Name: Marla Ann Morgan Date of Degree: May 23, 1965

Institution: Oklahoma State University Location: Stillwater, Oklahoma

Title of Study: CAPILLITIAL FORMATION IN THE MYXOMYCETES

Pages in Study: 26 Candidate for Degree of Master of Science

Major Field: Natural Science

Scope and Method of Study: This report was undertaken as a survey of the information available to date concerning capillitial formation in the Myxomycetes. Some attention was given to the phylogenetic and taxonomic position and the morphology of the group. The major theories advanced in explanation of this formation were treated in a historical context. Capillitial formation of the Stemonitaceae, Physarales and Trichiales was given detailed treatment. A brief account was given concerning environmental effects on the total fruiting process.

Findings and Conclusions: In the immature Trichialess and Physarales, the protoplasm becomes highly vacuolated. These vacuoles are formed by the liberation of water in which various materials furnishing the substances for capillitium formation within the vacuoles are dissolved. This vacuolar system corresponds to the appearance of the capillitium in a mature sporangium. In the Physarales the capillitial material is deposited on the surface of the vacuoles. In the Stemonitales and Echinosteliales the capillitium either forms as an outgrowth of the columella or is deposited in the cytoplasm without previous formation of a vacuolar system. Environmental influences can only be inferred from data regarding environmental effects on the total fruiting process.

ADVISER'S APPROVAL John E Thomas

CAPILLITIAL FORMATION IN THE MYXOMYCETES

By

MARLA ANN MORGAN

Bachelor of Arts

Kansas Wesleyan University

Salina, Kansas

1964

Submitted to the faculty of the Graduate School of
the Oklahoma State University
in partial fulfillment of the requirements
for the degree of
MASTER OF SCIENCE
May, 1965

CAPILLITIAL FORMATION IN THE MYXOMYCETES

Thesis Approved:

John E Thomas

Thesis Adviser

L. Herbert Bruneau

Dean of the Graduate School

PREFACE

Because of their often conspicuous fructifications, the Myxomycetes have long been familiar. Because of their questionable kingdom classification and phylogenetic position, however, much of the work done on them has been left to the mycologists and has been taxonomic in nature; in comparison, little work has been done on such topics as covered by this paper. The purpose of this study is to present a brief introduction to the Myxomycetes and bring together the work that has been done on capillitial formation in this group.

Special acknowledgement is given to Dr. John Thomas for initial introduction to mycology and continued assistance and interest in further work in this area. Mr. C. M Howland also provided valuable assistance in finding research materials on the Myxomycetes.

TABLE OF CONTENTS

CHAPTER I

AN INTRODUCTION TO THE MYXOMYCETES

Phylogenetic and Taxonomic Position

The Myxomycetes, with their conspicuous and often delicate fructifications, have long been familiar organisms. While older mycologists accepted them as fungi (though Fries did recognize the distinction between their plasmodial phase and the mycelium of other forms), it was only as a result of DeBary's (7) extensive investigations of the life history of certain species that the animal affinities of the slime molds were brought out and the name Mycetozoa proposed. Since DeBary's time the group has been included in works in both botany and zoology. Zoologists include the slime molds in the Protozoa; a representative treatment places them in the order Euplasmodida where, along with Acrasida and Phytomyxida, they are regarded as comprising the subclass Mycetozoa of the class Rhizopoda (in the subphylum Sarcodina). Botanists tend to include the slime molds among the Thallophyta as an independent group coordinate with the bacteria and fungi. Thus botanists and zoologists are agreed that the Myxomycetes show evidence of relationship with forms commonly included among the Protozoa.

If the fungi are thought of as descended from the green algae (either as a monophyletic or polyphyletic group), the Myxomycetes are excluded. On the other hand, if the fungi are considered as a monophyletic group descended from colorless flagellates, the Myxomycetes form a natural class, the lowest of four (the others being the Phycomycetes,

Ascomycetes and Basidiomycetes). The two major divisions in this class are the Exosporeae, in which the spores are borne externally on individual stalks, and the Myxogastres, in which the spores are borne internally in fructifications. It has been generally agreed that the Myxomycetes be regarded as a phylum which has not definitely developed into either flora or fauna, but may be grouped with the flora as a matter of convenience and in accordance with custom.[1]

Morphology of the Myxomycetes

> The Myxomycetes are fungus-like organisms characterized by an assimilative phase consisting of a naked, multinucleate, mobile mass of protoplasm, the plasmodium, and a reproductive phase, consisting in most instances of a membranous spore case. The latter often contains, in addition to the spores, a system of netted or free threads, forming the capillitium, and frequently bears, within or without, calcareous accretions of specific character.[2]

The Myxomycete spore, upon germination, emits a vesicle which gives rise to one or more swarm-spores, each characterized by an anterior flagellum. Or the swarm-spores may also be produced directly from the spore, without the formation of a vesicle. In either case, these feed and multiply, eventually function as gametes and fuse in pairs (or sometimes larger groups). This resultant zygote is the first stage of the plasmodium; it grows by karyokinesis and in some cases also by fusing with other plasmodia, and, under appropriate conditions, gives rise to the spore-producing fructification. The changes through which the plasmodium passes in transformation into a fructification have been followed in several species. By 1791 certain external features of this

---

[1] G. W. Martin, "Systematic Position of the Slime Molds and Its Bearing on the Classification of the Fungi," Botanical Gazette, XCIII (April, 1932), pp. 421-435.

[2] T. H. MacBride and G. W. Martin, The Myxomycetes (New York, 1934), p. 1.

process were noted and illustrated; it was not until 1859, however, that DeBary attempted to trace the details in the species Fuligo septica. Studies since, combining morphological and cytological detail, have shown the process to vary somewhat, depending upon whether the organism is plasmodiocarpous or sporangiate.

The essential parts of the sporangium are the enclosing wall and enclosed spores. A capillitium, composed of netted tubes or thread-like processes, is often present. In some forms this capillitium is lacking (as in the Exosporeae, Licea and Cribaria). In Badhamia it is a relatively crude and ineffective network of limy tubes while in Physarum and related genera the lime is aggregated into nodules which are connected by a network of almost or entirely limeless tubules. In Stemonitis, Comatrichia and Lamproderma the capillitium arises as branches of the columella. In Hemitrichia and Arcyria it takes the form of a network of elaborately sculptured tubes, while in Trichia the threads are like those of Hemitrichia but shorter and separate. Lycogala, Reticularia and Enteridium have a pseudocapillitium[3] composed of coarse tubes or frayed or perforated plates. In all cases, however, the capillitium is a group of non-living, hair-like structures which may be united to form a network attached to the columella or peridium, or which may consist of simple or branched filaments, unattached and independent of each other.[4]

---

[3]Cf. T. H. MacBride and G. W. Martin, The Myxomycetes (New York, 1934), p. 10: "The distinction is based on the method of formation, the true capillitium being formed of materials laid down by intra-protoplasmic secretion on the walls of vacuoles or tubular invaginations, while the pseudocapillitium is the direct product of the degeneration of a portion of the protoplasm itself."

[4]Constantine J. Alexopoulos, Introductory Mycology (New York, 1964), p. 91

The capillitium undoubtedly aids in spore dispersal, forming a spongy mat of threads, which may expand when the peridium has disintegrated, carrying the spores with it to a considerable height above the base of the fructification. The spores are then easily dispersed from this position by air currents. This does not preclude their taking, as noted, a great variety of forms--sometimes definite elaters with spiral markings, sometimes a simple basket-work of smooth threads of various shapes. The presence and type of capillitium are consequently important characteristics in Myxomycete classification, for example:

Key to the Order of the Myxogastres

A. Spores in mass pallid or brightly colored to dingy olivaceous

B. True capillitium and columella lacking . . . . Liceales

BB. Capillitium or columella characteristically present

C. Stalked, minute; columella present, rarely lacking . . . . . Echinosteliales

CC. Stalked or sessile, larger; columella never present. . . . . Trichiales

AA. Spores in mass black or deep violaceous to furriginous

D. Neither peridium nor capillitium calcareous. . Stemonitales

DD. Peridium or capillitium or both calcareous. . Physarales[5]

---

[5]Ibid., pp. 69-70.

CHAPTER II

HISTORICAL BACKGROUND AND MAJOR THEORIES

The nature of the capillitium as an intraprotoplasmic secretion was first recognized in 1884 by Strasburger (19), who noted the fundamental differences between the method of its formation and that of the structurally and functionally similar elaters of the liverworts and mosses. He described the capillitium of Trichia fallax as originating in cytoplasmic vacuolar spaces which elongate and take on the tubular form of the young capillitial threads. He attributed the formation of the wall and spiral thickenings to the deposition of granules, similar to those he believed were also found in the formation of the cell-plate in cell dividion in the higher plants. The essential point in his description is that the capillitial threads are not elongated cells, but are intracytoplasmic secretions or depositions.

DeBary (6) in 1887 first characterized the capillitia in several genera of the Mycetozoa. The capillitium of Physarum and its allies consists of thin-walled non-septate tubes which spread their branches in every direction and combine into a network. Many branches run from the periphery of the net-work to the wall and are firmly attached to it by their funnel-shaped extremities. The tubes are swollen and inflated at the nodes of the network, forming calcium carbonate cavities which may also contain pigment. All the Calcareae have a capillitium which is uniformly attached by the ends of its branches to the wall of the sporangium

in the manner just described. In Didymium the capillitium consists of very slender threads which are cylindrical or slightly flattened, solid or with some indication of a cavity in the form of a line in the longitudinal axis. The threads usually do not contain calcium carbonate; but in a few cases, they enclose single calcium carbonate granules. They run upward from below, usually straight in a radial direction from the insertion in the stalk to the upper and lateral wall, their anastomoses usually forming an acute angle. The capillitium of the Trichiae and Arcyriae consists of tubular threads which have no calcium carbonate deposits and are either not or only partially attached to the sporangial wall. In Arcyria it is a nonseptate tube separating into countless branches which form a net-work by their anastomoses. In most species the capillitium is not connected with the wall, but is fastened loosely by a few branches from the tubes which descend into the stalk. The capillitial tubes of Trichia and Hemiarcyria are united into a net-work with branches which at the same time have free extremities. The capillitia described, though of many and apparently very different kinds, DeBary (6) regarded as all being peculiar membranous or parietal formations secreted or excreted from the protoplasm. All that was known concerning capillitial development at that time he thought harmonious with the conception that they are totally or partially hollow and take up excreted matter into their cavity.

Kranzlin (14) in 1907 described the capillitial threads as arising from centrosomes of heteropolar spindles, which become an "elateroplast" marking the starting point of a capillitial vacuole. Her conception was that the capillitial threads are phylogenetically derived from flagella.

On the basis of their extensive work with two species of the Trichiales, Harper and Dodge (11) agree with Strasburger that the

formation of the capillitium begins with the appearance of vacuoles of oval or irregular outline which early become connected together to form series and anastomosing systems of openings in the cytoplasm. They found the cytoplasm immediately surrounding these vacuoles to become very dense, with many fibrils more or less radiately arranged. The nuclei, at first evenly distributed through the cytoplasm, simultaneously with vacuole appearance, take up a characteristic position which persists through the process of capillitial thread differentiation. They at first move away from the vacuoles to a rather constant distance; later the outer nuclei seem to migrate also, moving in toward the vacuoles, so that finally all are gathered in a definite layer around the forming capillitial threads. Between this nuclear zone and the vacuoles the cytoplasm is quite dense; beyond the nuclei it is much more openly reticulated in appearance. The nuclei evidently gather about the vacuoles in which the threads are to form but are crowded back out of the denser cytoplasm which immediately surrounds the vacuoles. This characteristic relation persists until the capillitial threads have attained their normal form and diameter. The vacuoles are at first angular and joined by narrow anastomosing extensions into series which wind through the cytoplasm in the manner of the future capillitial threads. If the mature capillitium is to be of simple non-branched threads (as in Trichia), the vacuoles form either a single series or one vacuole elongates to form a thread. If the capillitium is to form a reticulated net, a single vacuole may become connected with several others instead of with only two. The vacuolar membrane Harper and Dodge found with no special thickening or differentiation at this time; apparently they are ordinary boundaries enclosing sap like that in ordinary vacuoles. The capillitial vacuoles anastomose and come to have the constant diameter of the future thread. The pathway of the threads in the cytoplasm

is already determined at this stage. The series of connected vacuoles form a nodular thread, the vacuoles constituting a series of vesicular expansions on a continuous vacuolar opening whose course through the cytoplasm is that of the future thread. (At this stage the system of anastomosing vacuoles may be compared to the mature capillitium in Physarum and Badhamia. The latter may in fact represent a more primitive stage through which the capillitia of Trichia and Hemiarcyria pass in their development.) The stages following involve the "smoothing" of the vesicular expansions into tubular threads of constant diameter throughout. This apparently consists in the reduction of the diameter with a corresponding increase in length and thus a more extensive winding of the mature threads. The greater part of the change in form of the original vacuolar series seems to go to increase the length by reducing the transverse diameters.

Harper and Dodge (11) deem the most striking and characteristic feature in this total process as the appearance of fibrillar asters about the capillitial vacuoles. There is no question that these rays in the slime molds are actual fibrils and when cut transversely, they appear as points. (Certain cases involving radial systems of these fibrils probably led Kranzlin to regard these as astrospheres about real centrosomes.) The fibrils are commonly not oriented on the center of the capillitial thread due to the fact that they are really oriented on the granules. The fibers of one system may extend through the cytoplasm until they reach and mingle with those from the next adjacent system. The differentiation of the membrane of the capillitial thread goes on rapidly during this period while the radiating fibrils are conspicuous and the nuclei maintain their zonal distribution. The conditions suggest that the fibrils represent cytoplasmic streams which bring in material for formation of the

capillitial wall and its thickenings. In such case it would seem that the granules on which the rays are centered should be regularly distributed on the boundary of the forming capillitial thread. However, this is not the case and the granules cannot be regarded as at all completely representing the material brought in, even in case the fibrils are interpreted as having their origin as streams of cytoplasm. But the fact that the formation of the capillitium implies the deposition of materials in the vacuolar spaces first formed naturally suggests that these radially placed lines mark the pathways by which materials are brought in from the surrounding cytoplasm. The accumulation of the nuclei in a quite definite zone at a rather constant distance from the forming thread may be further evidence of their relation to the metabolic factors in the growth and morphogenetic processes and suggests that they may be concerned in some way in the production of the material to be used in capillitial formation.

Spirals when first formed are markedly granular. They constitute thickenings formed on the membrane of the capillitial tube. Apparently they form simultaneously along the thread rather than progressively or intermittently. The material of the spiral seems definitely to be deposited as granules. The granular material in the capillitial thread interior lessens as the wall thickens and spirals appear, and as the thread matures, it almost disappears. However, there is no evidence that granular material as such passes from the thread interior into the forming spirals. It is speculated that the stainable granules in the thread interior may be precipitation products formed in fixation and that in the living condition the capillitial cavity contains only materials in solution in the cell sap. These materials may be used up in the formation of the capillitial wall and spirals so that in later stages no such precipitation products are formed.

The deposition of materials in the vacuoles from which capillitial threads are formed is intraprotoplasmic secretion and is undoubtedly an adaptive morphogenetic process similar to that by which other soluble materials are deposited in the cell sap of vacuoles and may then crystallize out if the solution becomes sufficiently concentrated. Such crystals are regularly formed in the vesicular nodes of the capillitium of Tilmodoche, Physarum, and other types.[1]

The formation of the capillitial thread membrane with its sculpturings may be conceived as comparable to the ordinary processes of cell-wall formation. The materials of the capillitial wall are dissociation products of proteid, whether considered as set free by secretion or by direct transformation. If the chemical changes which result in the production of the solid elastic and hygroscopic capillitial thread out of the watery colloidal cytoplasmic mass involves a reduction in volume, tensions should be set up. The formation of vacuoles as the initial step in the development of the thread may be conclusive proof that the production of the solid materials of the wall of the thread involves the freeing of water which may start as containing considerable quantities of dissolved transition products. These dissolved materials presumably are used up in the process of building the thread. The chemistry of the process involved in capillitium formation then consists of at least three steps: the process is initiated by the liberation of water and the formation of vacuoles; the vacuolar sap at first contains materials in solution which later disappear and probably furnish material for the capillitial wall and spirals; the spirals are laid down as organized material, in a

---

[1]R. A. Harper and B. O. Dodge, "The Formation of the Capillitium in Certain Myxomycetes," Annals of Botany, XXVIII (1914), p. 8.

definite form on the outside of the thread next to the vacuolar membrane.[2] Gates (8) is in agreement that initiation is by water liberation and vacuolar formation, but elaborates that the deposition of these spiral bands must be determined by some rhythmic or repetitive process in the protoplasm.

---

[2]Ibid., p. 14.

CHAPTER III

CAPILLITIAL FORMATION IN SELECTED MYXOGASTRES

The formation of capillitia in the slime molds is in many ways a unique process and further, more recent studies have elaborated on the previously discussed basic pattern laid down by Harper and Dodge. Most of this work has been limited to studies of individual species and, although these species are grouped into related orders for convenience in study, obviously the findings concerning a particular species are not necessarily representative or characteristic for their order (though, of course, this is hoped for in a majority of cases).

Stemonitaceae

Bisby (4) was one of the earliest workers to confine his studies of capillitial development to selected species (Physarella mirabilis Peck and Stemonitis fusca Roth). From his work with Stemonitis, he concluded that the capillitial threads in S. fusca, at least, are hollow and that the method of deposit of capillitium is almost the same as found in Physarella. Bisby's observations are in accord with DeBary's in that the lumen of the columella is not continuous with the lumen of the capillitial thread. The attachment of capillitial threads to the central columella in Stemonitis displays a condition somewhat comparable to the attachment to the sporangium wall in Physarella. In Stemonitis the threads are in connection with the exterior deposition on the columella, pointing to the

fact that the threads are formed by a deposition no different from that forming the columella, nor from the wall itself. That the thread lumen is not continuous with the lumen of the hollow columella shows that in these instances, at least, the capillitial cavities were started to be formed sometime after the columella wall deposit had attained some degree of thickness.[1] Even though the capillitial thread exteriors in the two species studied contrasted sharply to those in certain of the other Myxomycetes (like Trichia), Bisby found the process of formation to be similar: deposition of hollow threads by plasma membranes lining tubular capillary spaces. In Physarella and Stemonitis, however, the capillitial cavities are very narrow, while in Trichia, they are relatively wide. Also, in Trichia and like genera, the capillitium begins in vacuoles in the interior of the protoplasm, while in Physarella and Stemonitis these spaces originate as invaginations of the external plasma membrane or that lining the capillitial or columellar cavities. Bisby thought this of fundamental importance to the exterior capillitial appearance. Also apparent from his study is that the cleavage furrows are influenced and defined to a considerable degree by the capillitial threads in the two species studied.

In 1949 Wolf and Wolf (21) also studied Physarella mirabilis and Stemonitis fusca. Their conclusions were somewhat similar to Bisby's: capillitium arises during sporangial cleavage among tubular spaces formed from invaginations; the plasma membrane lining these spaces progressively deposits substance that becomes the walls of capillitial threads.

The capillitium begins to form from the columella tip in Comatrichia nigra and Comatrichia elegans and from the stalk tip in Comatrichia

---

[1]G. R. Bisby, "Some Observations on the Formation of the Capillitium and the Development of Physarella mirabilis Peck and Stemonitis fusca Roth," American Journal of Botany, I (1914), p. 285.

fimbriata. The capillitial initials in their earliest stages are extremely fine hyaline threads radiating from the columella or stalk tip toward the periphery of the sporangium. It appears that the capillitial strands are continuous with the individual fibers in the columella. In the species with columella, the initial capillitial elements form at the apex; fibers in the lower parts of the columella then bend outward at right angles to form the lower capillitial branches. The earliest initials develop into the main branches of the capillitium, elongating at the ends until reaching the outer surface of the protoplasmic mass. Secondary branches quickly appear, developing in a wave from the interior toward the surface. The capillitial threads apparently thicken by means of protoplasmic deposition. Pigment appears to color the branches and the capillitium is then mature. Cellulose is definitely present in the capillitium and develops secondarily after a non-cellulosic skeleton has formed. This delay in cellulose formation is shown in sporangia with developing capillitium; the text for hydrocellulose is positive in the oldest portion of the threads and is negative in the newer net part.[2]

The apex of the stalk and columella and the ends of the capillitial threads of Stemonitis, Comatrichia and Lamproderma all appear to blend gradually into the cytoplasm surrounding them. New evidence indicates the stalk, columella and capillitium of members of the Stemonitaceae are formed as intraprotoplasmic secretions, not as secretions through a membrane or by the thickening of a pre-existing one. The difference in the mature capillitia of Stemonitis, Comatrichia and Lamproderma is revealed by the differences found in the development of the capillitia of these genera. In Comatrichia the lateral development of the capillitium

---

[2]D. C. Goodwin, "Morphogenesis of the Sporangium of Comatrichia," American Journal of Botany, III (1961), pp. 150-153.

begins by the outward bending of the tubes of the columella into the sporogenous protoplasm. Even though these tubes do not elongate further until secondary branching commences in the apex, they are already formed and can elongate very rapidly. Since each lateral branch develops individually there is little anastomosing of these main lateral branches and the other ends remain free. In Lamproderma the lack of much secondary branching enables the major capillitial threads to grow to the periphery directly from the columella with scanty anastomosing. In experiments conducted with Lamproderma arcyrionema, Ross (18) finds that from initial apical tubules to capillitial extension throughout the sporangium requires only ten minutes. It was not determined whether the development of the capillitium proceeds from the apical tubules outward or whether it is laid down all at once on a preformed system of tubes or vacuoles in the cytoplasm which then connects up with the apical threads. The initial capillitial threads are the apices of the stalk tubules which bend out into the protoplasm and have been formed by the gradual addition of material to their ends.

In contrast to the manner in which capillitium is formed in the species of Trichiales and Physarales which have been investigated, Ross finds no invaginations or vacuolar tubes in the seven species of Stemonitaceae which he studied, the capillitial threads in these species blending gradually into the protoplasm without evidence of any membrane surrounding them. He further reports some differences in capillitium formation between Comatrichia typhoides and two species of Lamproderma, on one hand, and four species of Stemonitis on the other. In C. typhoides the stalk is composed of a bundle of hollow tubes which elongate upward forming the columella. The outer tubes bend outward from the columella, grow, branch and form the capillitium. Thus the capillitium in this species originates

entirely from the columella. In the species of Stemonitis investigated, the capillitium originates both from the apex of the columella and independently from the surrounding protoplasm. Capillitial tubes which originate in the cytoplasm branch down the periphery of the sporangium and form the surface net. In Stemonitis there are no individual tubes capable of bending away from the columella to form lateral branches. Lateral branches do not arise from the columella until the columella has reached its full height, and then only concurrently as the network is forming independently in the periphery of the sporangium. The apical and peripheral portions of the capillitium form concurrently and the rapid wave of secondary branching and anastomosing is complete before the lateral outgrowths from the columella have had time to grow to the periphery. When the ends of the lateral branches do reach the periphery, the peripheral net is already there, and the ends of the lateral branches fuse with the net.

In the Stemonitaceae once the columella is mature, differentiation of the capillitia proceeds downwards. Until the upward differentiation of the columella is complete, the downward development of the capillitium is unable to begin.[3]

Physarales

In Physarella mirabilis when the plasmodium first begins to form lumps where sporangia are to occur, the protoplasm appears like that of the vegetative stage except that much of the extraneous substances has been extruded and left along a slimy trail. Shortly, however, spaces

---

[3] I. K. Ross, "Capillitial Formation in the Stemonitaceae," Mycologia IL (1957), p. 814.

appear in the protoplasm into which waste substances (largely lime granules) are excreted. As it becomes more granular, in sections of the protoplasm fine tubes can be detected, sometimes connecting the knot spaces with the exterior and occasionally without any discernable attachment to a developing lime knot. The membrane surrounding the tubular opening is continuous with the membrane surrounding a knot space (if any of the knot spaces are in connection with this opening). The lime knot, usually filled with cystolithic granules of calcium carbonate, and capillary tubules connected with it are bounded only by a plasma membrane continuous with the membrane at the external surface of the protoplasm. The threads are not all formed simultaneously. Spaces without deposition may be found concurrently with capillitial threads which are nearly mature.

In P. mirabilis tubular capillary spaces appear in early stages of sporangial development. These spaces may be filled with watery sap and aqueous waste since they are connected with lime-knot spaces and open upon the developing outer membrane. From the plasma membrane surrounding these capillitial primorida, wall substances are next secreted. The substance secreted to form the walls of these hollow threads is probably plastic for some time after formation. In addition, there may occur a wrinkling or folding of the thread during the process of drying, particularly in relatively broad regions. Frequently there are lumens within the thread, but solidity may occur when material is deposited in a tubular space of capillary proportions. The same method of deposit holds true in the formation of walls about both lime knots and capillitial threads as that in the formation of at least the inner part of the sporangial wall.

The results presented by Welden (20) in 1955 for capillitial formation in Badhamia gracilis and Didymium Iridis agree in most details with those presented by Bisby for P. mirabilis and S. fusca and those of

Cadman (5) for Didymium nigripes. In both B. gracilis and D. Iridis the capillitium is formed by the coalescence of tubular invaginations originating from the peridial walls and from vacuoles in the protoplasm of the developing sporangium. This system of tubes becomes filled with calcium carbonate and other excretory products, which, in B. gracilis, form a calcareous capillitium, whereas in D. Iridis they are transported to the exterior of the sporangium or to the columella. Thus the formation of capillitium in these two species of Physarales follows in its initial stages the pattern which had been established by Harper and Dodge for Trichiales with this difference: that in Hemitrichia clavata and Trichia sp. capillitial material is deposited on the walls of the vacuolar tube system, whereas in B. gracilis and D. Iridis capillitial material is deposited within the vacuolar tubes. However, the lime-knots seem to be formed as a result of the excretion of calcium compounds into the vacuoles resulting from protoplasmic condensation.

Howard (12) relates that a capillitium of elongated vacuoles of equal diameter characteristic of some Badhamia species precedes the formation of a typical physaroid capillitium of capillary threads joined to angular lime-knots. In B. gracilis this was not found to be true. The Physarum-resembling vacuoles and invaginations form directly without any intermediate stages. The capillitium of D. Iridis is composed almost wholly of small tubular invaginations and any vacuoles present either do not or only slightly elongate. The threads of Didymium, which have a very narrow lumen or no lumen at all at maturity, are at first hollow.

As noted, Strasburger believed the capillitium to be the result of intraprotoplasmic secretion and Harper and Dodge have also followed this interpretation. In B. gracilis and D. Iridis, however, Welden did not find this to be true. The threads arise as invaginations from the peridial wall

in Badhamia and from the peridial wall and columella surface in Didymium. The calcareous compounds are excreted into the vacuoles in solution and the water evaporates, leaving the calcium carbonate either on the peridium or in the capillitium or both.

Trichiales

The only extensive work with the Trichiales has been done by Harper and Dodge (11) with Hemitrichia and Trichia. Since this previously discussed work has served as the groundwork for comparison by most other researchers in their investigations, information concerning Trichiales capillitial development is included in this comparative capacity with the Stemonitaceae and Physarales.

CHAPTER IV

ENVIRONMENTAL EFFECTS ON CAPILLITIAL FORMATION

No published work has been carried out on the effects of environment upon capillitial formation in the Myxogastres. Work done in 1938 and in 1963 deal with environmental effects on fruiting, and until experimental evidence proves otherwise, it may be assumed that what holds true for fruiting in general may also apply for capillitial formation (10) (13).

With the species studied, it was found that yellow-pigmented Myxomycete plasmodial types require light in order to complete their life cycles while non-pigmented types and Didymium xanthopus fruit equally well in light or darkness. Preliminary investigation on Physarum gyrosum Rost. indicates that the presence of light and depletion of nutrients is necessary for initiation of fruiting, a condition similar to that with the pigmented plasmodia. (Since P. gyrosum has pigmented plasmodia only when grown in the light, the exact function of pigments in initiation of fruiting in this case is uncertain.)

Under controlled conditions of temperature, light and nutrient, fruiting periods of pigmented types assumed great regularity. Under conditions of constant temperature and continuous illumination the length of the vegetative phase of Physarum polycephalum and Polycephalum tenerum are conditioned by the total amount of light received. Under conditions of intermittent illumination the vegetative phase of P. polycephalum may be

lengthened, although the total amount of light necessary for a cycle to be completed may be greatly reduced. Fed cultures of P. polycephalum, when placed in lights of various wave lengths, formed sporangia only when exposed to the shorter wave lengths of the visible spectrum. The plasmodia of all yellow-pigmented types studied reportedly clumped and faded when exposed to light.[1]

---

[1]W. D. Gray, "The Effect of Light on the Fruiting of Myxomycetes," American Journal of Botany, XXV (July, 1938), p. 522.

CHAPTER V

SUMMARY

In the Trichiales and Physarales, when the sporangium is formed, but still immature, its protoplast becomes highly vacuolated. These vacuoles are formed by the liberation of water in which various materials furnishing the substances for capillitium formation within the vacuoles are dissolved. The appearance of this vacuolar system at capillitial formation initiation corresponds to the appearance of the capillitium in a mature sporangium. Consequently, if the capillitium is to be a network of filaments, the vacuolar system from which it will be formed develops into a tubular network. Likewise if the capillitium is to be made up of long threads, the vacuoles are elongated and possibly branched, but are scattered in the cytoplasm without coalescing. In the Physarales the capillitial material is deposited within the vacuoles, whereas in the Trichiales it is deposited on the surface of the vacuoles. In the Stemonitales and Echinosteliales the capillitium either forms as an outgrowth of the columella or is deposited in the cytoplasm without previous formation of a vacuolar system.

The effects of light, temperature, nutrition and other environmental influences on Myxomycete capillitial formation can only be inferred from data regarding environmental effects on the fruiting process in total.

SELECTED BIBLIOGRAPHY

1. Alexopoulos, Constantine J. Introductory Mycology. New York: John Wiley and Sons, 1964.

2. _____. "The Myxomycetes II." Botanical Review, XXIX (January, 1963), 1-78.

3. Bessey, Ernst A. Textbook of Mycology. Philadelphia: Blakiston's Son and Company, 1935.

4. Bisby, G. R. "Some Observations on the Formation of the Capillitium and the Development of Physarella mirabilis Peck and Stemonitis fusca Roth." American Journal of Botany, I (1914), 274-288.

5. Cadman, Elsie J. "The Life History and Cytology of Didymium nigripes Fr." Transactions of the Royal Society of Edinburg, LVII (1931), 93-142.

6. DeBary, Anton. Comparative Morphology and Biology of the Fungi, Mycetozoa, and Bacteria. Oxford: Clarendon Press, 1887.

7. _____. "Recerches sur le developpement de quelques champignons parasites." Annales des Sciences Naturelles Botanique et Biologie Vegetale, XX (May, 1863), 5-148.

8. Gates, R. Ruggles. "Adaptations in Cell Structure." Journal of the Royal Microscopical Society, L (January, 1931), 1-13.

9. Goodwin, Donna C. "Morphogenesis of the Sporangium of Comatrichia." American Journal of Botany, IIL (1961), 148-154.

10. Gray, William D. "The Effect of Light on the Fruiting of Myxomycetes." American Journal of Botany, XXV (July, 1938), 511-522.

11. Harper, R. A. and B. O. Dodge. "The Formation of the Capillitium in Certain Myxomycetes." Annals of Botany, XXVIII (1914), 1-18.

12. Howard, F. L. "The Life History of Physarum polycephalum," American Journal of Botany, XVIII (1931), 116-133.

13. Koevenig, James L. "Effect of the Environment on Fruiting in the Myxomycete Physarum gyrosum Rost." American Midland Naturalist, LXIX (February, 1963), 373-375.

14. Kranzlin, H. "Zur Entwicklungsgeschichte der Sporangien bei den Trichien und Arcyrien." Archiv fur Protistenkunde, IX (1907), 170-194.

15. MacBride, T. H. and G. W. Martin. The Myxomycetes. New York: Macmillan, 1934.

16. Martin, G. W. "Systematic Position of the Slime Molds and Its Bearing on the Classification of the Fungi." Botanical Gazette, XCIII (April, 1932), 421-435.

17. Ross, Ian K. "Capillitial Formation in the Stemonitaceae." Mycologia, IL (1957), 809-819.

18. _____. "Sporangial Development in Lamproderma arcyrionema." Mycologia, LII (1960), 621-627.

19. Strasburger, E. "Zur Entwickelungsgeschicht der Sporangien von Trichia fallax." Botanische Zeitung, XLII (May 16, 1884), 305-316.

20. Welden, Arthur L. "Capillitial Development in the Myxomycetes Badhamia gracilis and Didymium Iridis." Mycologia, VLII (1955), 714-728.

21. Wolf, F. A. and F. T. Wolf. The Fungi II. New York: Wiley and Sons, 1949.

VITA

Marla Ann Morgan

Candidate for the Degree of

Master of Science

Title of Study: CAPILLITIAL FORMATION IN THE MYXOMYCETES

Major Field: Natural Science

Biographical:

Personal Data: Born in Concordia, Kansas, on November 14, 1942, the daughter of Everett C. and Margaret Morgan.

Education: Graduated from Concordia High School, Concordia, Kansas, in 1960; in 1964, received the Bachelor of Arts degree from Kansas Wesleyan University, Salina, Kansas, with a major in biology; completed requirements for the Master of Science degree at the Oklahoma State University in May, 1965.