The Cytology of the Laboulbeniales.

BY

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INTRODUCTORY.

A PRELIMINARY note on the cytology of the ascus of the Laboulbeniaceae was published by the writer in 1906. Since then a considerable quantity of material has been accumulated and the earlier studies on this exceedingly interesting group have been extended to many additional forms and to the cytological phenomena of their entire life cycle. In the course of these studies the observations first recorded have been repeatedly verified, and many new facts have come to light. Several features are still under investigation. This introductory account of the researches so far accomplished will be followed by others dealing in greater detail with the topics presented below.

I wish here to express my obligations to Professor Roland Thaxter for his generous interest and kindnesses throughout, and to Professors Farlow and Thaxter for the facilities of the laboratories of Cryptogamic Botany of Harvard University so kindly placed at my disposal during several months of last year.

SPORES.

The spores are uninucleate in their earliest stages. The nucleus divides once before the spore is mature, but a septum immediately effects the separation of the spore contents into two cells. In *Amorphomyces* alone of all the genera examined does this septum not form, in which case the lower of the two daughter nuclei (with reference to the orientation of the spores in the ascus) at once degenerates, so that when the spores are shed they are non-septate and contain but a single nucleus.

THALLUS.

The cells of the thallus are characteristically monoenergid. After the thallus has completed its normal growth, the nucleus in the larger cells of the receptacle of certain genera may undergo one or several divisions. This

phenomenon has been noted frequently in *Ceratomyces* and *Laboulbenia*. The same thing is true of the nuclei of the richly stored inner cells of the perithecium.

The nucleus divides mitotically, not only in the young spores and thalli, but also in the older cells. An ordinary spindle is formed at each division, on which are arranged the chromosomes, and at each end of the spindle there is a central body.

The entire plant body is enclosed by a thin chitinous membrane that is exceedingly resistant to the penetration of fixing reagents. The walls of the cells are thick and laminated. Those that separate cells of common origin contain a single deep pit, interrupted only by the middle lamella. There are protoplasmic bridges, but sometimes, as in the receptacle and perithecium of *Laboulbenia chaetophora*, they are very tenuous.

The cytoplasm is finely granular or spongy-reticulate, and often contains abundant granular inclusions, or globules of oil. Very often, especially in *Laboulbenia*, one finds a more or less clearly defined organization of cytoplasmic strands bearing a definite relation to the pits or to the nuclei.

THE ANTHERIDIA.

The antheridia, as is well known, are of two general types—*exogenous*, as in *Zodiomyces*, and *endogenous*, as in *Laboulbenia*. The endogenous are again of two sub-types—simple, as in *Stigmatomyces*, and compound, as in *Dichomyces*. The antheridia are usually borne along with the female organs on the same plant, but in *Amorphomyces* and a few others the sexes are separate.

Exogenous antheridia were studied in *Rhyncophoromyces* and *Zodiomyces*. They were found to be uninucleate. The spermatia are formed as short lateral branches at the upper end of the antheridia, and they, too, are uninucleate. There are indications, in my preparations of *Rhyncophoromyces*, that the spermatial rods, as soon as they drop off, are replaced by the outgrowth of others from the same base, in which case the antheridial nucleus must undergo repeated divisions in order to supply each spermatium in turn.

Simple endogenous antheridia were studied in *Stigmatomyces*, *Dioichomyces*, *Amorphomyces*, and *Laboulbenia*. The antheridium is invariably occupied by a single nucleus. Prior to the formation of a spermatium the nucleus divides mitotically, and the chromatin destined for the upper daughter nucleus, the nucleus of the male element, is literally pushed during the telophase stage of division up to the mouth of the efferent tube by the remarkably orientated and elongated spindle fibres. This phenomenon is regularly repeated at the birth of each spermatium. The spermatia contain a relatively large nucleus and a small amount of cytoplasm, and appear to be covered by nothing more than a thin protoplasmic membrane.

The compound antheridia of three genera were examined—*Dichomyces*, *Dimorphomyces*, and *Enarthromyces*. The nucleation observed was seen to differ in no way from that of the simple antheridia. The nature of the common chamber into which the efferent passages of the individual antheridia open was not determined. But an examination of specimens of *Enarthromyces* kindly loaned me by Professor Thaxter seems to show that they are, in this form at least, modified cells. It is possible, too, that the compound antheridium has originated quite independently more than once in the course of the evolution of the forms bearing simple antheridia, and in different ways, that is, on the presumption that the latter is the more primitive type.

THE PROCARP.

The procarp of several genera has been examined, but that of *Dioichomyces*, *Amorphomyces*, *Stigmatomyces*, and *Laboulbenia* has received most careful attention. There are many difficulties attendant on the elucidation of the nuclear phenomena, so that except in the case of *Laboulbenia chaetophora* I am not yet in a position to state with sufficient positiveness the origin of the pair of nuclei found eventually in the carpogenic cell.

The procarp has its beginnings as a single uninucleate cell, an outgrowth from the receptacle. It develops into a structure that consists of three parts—a uninucleate carpogenic cell, a uninucleate trichophoric cell, and a trichogyne. The trichogyne, as in *Stigmatomyces*, is unicellular and uninucleate, or, as in several species of *Laboulbenia*, is a more or less highly branched and septated organ. About the time the carpogonium becomes binucleate the trichogyne withers, and then the trichophoric cell begins to degenerate. I have seen spermatia attached to trichogynes, but, as yet, have not been able to demonstrate their entrance into or fusion with them, possibly on account of the dense stain taken by the receptive cells of the trichogyne at this stage. Nor have I been able to detect a nucleus migrating down through the trichophoric cell.

The carpogenic cell does acquire a second nucleus, and the ascogenic cells, too, in all the genera that have come under observation, are binucleate. In some forms the intermediate stages have been followed more or less completely, showing that the binucleate condition is maintained. I have seen no evidence of a nuclear fusion in the carpogenic cell or ascogonium, though the possibility of the occurrence of such a fusion is not precluded.

As for *Laboulbenia chaetophora*, it is possible to give a practically complete account of its developmental sequence. This species, like its near relative *L. Gyrinidarum*, is interesting because of the lack of antheridia, or of any organs that might function as antheridia. The trichophoric and carpogenic cells are uninucleate at the outset. The nucleus of the latter very soon divides, and one daughter passes to the lower end of the cell,

which is subsequently cut off as the inferior supporting cell, the other to the upper end. The nucleus of the trichophoric cell now moves down next to the carpogenic cell, and divides mitotically. The membrane separating the two cells at this time disappears. One daughter of the trichophoric nucleus next moves back to the earlier position occupied by the mother nucleus, and is later cut off by a septum; the other remains with the upper nucleus of the carpogenic cell. This pair now undergo division. A transverse partition then cuts the carpogonium into a binucleate superior supporting cell and a binucleate ascogonium. Presumably the nuclei in the ascogonium again divide, to supply a binucleate secondary inferior supporting cell which is cut off from the lower end of the ascogonium. I cannot speak with certainty of the nucleation of the supporting cells in all instances. There may be variations such as have been found to be the case in the cells adjoining the ascogenic cells in many other Ascomycetes. The binucleate ascogonium now usually divides by a nearly vertical wall into a pair of binucleate ascogenic cells, but may at once, without dividing, begin to bud off asci.

THE ASCUS.

The two nuclei of an ascogenic cell divide simultaneously and mitotically at the advent of each ascus. A daughter of each passes into the young ascus, where they fuse. The definitive or fusion nucleus of the ascus now enters on a long period of growth, and finally attains a large size. Eventually it undergoes three successive mitoses. The first exhibits clearly the phenomena said to be characteristic of meiosis, except that neither here nor in the two subsequent divisions is there any change in the number of chromosomes. The central body is present and lies outside the nuclear membrane. In the prophases of mitosis its relation to the chromosomes is very evident. The second division follows rapidly on the first, but the third takes place more leisurely.

Directly after the third division spore formation begins, which differs in no respect from the method characteristic of sac fungi. The astral rays are thin, long, and quite conspicuous, and are to be seen within the spore for some time after its delimitation. They do not unite to form the protoplasmic membrane bounding the young spore, and, apparently unmodified, have been observed in some cases twisted about the long neck of the nucleus while the central body of the latter was still in connexion with the spore membrane. The cavities in which the spores lie are also lined by what appears to be a protoplasmic membrane. The spores of all the forms examined, with the exception of *Amorphomyces*, as already noted, become two-celled.

Four spores only are formed, four nuclei of the last division passing to the apex of the ascus, where they function no further, and finally disintegrate. The functional nuclei, in *Laboulbenia chaetophora* at least, are the

lower ones on the spindles of the last mitosis. There are some reasons for believing that the same is true of *Amorphomyces* and *Dioichomyces*, in which case sexual differentiation of the spores might be determined in the second division.

RELATION TO HOST, AND OTHER FACTORS.

The foot of such forms as *Laboulbenia Gyrinidarum* and *L. chaetophora* lies closely appressed on the surface of the host, but does not penetrate its chitinous covering or produce any visible changes in its underlying tissues. This is not true of all, however, as, for example, of *Stigmatomyces*, *Dimero-mycetes*, and *Dioichomyces*. In the last there is a distinct hypertrophy of the tissues in the neighbourhood of the point of attachment of the fungus, and in the two former there is, especially under the older and larger tufts, often a disorganization of a more or less extensive patch of cells, which sometimes extends through the entire body wall. I have not had the opportunity of examining any species possessing rhizoids.

Whatever part the appendages play in the life of the fungus, that is to say, as to whether or not they act to a certain extent as absorbing organs, it may be stated here that their cells are well nourished throughout, exhibit some power of regeneration, and do not show signs of senescence often seen in the larger cells of the receptacle.

The members of several species—for example, of *Stigmatomyces* and *Dioichomyces*—lie flat against the hosts in their earlier stages of development. At maturity, however, the stalk cell of the receptacle bends so as to bring the plant into a position approximately at right angles to its former one. The young plants thus appear to enjoy the advantages of greater security against desiccation, and in the later stage spore dissemination is facilitated.

The moisture relation also exhibits itself in the relative thickness and permeability of the chitinous general envelope. In *Zodiomyces* and other aquatics this membrane is usually much thinner and more permeable than in terrestrial forms. The same may be said of species that grow on the under side of the body in comparison with those that grow in more exposed situations. This fact may be readily confirmed by reference to species of *Dioichomyces*, two or three of which are often to be found on the same insect, or to individuals of a species not restricted to a limited position on the host.

THEORETICAL.

One of the most obvious conclusions to be drawn from a cytological study of the Laboulbeniales is the fact of their evident Ascomycetous nature. The spore sac has quite the same right to be designated an *ascus* as has the spore sac of the most typical Ascomycetes. As to their place

among the Ascomycetes, if the possession of a perithecium is the one distinctive character of the Pyrenomycetes, then there is no good reason why the Laboulbeniales should not constitute a well-marked subdivision of this order.

The resemblance of the procarp to that of the Florideae, on the one hand, and to that of certain Fungi on the other, has long been recognized. Cytologically, it stands nearer the latter. The phenomena of conjugate nuclear division, and in *L. chaetophora* of a reduced type of sexuality, suggest similar phenomena in the rusts and certain Ascomycetes.

The nuclear phenomena in the antheridia appear to be of far-reaching import. The gap between the exogenous and the endogenous types is bridged by such a form as *Coreomyces*. Such features as a uninucleate antheridium, the possibility of proliferation of spermatia from the same antheridium, and the exogenous type of spermatium organization, suggest similar phenomena in the rusts, many Ascomycetes, and the Florideae. But further investigations are needed on the antheridia of all of these groups.

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