. Adopting, however, the oldest known specific name applied to any stage, it becomes *Pezizella lythri* (Desm.) new combination.

This fungus in one or another of its stages has been found on about fifty different host plants widely distributed through North America and Europe, and is also found in South America.

The cultural and morphological characteristics of the various stages are described.

Cross inoculation experiments show that the fungus is a weak parasite and passes readily under favorable conditions from one host to another.

The chaos which at present prevails in the taxonomy and morphology of the ascomycetes is discussed and the imperative need of establishing a more stable system of nomenclature pointed out. The application of the type method, it is believed, would accomplish this end.

The great need and importance of life history studies is emphasized, as such studies will supply important data for determining the natural relationships of the genera and species of fungi and also furnish information of exceeding value and direct bearing on phytopathological problems.

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EXPLANATION OF PLATES 8–10

PEZIZELLA LYTHRI (Desm.) Shear & Dodge

PLATE 8. Conidial stage, *Hainesia lythri* (Desm.) v. Höhn.

Fig. 1. Small sporodochia on white carpel of dewberry, also mycelia of moulds that often follow this fungus. × 10.

Fig. 2. Large sporodochia on red raspberry, two showing irregularly lobed margin. × 15.

Fig. 3. Sporodochia on strawberry showing conical mass of conidia. × 10.

Fig. 4. Typical forms on strawberry. × 15.

Fig. 5. Two sporodochia from old cultures on cut surface of apple. The one at left developed normally, that on right remained closed and became darkened. It contained mature spores. × 15.

Fig. 6. Sporodochia from the same cultures as fig. 5. These resemble pycnidia with large ostioles from which broad, white cirrhi of spores are protruding. × 15.

Fig. 7. Mature sporodochia on agar. The spore masses have become heavy so that most of the sporodochia have fallen over showing the stalk-like basal portions. × 10.

FIG. 8. Sporodochium from the same culture as fig. 7, after the spore mass was removed showing the cup shaped body with lobed margin. × 20.

Fig. 9. Section of young cylindrical sporodochium from strawberry. The sporophores from the base are much longer than those from the sides. × 100.

Fig. 10. Section of a conidial fructification from strawberry. The spore mass free from the sporophores. × 300.

PLATE 9. Pycnidial stage, *Sclerotiopsis concava* (Desm.) Shear & Dodge

Fig. 11. Pycnidia on cane of black raspberry. Note the lines radiating from each pycnidium showing the effect of the fungus in causing a wrinkling of the host tissues.

Fig. 12. Pycnidia on dead leaf of *Steironema ciliatum* showing concave condition of the mature, dried fruit body, dehiscence not yet occurred. × 2½.

Fig. 13. Immature pycnidia on leaf of *Epilobium*. × 12.

Fig. 14. Pycnidia on dewberry canes. The longitudinal cracks show where the cuticle has ruptured. The walls of the pycnidia are still unbroken. × 15.

Fig. 15. Pycnidia from the specimen shown in Fig. 11, but more highly magnified to show the irregular cracking of the pycnidial wall in dehiscence.

Fig. 16. Section of a very small mature pycnidium showing the original orientation of cells in the upper wall and the middle, dark colored tissue in the basal wall. × 240.

Fig. 17. Cross section of an overwintered pycnidium on dewberry cane, showing the cuticle and the cuticularized layer of the epidermis tightly stretched, and region at the center showing where the walls of spores are being transformed into a mucilaginous substance the swelling of which bursts the pycnidium. × 80.

PLATE 10. Ascogenous stage, *Pezizella lythri* (Desm.) Shear & Dodge (except fig. 18).

Fig. 18. An old sporodochium (*a*) and a young pycnidium (*b*) on rotting strawberry. The spore cavity in the pycnidium is just being formed. The dark colored middle layer of the wall along the base is well shown here. × 80.

Fig. 19. Section of a mature discocarp from dewberry. The spores are deeply stained. × 300.

Fig. 20. Section of a discocarp showing a stalk-like base, from leaf of wild blackberry. The discocarps originate intraepidermally. This is evident as portions of epidermal cells are clearly seen at the base. × 150.

Fig. 21. Part of a section of a discocarp highly magnified, showing the arrangement of the spores in the asci, and the paraphyses projecting above the asci. × 600.

Fig. 22. Small but old discocarp from dewberry leaf showing portions of the epidermis among the cells at the base. × 150.