Researches on the Life-history of Parasitic Fungi.

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With Plate XXIV.

I. CLADOSPORIUM HERBARUM, Link.

THE genus *Cladosporium* is a comparatively old one, having been founded by Link in the year 1791. The species *Cladosporium herbarum* was described by the same observer in the following terms:—‘atrovirens, densum, effusum, floccis septatis.’

The species is of somewhat wide occurrence; almost everywhere the dead remains of plants can be seen to be covered with dark, sometimes almost black patches formed of its conidiophores. The conidiophores are olive and are arranged in tufts which are frequently large and dense. The conidia are olive, continuous at first and becoming later typically once septate; they measure on the average $18-20 \times 8-10 \mu$, and are produced at the tip of the conidiophore in short chains which sometimes remain attached so that they may become larger and twice or even thrice septate. *Cladosporium herbarum* in its life-history will be shown to be connected with another conidial form belonging to the form-genus *Hormodendron*; this form *Hormodendron* will be shown to be parasitic on several plants, causing disease, and it is proposed first to treat with this disease and after to deal with the relations of the conidial form to *Cladosporium herbarum*.

The disease caused by the form *Hormodendron* and the evidence of its parasitic nature.

For some time past the green foliage of many different species of plants has been seen to be suffering with a disease which takes the form of large, irregular holes in the lamina of the leaf. The damp summer of last year seems to have been particularly favourable to the spread of the disease. Of the species which have frequently been found to be affected in this way the following are given:—

Brassica oleracea (Cabbage), *Cucumis sativa* (Cucumber), *Cucumis Melo* (Melon), *Arctium Lappa* (Burdock), *Catalpa bignonioides*, *Althaea rosea*,

Malva sylvestris, *Circaea lutetiana* (Enchanter's Nightshade), *Funkia* spp., *Digitalis purpurea* (Foxglove), and *Phlox* spp.

Since it attacks such plants as Cucumber, Melon, and Cabbage, the fungus is one of economic importance; the assimilating surface of plants attacked may be considerably reduced, and further, in the case of Cabbage, the disease may render the 'heads' quite unsaleable. At times the disease has taken the form of an epidemic in Cucumber houses in this country. When a leaf is attacked small perforations make their appearance; these increase in size and frequently run together so that they eventually become large, irregular holes. The largest holes which have been recorded measured about three-fourths of an inch. Surrounding each hole there is usually a small, brownish area formed of the dead tissues of the leaf; the remaining parts appear to be green and healthy. Along with the rest of the tissues the smaller veins perish; the larger veins, however, as a rule remain. It is interesting to note that in its progress this disease differs markedly from the so-called 'leaf-spot' diseases; in the latter the tissues of isolated spots are killed and fall away, leaving holes in the leaf, whereas in the former the tissues appear to be eaten away and the holes continue to increase in size. An examination of the tissues of the leaf bordering on the hole shows that the cells are apparently exhausted of their contents and dried; it might be thought that the formation of the holes and their increase in size were due to the falling away of these dead cells, but this is apparently not so in this case. From the very commencement of the disease a perforation appears, not a dried spot from which the dead tissues fall away leaving a hole; in fact, it seems as if the tissues of the leaf are not merely killed but devoured. This mode of action is most unusual for a fungus and resembles that of an animal; it would point to the occurrence of ferments of the cytase, protease, and diastase classes, and it is hoped that further work on the ferments present in this parasite will throw some light on its action on the tissues of the leaf.

The mycelium of the fungus is most abundant in that region which is in close proximity to the holes; further away from the holes the tissues contain little or no mycelium. The hyphae run through the cells; they are colourless when young, become darker in colour as they grow older, are variously branched, measure about 4μ in width, and are without haustoria. The conidiophores arise from the hyphae in the tissues of the leaf bordering on the holes; they are short, lateral branches of the hyphae, are simple, almost hyaline, continuous or sparingly septate, and bear at their tips branched chains of conidia. The branched chain arises thus:—from the tip of the conidiophore three conidia are usually formed; each of these bears two conidia of a second order, and each conidium of the second order can bear one or two of a third order of branching, and so on. The conidia are hyaline or almost hyaline, continuous, elliptical, and measure $8-9 \times 4\mu$.

From the structure and arrangement of the conidia the fungus was found to correspond with the form-genus *Hormodendron*.

An account will now be given of the infection experiments which show that the form *Hormodendron* is the cause of the disease described above. Before actually carrying out the infections a pure culture of the fungus was made in order to ensure the exclusion of any spores other than those of the form *Hormodendron*. First, some of the conidia were taken from an infected leaf of *Catalpa bignonioides* and were transferred to pure water in a 'hanging-drop'; they were thus kept in water in a chamber which was constantly moist. In from one to two days they were found to have germinated. Each emitted one hypha, as a rule, which became septate and branched; the absence of food-material prevented any further growth of the hyphae. A cultural medium composed of 4 per cent. of the expressed juice of fresh grapes and 6 per cent. of gelatine was found to be favourable to the growth of the fungus. This nutrient gelatine was sterilized by heating in a steam-oven for four hours each day on three successive days. Five Petri dishes and a boiling-tube, into which a plug of cotton-wool had been inserted so as to close its mouth, were sterilized by heating in an air-oven at 100° C. for five hours each day on two successive days. Some of the nutrient gelatine was transferred to the boiling-tube, and to this were added some conidia taken from a previously made, impure culture; the needle used for transferring the conidia had been previously heated to a red heat and allowed to cool. The liquid in the boiling-tube was shaken, and some of it was poured into a Petri dish. The remainder of the liquid in the boiling-tube was then diluted by one-half, it was shaken and some was transferred to another Petri dish; this process of diluting, shaking, and transferring some of the fluid to a Petri dish was repeated three times. Care was taken to keep the boiling-tube closed as much as possible, and before removing the plug of cotton-wool the part of the plug which was exposed to the air was slightly burnt on each occasion so as to prevent any spores which had fallen on it from the air from dropping into the liquid in the tube. The last Petri dish was found to contain a pure culture derived from the growth of a single conidium. The growth and development of the mycelium in the pure culture was carefully followed. The hyphae when young were colourless, but as they grew older they assumed an olive colour; they were septate at fairly short intervals and were variously branched. From them there arose abundant lateral branches which grew above the surface of the nutrient gelatine and bore branched chains of conidia. The conidia in their structure, mode of formation, and arrangement corresponded with those observed on the infected leaves and described above.

Conidia taken from the pure culture were used for infecting living plants. Two methods were made use of for transferring them to the leaves ;

in the one a sterilized needle was used, in the other they were mixed with sterilized water in a spraying-apparatus which had been previously washed out with absolute alcohol and allowed to dry. Six young Cabbage plants were selected as being healthy and intact and were arranged in two lots of three each. In one experiment the leaves of three plants were sprayed with the conidia; in the other experiment the conidia were transferred to definite spots on the leaves of the other three plants and the spots were moistened with distilled water. Each lot of three plants was covered with a bell-jar of which the inner surface had been cleaned with absolute alcohol. In from four to five days the leaves thus treated were found to have perforations in them; the leaves of those plants which had been sprayed showed numerous perforations, while in the others the perforations were limited to the spots on which the conidia had been placed. The perforations increased in size and soon became large holes. A microscopic examination showed that the conidiophores of the fungus were arising from the tissues of the leaf surrounding the holes and were producing conidia abundantly. The symptoms developed by these plants which had been artificially infected were similar to those observed naturally on the infected plants. All of the six plants yielded the same results, while a control in the form of a young Cabbage plant kept under a sterilized bell-jar and to which no conidia had been transferred showed no signs of infection.

Another series of experiments was made for the purpose of determining with what degree of facility the fungus could be transferred from one host to another. For this purpose excised leaves were used; the leaves were placed on filter papers in Petri dishes and the filter papers were moistened with distilled water, the Petri dishes and filter papers having been previously sterilized by heating in an air-oven at 100°C. for five hours each day on two successive days. Conidia were taken from an infected leaf of one species and were placed on definite spots of a leaf of another species in the Petri dish; the spots were moistened with distilled water. The experiments showed that conidia from one species would grow on another with apparent facility. The fungus on Cabbage could be transferred to *Catalpa*, that on Melon to Cabbage and vice versa, that on *Catalpa* to Mallow and vice versa, and that on *Catalpa* to Melon. It is concluded that the form *Hormodendron* has not adapted itself closely to any one host, at least in the case of the species experimented with. Further, it may be mentioned that the disease caused by this form would be particularly difficult to exterminate, since the fungus attacks many species of plants and can apparently pass from one species to another, and this apart from its connexion with *Cladosporium herbarum*, which is so common everywhere on the dead leaves of plants.

The origin of *Cladosporium* from *Hormodendron*.

An examination of the old cultures of *Hormodendron* showed that the production of conidia of *Hormodendron* had ceased. The mycelium remained the same, but from some of the hyphae lateral branches had been produced which bore pale olive conidia at their tips. These fertile hyphae were thicker than those which had borne conidia of *Hormodendron* and were three or four times septate. The conidia were borne in short chains and were typically once septate; sometimes they were twice or thrice septate. They were similar in their structure and mode of origin to those of *Cladosporium herbarum*. Some of them were seen to have germinated in the medium of the culture; each emitted two hyphae, as a rule, which were septate at somewhat short intervals and were usually unbranched. At the tips of the hyphae were borne short chains of conidia of *Cladosporium*. The examination of the cultures, therefore, showed that the mycelium of *Hormodendron* after having produced conidia of *Hormodendron* gave rise to conidia of *Cladosporium*, which after germination in the medium of the culture reproduced themselves.

The production of *Hormodendron* from *Cladosporium*.

The origin of *Cladosporium* from *Hormodendron* shown above led to a careful examination of the leaves of plants which were attacked by *Hormodendron*, for the purpose of finding out whether *Cladosporium* occurred on them. On the living leaves no *Cladosporium* was observed, but the waning or dead leaves showed *Cladosporium* to be present in abundance. Whereas from these leaves *Hormodendron* had evidently disappeared, tufts of the conidiophores of *Cladosporium* could be seen growing around the holes previously made by *Hormodendron* as well as on other parts of the leaves which showed no signs of having been affected with *Hormodendron*. The dead or waning leaves of all the species which had been attacked by *Hormodendron* showed *Cladosporium* on them.

Conidia of *Cladosporium* were taken from the leaves and were mounted in 'hanging-drops' in a weak solution of cane sugar. Whether they were continuous or once, twice, or thrice septate the conidia were found to be capable of germinating; it is, therefore, interesting to note that the mature conidium is not necessarily septate, that is if the power of germinating is to be taken as the significance of maturity. Each conidium emitted usually two hyphae; the hyphae grew, branched, and on the lateral branches were borne branched chains of conidia of *Hormodendron*. Sometimes a hypha was observed to bear conidia of *Hormodendron* when quite short and unbranched. The results of the germination of conidia of *Cladosporium* taken from different species of plants were the same; in the experiments conidia of *Cladosporium* were taken from the leaves of Cabbage, Oak, *Catalpa*, *Funkia*, Melon, and other plants.

The action of different media was tried for the purpose of ascertaining whether the composition of the medium in which germination took place would have any effect on the production of conidia of *Hormodendron*. The following media were employed:—

1. Distilled water.
2. A solution of mineral salts in water consisting of equal weights of potassium phosphate, calcium chloride, and magnesium sulphate, and amounting to 2 per cent. total salts.
3. A 2 per cent. solution of pure cane sugar.
4. A decoction of dried leaves of *Catalpa* and Cabbage made by grinding the leaves in a mortar with the addition of a little water, filtering through muslin and adding more water to make up to a 4 per cent. solution of the expressed juice of the leaves. In these media the germination of conidia of *Cladosporium* taken from leaves of Cabbage, *Catalpa*, Oak, and *Funkia* was carried out in 'hanging-drops'. It was found that whatever medium was employed the same result attended the germination of the conidia, viz. the formation of conidia of *Hormodendron*.

The conidiophores and the small masses of cells produced by the mycelium of *Cladosporium* were also found to be capable of giving rise to conidia of *Hormodendron*. When some of the conidiophores of *Cladosporium* were mounted in a 'hanging-drop' in a 2 per cent. solution of cane sugar it was found that occasionally from the broken end of a conidiophore there arose a hypha which branched, and at the tips of the branches were borne conidia of *Hormodendron*. The small masses of cells produced by the mycelium of *Cladosporium* were also found to be capable of giving rise to hyphae which bore conidia of *Hormodendron*.

These experiments showed that not only can conidia of *Hormodendron* be produced by *Cladosporium*, but also that there is a great tendency on the part of *Cladosporium* to give rise to conidia of *Hormodendron*, and that this tendency has made itself manifest, in the case of the species of plants used as the source of *Cladosporium*, independently of the nutrient medium employed for germination.

By making use of the method described above for the preparation of a pure culture, it was found possible to obtain a pure culture of *Cladosporium*. The medium used consisted of 4 per cent. of the extracted juice of fresh grapes and 6 per cent. of gelatine. In the pure culture the growth and development of the mycelium were followed. The hyphae were at first colourless and became later olive in colour. The general nature and appearance of the mycelium and of its component hyphae were similar to those of the mycelium and hyphae in the cultures of *Hormodendron* described above. From the hyphae there arose lateral branches which grew above the surface of the nutrient gelatine and produced conidia of *Hormodendron*. The production of conidia of *Hormodendron* was not

abundant, and was much less than in the cultures of *Hormodendron*. Soon conidia of *Cladosporium* began to be formed; they were found to arise in a similar way to those described above in the cultures of *Hormodendron*. On germination these conidia gave rise to conidia of *Cladosporium* again.

The following conclusions are based on the comparison of the cultures of *Cladosporium* and *Hormodendron*:—the characters of the mycelium and of the component hyphae are similar in both cases; there is a production of conidia of *Hormodendron* which is more abundant in the latter case than in the former; this is followed in both cases by the formation of conidia of *Cladosporium*, and these conidia of *Cladosporium* on germination reproduce themselves; of the two conidial forms, *Cladosporium* and *Hormodendron*, each can give rise to the other and each can also reproduce itself; the tendency on the part of *Hormodendron* in an artificial matrix to pass to *Cladosporium* is clear.

The effect of a lower temperature on the germination of conidia of *Cladosporium*.

In the experiments described above, in which 'hanging-drops' were employed, the conidia of *Cladosporium* had been germinated at the temperature of the laboratory, i. e. at 60° F. and above, and it has been shown that they always gave rise to conidia of *Hormodendron*. Further experiments were conducted for the purpose of ascertaining whether a lower temperature would in any way influence the formation of conidia of *Hormodendron*. The hosts used were Cabbage, *Catalpa*, and *Funkia*; one or two conidia from each were mounted in a 'hanging-drop' in a 2 per cent. solution of cane sugar. The 'hanging-drop' cultures were placed on a box outside of the building, and near to them were placed a maximum and a minimum thermometer. During the space of five days the thermometer recorded the following temperatures:—

Date.	Maximum Temperature.	Minimum Temperature.
November 10	49° F.	35° F.
" 11	50° F.	32° F.
" 12	55° F.	33° F.
" 13	54° F.	30° F.
" 14	56° F.	31° F.

The highest temperature attained was 56° F. on the last day, and the lowest temperature was 30° F. on the fourth day; the average temperature for the five days was 42° F. All of the conidia germinated, and each gave rise to hyphae which were septate at somewhat short intervals, were sparingly branched, and bore conidia of *Cladosporium*. In some cases not only were the conidia borne at the tip of the hypha, but the hypha became converted

into a chain of conidia. Other 'hanging-drop' cultures were prepared as controls, and were kept at the temperature of the laboratory; in these the production of conidia of *Hormodendron* was found to take place in the ordinary way. At the lower temperature, then, the formation of conidia of *Hormodendron* was completely suppressed.

The microsclerotia of *Cladosporium*; their growth and development.

Each tuft of conidiophores of *Cladosporium* springs from a cellular mass produced by the approximation and repeated division of the hyphae. When the conidiophores fall away this mass of cells remains and forms what has been called a microsclerotium. The microsclerotium is somewhat rounded and measures, when fully formed, about 160 μ across. Its surface is corrugated, and there can be seen projecting from the main mass a few outlying cells which are more or less transparent. The main mass of the microsclerotium is black or of a very dark brown colour, and is composed of cells which are more or less rounded, dark brown in colour, and have rather thicker walls than the hyphae from which they were formed. It is conceivable that the microsclerotia do not necessarily always arise at the base of a tuft of conidiophores; the hyphae in the tissues, in their later stages at any rate, show a tendency to form masses of cells, and these probably also develop into microsclerotia. The microsclerotium is regarded as a resting-stage of *Cladosporium*, or rather as a stage which is capable of enduring a period of inactivity.

The growth of microsclerotia taken from leaves of Oak, *Catalpa*, Cabbage, *Funkia*, Plantain, and other plants, was observed; they were allowed to germinate in 'hanging-drops' in water. Each superficial cell by the rupture of its thick wall was found to be capable of emitting a hypha; the hypha grew, became septate, and seldom branch 1. From its tip there arose a short chain of conidia of *Cladosporium*. The microsclerotium was thus seen to be capable of producing conidiophores which bore conidia of *Cladosporium*, and this was found to occur in the case of all of the species of plants used. Some of the smaller masses of cells had been seen, as was stated above under the section dealing with the origin of *Hormodendron* from *Cladosporium*, to give rise to conidia of *Hormodendron*, but these are not regarded as fully formed, true microsclerotia.

Some of the conidia of *Cladosporium* derived from microsclerotia were germinated in 'hanging-drops' in a 2 per cent. solution of cane sugar; they were found to give rise to conidia of *Hormodendron*. This was observed in the case of conidia produced by microsclerotia which had been taken from all of the species mentioned above. It is, therefore, concluded that this is the means by which *Hormodendron* is naturally regenerated in the spring.

Before discussing the relations of the two conidial forms, *Cladosporium* and *Hormodendron*, to each other, it may be well to describe briefly the experiments which were conducted on the infection of living leaves with conidia of *Cladosporium*. For this purpose excised leaves were used, and the experiments were conducted in a similar way to those described above in which the leaves were placed on filter papers in Petri dishes, and the conidia transferred to definite spots on them by means of a needle. The conidia were taken from the leaves of *Catalpa* and of Cabbage. After four days an examination of the spots showed that conidia of *Hormodendron* were being produced; later on, the leaves died and commenced to rot, and the conidia of *Hormodendron* ceased to be formed; conidia of *Cladosporium* were then found to be present in abundance. The infection of the leaves of Cabbage and *Catalpa* yielded similar results, and led to the following conclusions:—

Conidia of *Cladosporium* placed on living leaves give rise to conidia of *Hormodendron* which are capable of infecting living leaves; direct infection by conidia of *Cladosporium* is not possible when the leaves are living; when the leaves die, *Hormodendron* disappears, and *Cladosporium* then makes its appearance.

The relations of *Cladosporium* and *Hormodendron* to each other and the nature of the life-cycle.

It has been shown above that if healthy leaves are infected artificially with conidia of *Hormodendron*, they develop symptoms of disease which are similar to the symptoms observed in the case of leaves which have been infected naturally with *Hormodendron*. It is, therefore, concluded that *Hormodendron* is capable of living as a parasite on the green leaves of plants and of causing disease.

Hormodendron attacks many plants which exhibit no close relationship to each other; in its range it is not confined to species of one family or even of closely allied families, and it can be transferred from one species of host to another without any difficulty. This shows that it is only weakly parasitic, in the sense that it represents no highly developed form of parasitism.

The cultural experiments have shown that the same mycelium which had previously formed conidia of *Hormodendron* gives rise later to conidia of *Cladosporium*, while observations on the leaves of plants attacked by *Hormodendron* in nature have shown that when the leaves commence to wane and die *Hormodendron* disappears, and *Cladosporium* makes its appearance. It is inferred that *Cladosporium* occurring on waning or dead leaves has its origin from *Hormodendron* which attacks the leaves when they are living. Also, since on the dead leaves *Hormodendron* passes

to *Cladosporium* and the same change occurs in an artificial medium, *Hormodendron* is considered to require a living matrix for its further continuance.

The occurrence of *Cladosporium* on dead leaves, its production in an artificial, cultural medium, and its tendency to reproduce itself in such a medium show that it is to be regarded as a saprophytic form. In the life-history of many fungi when two forms are concerned, the one a parasite and the other a saprophyte, it is customary for the saprophytic form to be ultimately produced in an artificial medium and to continue to reproduce itself in such a medium. In the genus *Ustilago*, for example, the secondary spores produced by the so-called *Ustilago*-spores continue to reproduce themselves in an artificial medium, and it is only when they are transferred to the host-plant that they give rise to the parasitic form from which the *Ustilago*-spores are again produced.

Conidia of *Cladosporium*, when germinated at a temperature of 60° F. or above, give rise to conidia of *Hormodendron*. This is considered as a means by which *Hormodendron* is produced for the purpose of infecting living leaves during the summer; there are, then, two sources from which *Hormodendron* is derived during the summer, namely, conidia of *Cladosporium* and conidia of *Hormodendron*. A lower temperature has been shown to suppress the production of conidia of *Hormodendron* and to favour the formation of conidia of *Cladosporium*. This points to *Hormodendron* being a summer form and to *Cladosporium* being a later form.

The fully formed microsclerotia have been shown to produce conidiophores which bear conidia of *Cladosporium*, and these conidia of *Cladosporium* have been shown to give rise to conidia of *Hormodendron* after germination. This is considered to afford the means by which *Hormodendron* is regenerated in the spring of each year. The microsclerotia are formed in late autumn, after the conidiophores of *Cladosporium* have disappeared, and exist through the winter in a state of inactivity. On the recurrence of spring they germinate to give rise to conidia of *Cladosporium*, from which conidia of *Hormodendron* are produced, and so can infect the living leaves of plants during the summer.

From the experimental results and from the conclusions based on them, the life-history of *Cladosporium herbarum* is considered to include two conidial forms, the one a parasitic form, *Hormodendron*, and the other, *Cladosporium*, a saprophytic form. The latter form is capable of existing in an inactive condition through the winter. Such a life-history, which is made up of two conidial forms only, is unusual among the Fungi. Each form has been shown to be capable of giving rise to the other, and an attempt has been made to elaborate the conditions under which one form tends to pass into the other. The life-cycle appears to be complete, and the intervention of any other spore-form would be unnecessary.

The species of *Cladosporium* dealt with in this article has been regarded as *Cladosporium herbarum*; hitherto it has been customary to regard the species occurring on *Quercus*, *Platanus*, *Populus*, and a few others, as *Cladosporium epiphyllum*, Nees, and that occurring on the dead remains of plants generally as *Cladosporium herbarum*, Link. It is considered to be advisable to include these two hitherto distinct species under one specific name, partly because the differences in the nature of the conidia and conidiophores are not thought to be sufficiently great to warrant their separation as two distinct species, and also because the conidia taken from *Quercus*, or from any of the other species of plants worked with, have yielded similar results; the name of the older form, *Cladosporium herbarum*, Link, is accepted as the name of the species.

Previous work on *Cladosporium herbarum*.

Cladosporium herbarum has afforded material for the work of several authors; reference will now be made to a few of these. M. Janczewski obtained a giant and a dwarf form of *Hormodendron* from *Cladosporium herbarum*; the same observer has also obtained an ascigerous stage which he has named *Sphaerella Tulasnei*. M. Laurent obtained *Hormodendron cladosporioides*, Sacc., *Dematium pullulans*, De Bary, and a *Fumago* form, all being forms of *Cladosporium herbarum*. M. Berlèse, on germinating conidia of *Cladosporium herbarum* taken from a number of species of plants, always obtained the form *Hormodendron*, which he regards as essentially the saprophytic form of *Cladosporium herbarum*. Other observers have obtained several other forms.

In the life-history given above the only other form mentioned is the form *Hormodendron*; this was the only other form obtained in the cultures or observed on the leaves of plants examined, except in one instance which will now be mentioned. On germinating conidia of *Cladosporium* taken from the leaves of *Eucalyptus globulus* in a 2 per cent. solution of cane sugar in 'hanging-drops', there was produced, in addition to the small form *Hormodendron*, a larger conidial form of which the conidia measured $18 \times 8 \mu$. The conidia were borne in branched chains not only at the apex of the conidiophore, but also at other points of its axis. In their method of origin, therefore, the conidia of the larger form differed from those of the small form which were borne only at the apex of the conidiophore. In both the smaller and larger forms, however, the conidia differed somewhat from those of the form *Hormodendron* occurring on other species of plants, in that instead of being elliptical they were nearly circular in shape. It must be borne in mind that *Eucalyptus globulus* is an exotic species, and more work is needed to determine whether the species of *Cladosporium* occurring on it is a different species from *Cladosporium herbarum*.

The work of the authors mentioned above would show that *Hormodendron* is a saprophytic form, while the experiments described in this article would point to its being a parasitic form. With reference to the ascigerous stage, *Sphaerella Tulasnei*, mentioned above, it may be said that there is no record of its occurrence in Britain, and, further, that the life-history of *Cladosporium herbarum* has been shown to be complete without the intervention of an ascigerous stage.

Cladosporium herbarum has been described by several observers as, in certain circumstances, a parasite. Prilleux and Delacroix consider it to be parasitic on Apple trees and Raspberry bushes, Cavara on Raspberry, Cycads, and other plants, Sorauer on Peas, Lopriore on Wheat, and Ritzema Bos on Oats.

On the whole the work of various authors tends to show that there are several races or species included under the name *Cladosporium herbarum* which are separated from each other, not by the characters of conidia, conidiophores, or hyphae, but by virtue of the other spore-forms which they can give rise to.

The following is given as a brief summary of the life-history as worked out in the above pages :—

1. The life-cycle is composed of two conidial forms, *Hormodendron* and *Cladosporium*.
2. *Hormodendron* is a parasitic and summer form ; in the summer it produces a disease of the green leaves of several species of plants. When the leaves die it passes to the other form, *Cladosporium*.
3. *Cladosporium* is a later form and exists as a saprophyte on the dead leaves which have been previously attacked by *Hormodendron*. It can give rise to *Hormodendron* if the temperature be moderately high ; but at a lower temperature it reproduces itself.
4. In the winter *Cladosporium* exists in the form of microsclerotia which on the advent of the spring germinate to produce conidia of *Cladosporium* ; these conidia of *Cladosporium*, after germinating, give rise to conidia of *Hormodendron* which serve to continue the disease caused by *Hormodendron* during the summer.

A list of the species which are regarded as synonymous with *Cladosporium herbarum* is appended.

Cladosporium epiphyllum, Nees. Das Syst. der Pilze und Schwämme.

Cladosporium nigricans, Fr. Syst. Myc., iii, 370.

Cladosporium solutum, Link. Spec., i, 39.

Acladium herbarum, Link. Obs., i, 10.

Byssus caespitosa, Roth. Fl. Germ., iv, 566.

Byssus herbarum, DC. Fl. Fr., vi, 11.

Byssus nigricans, Roth. Catal., i, 126.

- Dematium articulatum*, Sow. Fung., T. 400, F. 8.
Dematium Brassicae, Pers. Syn. Fung., 699.
Dematium conicum, Schum. Fl. Saell., ii, 445, Nr. 2171.
Dematium epiphyllum, Pers. Syn. Fung., 695.
Dematium fungorum, Pers. Ibid., 699.
Dematium graminum, Pers. Myc. Eur., i, 16.
Dematium herbarum, Pers. Dispos. Fung., 75; Alb. et Schw. Consp. 1104.
Dematium Hippocastani, Pers. Syn. Fung., 698.
Dematium vulgare, Pers. Sec. Steud.

My thanks are due to Lieut.-Col. Prain, C.I.E., F.R.S., Director, Royal Botanic Gardens, Kew, for kindly permitting the work in connexion with this article to be carried out in the Jodrell Laboratory, and also to Mr. G. Massee, F.L.S., for his kind assistance.

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DESCRIPTION OF PLATE XXIV.

Illustrating Mr. Bancroft's Paper on *Cladosporium herbarum*.

Fig. 1. A tuft of hyphae of *Cladosporium herbarum* springing from a mass of cells and bearing conidia.

Fig. 2. A diseased leaf of *Catalpa bignonioides*, showing the effects of the disease caused by the form *Hormodendron*.

Fig 3 a. A conidium of *Cladosporium* which has germinated, and is producing conidia of *Hormodendron*.

Fig. 3 b. Another conidium of *Cladosporium* giving rise to *Hormodendron* after germination.

Fig. 4. Production of conidia of *Hormodendron* from a conidiophore of *Cladosporium* in a 'hanging-drop'.

Fig. 5. Early stages in the germination of conidia of *Hormodendron*.

Fig. 6. Hyphae of the mycelium of *Hormodendron* producing conidia in a culture in nutrient gelatine.

Fig. 7. Later production of conidia of *Cladosporium* from the same mycelium as in Fig. 6.

Fig. 8. Germination of a conidium of *Cladosporium* in a culture in nutrient gelatine with formation of conidia of *Cladosporium*.

Fig. 9 a. Production of conidia of *Cladosporium* by a conidium of the same form which has germinated at a low temperature.

Fig. 9 b. The same as in Fig. 9 a.

Fig. 10. Germination of a microsclerotium.

Fig. 11. A conidium produced by a microsclerotium giving rise to conidia of *Hormodendron* after germination.

Fig. 2 natural size; Fig. 10 magnified $\times 400$; the others magnified $\times 600$ (about).

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