PARASITISM OF MYXOMYCETE PLASMODIA ON THE SPOROPHORES OF HYMENOMYCETES

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With plates 48 and 49 and two text figures

THE interest of authors was aroused in the subject of the parasitism of Myxomycetes when they found plasmodia creeping over and destroying the fruitbodies of mushrooms and polypores in the forests. Because Myxomycetes are usually found on decaying wood, dead leaves, and other organic debris, the notion is current that their nourishment is derived chiefly from the bacterial and fungous decomposition of these substrata. Even though myxomycetous sporangia are occasionally found on disintegrating fructifications of polypores, mushrooms, and other fungi in the forests, collectors rarely conceive of the disintegration observed as being due to the plasmodia from which the sporangia are formed. There are students of the Myxomycetes, however, who have been impressed by the possibility of their active parasitism on fungi, as is pointed out in our résumé of the literature. The authors of the present paper have independently made extensive observations on the mycophagy of the slime molds in the field and supplemented them with tests in the laboratory. The results, dealing with the nutritional relationships of a considerable number of the Myxomycetes to the sporophores of fungi, and the process by which the plasmodia digest the fungal tissues, are presented here.

The general method used to obtain plasmodia for this study was, either to collect them upon Hymenomycetes or other substrata and to bring them into the laboratory, or to grow them from spores in culture upon suitable nutrient agar media. During the season when mushrooms were available, as many different kinds as possible were gathered, identified, and placed in large petri or crystallizing dishes lined with moist filter paper or paper toweling. The sporophores were inoculated by placing a piece of plasmodium varying from 0.5 to 2.5 sq. cm. in area upon the apex of the stipe of stipitate fruitbodies or at the base of sessile forms. Notes were taken daily upon the virulence of the attack and the nature and extent of the tissues of the host being digested. Details of the process of destruction of the fungous tissues were obtained, either from microscopic examination of living material, or from examination of material fixed in Navaschin's, Bouin's, or chrom-acetic solution, cut into sections 3 μ to 10 μ thick after embedding in paraffin, and stained with Flemming's triple or with iron-alum-haematoxylin.

The observations reported in this paper are the result of two independent investigations upon this subject. The junior author, now Mrs. Gordon Edwards, carried on her work as a graduate student in the Botanical Laboratories of the University of Toronto, during the years 1919–1921, under the direction of Professor J. H. Faull, now Professor of Forest Pathology at the Arnold Arboretum, Harvard University. The observations contributed by the senior author were made at Harvard University under the sponsorship of Professor W. H. Weston, Jr., during the tenure of a National Research Fellowship in the Biological Sciences, 1930-1931.

REVIEW OF THE LITERATURE

The literature contains several references to plasmodia attacking Hymenomycetes which indicate that mycophagy is not uncommon among the Myxomycetes. For the first reference to their parasitism we must look to A. Lister (8), who in January 1877 was led to investigate the parasitism of fungi by the Myxogastrales upon finding *Corticium puteanum* fruitbodies being consumed by a plasmodium of *Badhamia utricularis*. He kept this plasmodium in culture by feeding it sporophores of several species of Basidiomycetes, and although he found that the plasmodium could make use of the majority of these, it showed preferences. In some cases almost the entire fruitbodies were assimilated but in others merely the soft superficial tissues were used. The Myxomycete flourished on *Corticium puteanum*, *Polyporus versicolor*, *P. adustus*, *Merulius* sp., and *Daedalea* sp.; was most luxuriant on *Stereum hirsutum;* rapidly consumed *Boletus flavus* and *Agaricus* (*Psalliota*) *campestris;* slowly attacked *Agaricus* (*Armillaria*) *melleus;* and with great difficulty attacked *Agaricus* (*Amanita*) *rubescens* and *Agaricus* (*Hypholoma*) *fascicularis*. Lister observed that the decomposition products of the attacked fungi many times had a deleterious effect on the plasmodium. He noticed also that there was usually a heavy mucus-like residue which varied in amount with the species of Basidiomycete and in which Mucors and other fungi were apt to grow. He made a microscopic examination of the plasmodium attacking hyphae of *Stereum hirsutum* and found that the threads dissolved and broke in pieces as the hyaloplasm advanced over them.

Blytt (1) in 1879 collected the type of *Clastoderma Debaryanum* on a dead *Polyporus* sp., and Brunaud (2) in 1890 reported finding sporangia of *Enerthenema papillatum* on the debris of a *Corticium*, *Fuligo septica* on the pileus and hymenium of a Polypore, and *Stemonitis fusca* on the debris of *Polyporus versicolor*, but neither observer suggests that these Myxomycetes may be parasitic upon the fungi concerned. Likewise, Jahn (7) reports Möller as finding *Trichamphora pezizoides* fruiting on a pileus of *Lentinus villosus*.

Macbride (9) reported the second recognized case of a mycophagous myxomycete when he found that the plasmodium of *Physarum polycephalum* would rapidly digest sporophores of *Agaricus* (*Pleurotus*) *sapidus*.

Harshberger (6) shortly afterwards discovered a bright yellow plasmodium attacking *Pleurotus sapidus* sporophores in the field. Upon bringing the plasmodium, which he named *Fuligo septica*, into the laboratory he found that it would attack and digest pieces of *Coprinus comatus*, *C. atramentarius*, *Hypholoma perplexum* and the gleba but not the stipe of *Phallus impudicus*.

Atkinson in 1916 presented a paper before the Mycological section of the Botanical Society of America upon a slime mold parasitic on mushrooms, which was believed to be a *Badhamia*, but this paper has never been published.

Elliott (4) collected further data regarding the action of *Badhamia utricularis* on fungous tissues. He noted the same discrimination for various species of mushrooms as that described by Lister (8). Elliott experimented with *B. utricularis* on *Polystictus versicolor*, *P. hirsutus*, *Polyporus dryadeus*, *Amanitopsis vaginata*, *Amanita rubescens*, *Collybia dryophila*, *Coprinus micaceus*, *Laccaria* (*Clitocybe*) *laccata*, *Marasmius oreades*, *Panus stipticus*, *Psilocybe semilanceata*, *Russula furcata*, *R. rubra*, *R. emetica*, *Stropharia semiglobata*, *Boletus scaber*, *B. flavus*, and *Lycoperdon gemmatum*. Elliott observed that unless the plasmodium is able to move away from its host after the decomposition of the fungus sets in, it is killed. In conclusion, he writes that the plasmodium of *Badhamia utricularis* can assimilate nearly all of the fleshy fungi, whether poisonous or otherwise. In a later paper with Jessie S. Elliott (5) he describes the sequence of fungi and Myxomycetes upon a large oak branch subsequent to its fall in 1912. Fruitbodies of *Bulgaria polymorpha*, *Coryne sarcoides*, *Stereum hirsutum*, *Panus stipticus*, and *Hypholoma fascicularis* (*H. fasciculare*) appeared in order upon the branch, but only those of *H. fasciculare* and *S. hirsutum* were in evidence in 1919 when the first Myxomycete, *Physarum nutans* Pers., made its appearance. Sporophores of *Phlebia merismoides*, *Hypholoma sublateritium* and one of *Pluteus cervinus* were new additions before other crops of *Physarum nutans* appeared in June 1920. In July 1920 the white plasmodium of *Stemonitis* *fusca* emerged from the branch but nothing is said regarding its parasitism. The complete disappearance of *Bulgaria polymorpha* and *Coryne sarcoides* is attributed to the destruction and absorption of their mycelia within the wood by *Physarum nutans*.

Currie (3) in 1919, besides reporting *Badhamia utricularis* and *Physarum polycephalum* to be mycophagous, added three more species to our list of Myxomycetes which parasitise fungi, namely: *Badhamia foliicola* List., *B. magna* Peck, and *Physarum flavicomum* Berk.

Sanderson (11, 12) further supplemented the list by reporting two Myxomycetes which attacked fungous sporophores in Malaya. He observed the plasmodium of *Physarum viride* var. *rigidum* (*P. rigidum* G. Lister) attacking the fructifications of *Schizophyllum commune* and *Hirneola hispida* but not the fructifications of *Daldinia concentrica*, *Ustulina zonata*, and *Nummularia pithodes*. Likewise, he observed the dirty gray plasmodium of *Trichamphora pezizoides* covering and feeding upon the fruitbodies of *Schizophyllum commune*, "*Tremellina* sp.", *Daldinia* sp., and *Ustulina zonata*.

An examination of the foregoing résumé of the literature shows that of the seven mycophagous species of Myxomycetes reported, all belong to the family *Physaraceae* and that yellow-colored plasmodia predominate. Species classified in other families have been observed by the authors to be parasitic upon fungous tissues, to an account of which we now turn.

MYXOMYCETES FOUND TO BE PARASITIC AND THEIR FUNGOUS HOSTS

During these investigations, thirty-three different plasmodia were tested for their parasitism upon fruitbodies of Hymenomycetes. Fifteen species, representing four families of the Myxomycetes, were identified as follows: *Badhamia foliicola* List., *B. magna* Pk., *B. rubiginosa* Rost., B. *utricularis* Berk., *Fuligo septica* Gmel., *Physarum flavicomum* Berk., *P. polycephalum* Schw., *P. tenerum* Rex., *P. virescens* Ditm., *Leocarpus fragilis* Rost., *Brefeldia maxima* Rost., *Lindbladia effusa* Rost., *Lycogala epidendrum* Fr., *Hemitrichia clavata* Rost., and *Trichia decipiens* Macbr. Of the eighteen remaining plasmodia used, one was found to belong to the genus *Lamproderma* and another to the genus *Physarum*, but the others either failed to form sporangia or the sporangia were so aberrant that they could not be identified. These unidentified plasmodia were white, gray, yellow, and red in color, and were proved to be but weakly parasitic with one exception, plasmodium BFU, whose host range will be given later. Notes on the parasitism of the various identified species, as exhibited in the forest and by laboratory tests, are presented in the following paragraphs.

Badhamia foliicola List. was found creeping over and feeding upon many fruit-bodies of *Polyporus resinosus* by A. W. McCallum in the late autumn of 1918. The bright yellow plasmodium was eroding and channeling the pore surface noticeably.

Badhamia magna Pk. seems to be selectively parasitic, since the plasmodium grew rapidly at the expense of the tissues of *Collybia succosa* and *Trametes pini*, slightly increased in size but did little damage to *Fomes applanatus*, and died upon sporophores of *Collybia hygrophoroides*, *Coprinus micaceus*, and *Mycena galericulata*.

Badhamia rubiginosa Rost. increased slightly in size upon *Collybia hygrophoroides*, *C. succosa*, and *Polyporus versicolor*, but failed to attack *Amanita flavoconia*, *Coprinus micaceus*, *Cortinarius lilacinus*, *Hypholoma sublateritium*, *Mycena galericulata*, *Pleurotus ostreatus*, *P. sapidus*, *Polyporus betulinus*, and *P. sulphureus*.

Badhamia utricularis Berk. apparently may frequently attack *Polyporus resinosus* in the forest, since four collections of eroded sporophores of this fungus bearing *Badhamia utricularis* sporangia are represented in the University of Toronto herbarium. One very large sporophore of *Polyporus resinosus*, consisting of several subimbricate laterally connate brackets, the largest 16 cm. wide and the smallest 8 cm. wide was collected by Professor Faull. Practically the whole of the pore surface was demolished and the upper surface was furrowed where all of the fluffy superficial tissues had been consumed.

Physarum flavicomum Berk. was found attacking a fresh fruit-body of *Lentinus lepideus* in the field in October 1919 by J. H. Faull. The greenish-yellow plasmodium had reduced the gills to a slimy bacteria-infested mass. Later the same species was found on one occasion attacking the pore surface of *Polyporus lacteus* and on another, rapidly destroying a large group of *Merulius tremellosus* sporophores. These plasmodia were brought into the laboratory, kept in culture upon agar media, and used to inoculate other species of mushrooms. Although the plasmodium is a gross feeder it does not attack all of the fungi with equal intensity, so, for convenience, the fungi are grouped according to the character of the attack by the Myxomycete. Included in the group of Hymenomycetes upon which the plasmodium flourished especially, so that it rapidly increased in size and more or less eroded the whole fruitbody before moving away, are: *Flammula polychroa*, *Lentinus* *lepideus*, *Merulius tremellosus*, *Pleurotus ostreatus*, *P. serotinus* (Plate 49, fig. 9), and *Polyporus resinosus*. In the group upon which the plasmodium became so sluggish that it rarely moved away before both the sporophore and itself were attacked by secondary invaders are: *Collybia velutipes*, *Hypholoma sublateritium*, *Mycena* sp., *Pholiota marginata*, *Psalliota campestris*, *Polyporus adustus*, and *P. pargamenus*. A third group, *Armillaria mellea*, *Claudopus nidulans*, *Clitocybe multiceps*, and *Pleurotus ulmarius* were only slightly attacked by the plasmodium which usually died before it caused much damage. The last group includes those sporophores which the plasmodium failed to attack, namely; *Gyrocephalum* sp., *Lycoperdon* sp., *Tremella* sp., and *Tricholoma personatum*.

Physarum polycephalum Schw. plasmodia are quite frequently found destroying mushrooms and Polypores in the woods. Sporangia were collected in the summer of 1917 by J. H. Faull at Alexandria, Pa., and at Ithaca, New York, where before forming spores the plasmodia had been feeding on *Pleurotus ostreatus*. In July 1921 a large maple log was discovered bearing hundreds of *Pleurotus ostreatus* sporophores most of which were reduced to slimy pendant masses by the yellow plasmodium of *Physarum polycephalum*. Intermixed with the *Pleurotus* fruitbodies were fresh sporophores of *Fomes applanatus* and nearby was a cluster of *Mycena Leaiana* which were untouched by the plasmodium. Ten days later, on another maple log fifty yards from the one upon which the former collection was made, a large number of sporophores of *Pleurotus petaloides* was found scarcely one of which was not attacked by *Physarum polycephalum*. Again in early September of the same year a dead Elm tree was discovered with clusters of *Pleurotus ostreatus* intermixed with *Fomes applanatus* at its base, and while the former were being consumed by the plasmodium of *Physarum polycephalum*, the latter were untouched. One of the sporophores of *Fomes applanatus* was brought into the laboratory and there inoculated with a plasmodium which rapidly attacked the hymenium, as shown in plate 49, fig. 10.

The results of inoculations of fungous fruitbodies show that with *Physarum polycephalum*, as is also true for the other species investigated, the plasmodium does not attack all fungi with equal intensity. Some plasmodia may attack only the hymenial surface or the trama of a pileus while others may destroy the entire sporophore, none will wholly consume any fruitbody—there is always an undigested residue even though it be but the merest outline.

The fungi inoculated with the plasmodium of *Physarum poly-*

cephalum are grouped according to the ability of the Myxomycete to parasitise them. Those on which the plasmodium increased rapidly in size by digesting a large part of the sporophore are: *Amanita flavoconia, A. muscaria, A. phalloides, A. verna, Amanitopsis vaginata, Armillaria mellea, Cantharellus cibarius, Claudopus* sp., *Clitocybe dealbata, C. illudens, C. multiceps, Clitopilus prunulus, Collybia dryophila, C. radicata, Coprinus atramentarius, C. micaceus, Cortinarius lilacinus, Hygrophorus Peckianus, Hypholoma sub*

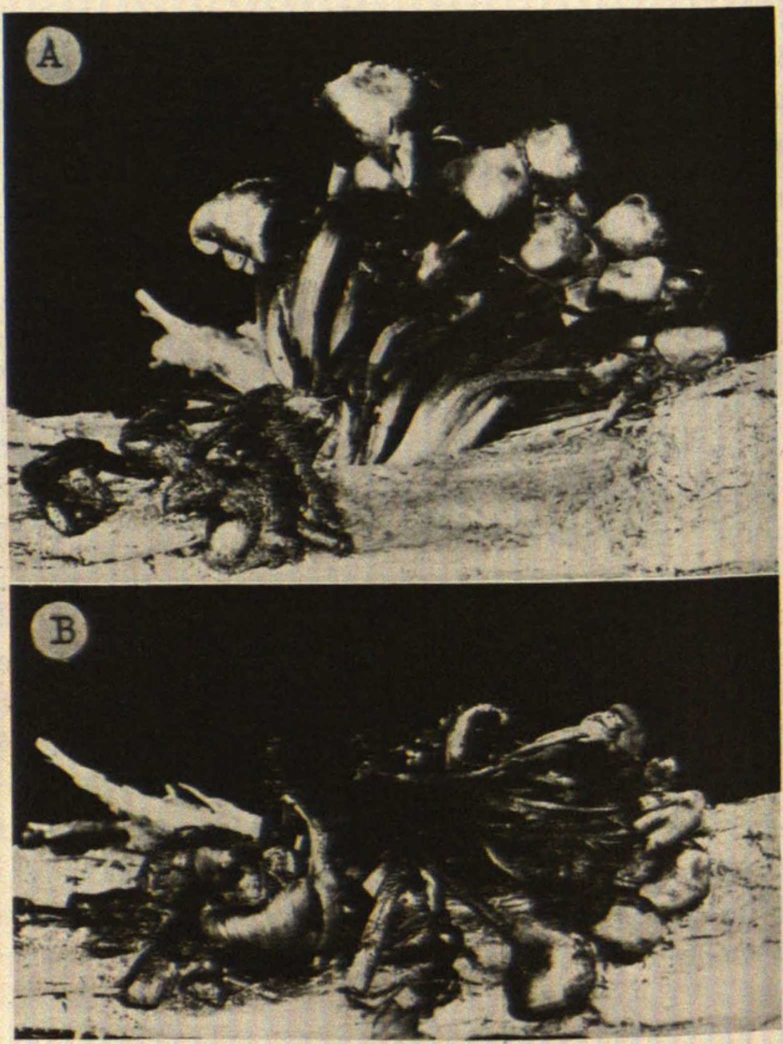

Fig. 1. *A*. Sporophores of *Mycena alcalina* inoculated twelve hours previously with the plasmodium of *Physarum polycephalum*. Several fruitbodies on the left have been enveloped by the plasmodium and have collapsed on the substratum. *B*. Twenty-four hours later practically every sporophore has been attacked and many have been left as soft black masses of tissue.

lateritium, Lactarius volemus, Lepiota brunnea, L. naucina, Mycena haematopa, Pleurotus petaloides, P. serotinus, P. ostreatus, Pluteus cervinus, Russula roseipes, Tricholoma album, Boletus scaber, B. speciosus, Merulius tremellosus, and *Polyporus betulinus*. It seems strange that *Polyporus betulinus*, although much firmer in texture than other members of the above group, is hardly surpassed as a host for *Physarum polycephalum*.

The fungi which were attacked more slowly, but on which the plasmodium fed for a comparatively long time, are: *Fomes applanatus* (Plate 49, fig. 10), *Lenzites betulina*, *Polyporus adustus*, *P. frondosus*, *P. hirsutus*, *P. pargamenus*, *P. resinosus*, *P. Schweinitzii* (Plate 48, figs. 3–4), and *P. versicolor*. The sporophores which *Physarum polycephalum* attacked virulently, but oftentimes from which the plasmodium moved so sluggishly that when putrefaction

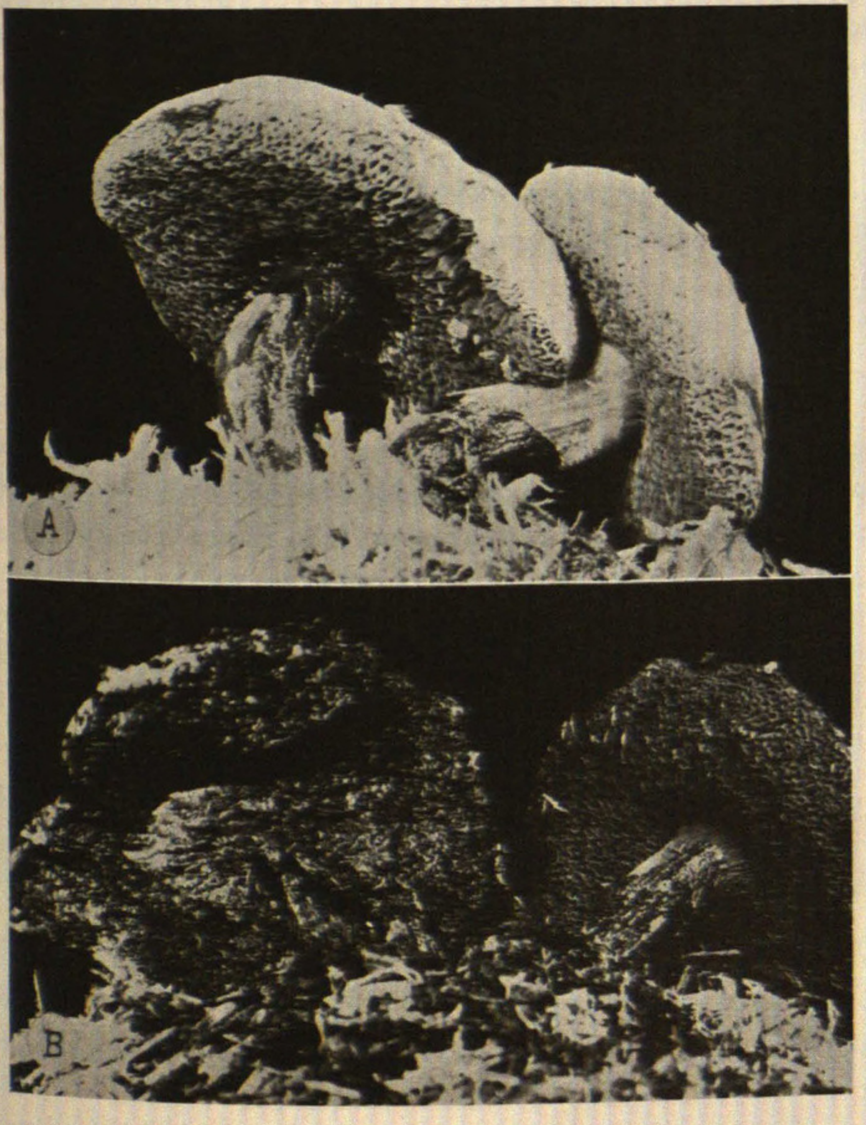

Fig. 2. *A*. Sporophores of *Boletus subtomentosus* twelve hours after inoculation with *Physarum polycephalum*, showing the plasmodium eroding the stipe and destroying the adjacent pores of the fruitbody on the left, and moving over the stipe of the one on the right. *B*. Twenty-four hours later the pileus at the left is a soft disintegrating black mass. The pores of the pileus on the right are about to be attacked.

began it disintegrated with the host, are: *Collybia succosa* (Plate 48, figs. 1–2), *Flammula polychroa*, *Hypholoma appendiculatum*, *H. velutinum*, *Mycena alcalina* (Text-fig. 1), *Pholiota praecox*, *Pleurotus sapidus*, *Psalliota campestris*, *P. placomyces*, *P. Rodmani*, *Russula fragilis*, *Boletus felleus*, *B. subtomentosus* (Text-fig. 2), *Strobilomyces strobilaceus*, *Polyporus sulphureus*, *Hymenochaete badio-ferruginea*, *Hydnum repandum*, *H. septentrionale*, *Hydnellum scrobiculatum*, *Clavaria aurea*, *C. fusiformis*, *C. Kunzei*, and *Tremella lutescens*. The plasmodium of *Physarum polycephalum* failed to attack *Claudopus* sp., *Clitocybe pithyophila*, *Pleurotus ulmarius*, *Tricholoma personatum*, *Poria corticola*, and *Lycoperdon* sp.

Positive statements regarding the intensity of the plasmodial attack upon a certain fungus host are difficult to make, since the maturity and condition of each sporophore tested may make a difference. In some trials *Hydnum septentrionale* was not attacked after inoculation with the plasmodium of *Physarum polycephalum*, while in other trials the plasmodium consumed almost the entire sporophore. The same was true of *Amanita phalloides* and of *Russula emetica*. A good example of the effect of the maturity of the sporophore upon the parasitism of the Myxomycete was shown by *Physarum polycephalum* upon *Coprinus micaceus*. If the plasmodium was placed upon the gills of a young pileus, the plasmodium grew rapidly at the expense of the gills and trama, but if the gills had changed in color from white to reddish purple or had begun to deliquesce, the plasmodium was killed.

Physarum tenerum Rex. rapidly attacked *Merulius tremellosus*, but very slowly attacked *Coprinus atramentarius*, *Lepiota brunnea*, *Polyporus adustus* and *P. pargamenus*.

Physarum virescens Ditm. was unable to attack *Coprinus micaceus*, but made a slight growth upon *Collybia succosa*.

Fuligo septica Gmel. failed to attack the sporophores of *Clitocybe multiceps* and *Clitopilus prunulus* when the typical yellow plasmodium was used as inoculum. When two white plasmodia, whose aethalia formed in cultures have been identified as *Fuligo septica*, were tested on fungi, they destroyed the tissues of some fruitbodies. The sporophores of *Amanita muscaria*, *Pleurotus petaloides*, *Tricholoma album*, *Boletus scaber* and *Merulius tremellosus* were rather rapidly attacked, while those of *Amanita phalloides*, *A. verna*, *Lactarius volemus*, *Lepiota naucina*, *Pleurotus ostreatus*, *Boletus speciosus*, *Polyporus Schweinitzii*, and *Tremella lutescens* were attacked more slowly. The fruitbodies of the following fungi were not attacked: *Hygrophorus Peckianus*, *Russula emetica*, *Polyporus betulinus*, *P. sulphureus*, *Poria corticola*, and *Hydnum septentrionale*.

Leocarpus fragilis Rost. increased slightly in size upon sporophores of *Collybia succosa*, but fruitbodies of *Coprinus micaceus*, *Mycena galericulata*, *Fomes applanatus*, and *Trametes pini* inoculated with the plasmodium were unattacked.

Brefeldia maxima Rost. made a slight growth upon *Collybia hygrophoroides* and *Fomes applanatus*, but none on the pilei of *Coprinus micaceus*.

Lindbladia effusa Rost. failed to grow on *Mycena galericulata* and *Coprinus micaceus*.

Lycogala epidendrum Fr. made a slight growth upon the apothecium of a *Peziza* and upon the mushroom *Mycena galericulata*, but it failed to attack *Mycena Leaiana* and *Coprinus micaceus*.

Hemitrichia clavata Rost.; the plasmodium attacked sporophores of *Mycena galericulata* and made a fair growth upon them, but it failed to attack *Collybia hygrophoroides*, *C. succosa*, *Coprinus micaceus*, and *Mycena Leaiana*.

Trichia decipiens Macbr. grew quite rapidly at the expense of the tissues of *Mycena Leaiana*, grew slightly upon *Mycena galericulata* and *Collybia hygrophoroides*, but did not attack *Coprinus micaceus*.

Lamproderma sp. seemed to attack *Hypholoma sublateritium* slowly but proved innocuous on *Pleurotus ostreatus*, *P. petaloides*, *P. sapidus*, *P. ulmarius*, and *Poria corticola*.

An unidentified yellow plasmodium (BFU) proved to be extremely parasitic and rapidly destroyed *Coprinus atramentarius*, *Hypholoma sublateritium*, *Lepiota brunnea*, *Pleurotus ostreatus*, *Russula emetica*, *Boletus scaber*, *Merulius tremellosus*, *Polyporus betulinus*, *P. adustus*, *Poria corticola*, *Daedalea confragosa*, and *Hymenochaete badio-ferruginea*.

The number of Myxomycetes whose plasmodia utilize fungi for food is far from being known and must await the cumulative observations of more workers in the future. Likewise, the complete range of fungi one species of plasmodium may parasitise is not known, but we may safely conclude from the long list of fungi that *Badhamia utricularis* and *Physarum polycephalum* are known to attack, that some species are very general parasites. Other species, as yet, appear to be non-parasitic upon fungi.

The tougher, more resistant tissues of the woody Polypores account for the slower attack by plasmodia upon them. The plasmodia move over the surface of the pores digesting the basidial layer and sometimes completely destroying the pores, as seen in Plate 48, figs. 3–4. As a contributing factor of great importance in the destruction of the sporophores, it should be noted that all the observed plasmodia remove the surface layers and leave the Polypore with a moist slimy coating; a very favorable substratum for the development of Mucors, bacteria, and other secondary invaders.

This parasitism of Myxomycetes on fructifications of fungi is not confined to the laboratory, for during one season (1931) twenty-two plasmodia were found in the forest apparently feeding on the fungi with which they were associated. Birch and maple logs, decayed by various Polypores and Agarics, proved to be a favored haunt of the majority of these plasmodia, but three were found destroying fungi on an oak stump, one on a dead standing Chestnut (*Castanea dentata*), and another on a dead standing Pine. Although field observation of the parasitic habit of plasmodia first aroused our interest in this problem, study in the laboratory has given us some details of the method of attack.

DISCUSSION OF THE METHOD OF ATTACK

Microscopical examination of both living and sectioned material shows that the attack of plasmodia upon all of the sporophores examined to be both pathogenic and parasitic; pathogenic in that the plasmodium may cause necrosis of the living fungous tissues with which it comes in contact, and parasitic in that the fungous tissues are digested and then absorbed to furnish nutrients for the growth and activities of the plasmodium.

Pinoy (10) doubts that plasmodia have the power of digesting fungous mycelium. He believes that the breakdown of the fungous tissues is due to associated bacteria and to the water absorbing power of the plasmodium which is supposedly able to dry up and kill the mycelial filaments without digesting them. Some of the evidence found by the authors to oppose this view is: 1, living hyphae with no signs of bacteria surrounding them can actually be seen to dissolve throughout their length when covered by the plasmodium, 2, stained sections (Plate 48, figs. 6–7) have failed to reveal bacteria digesting the hymenial layer in order that the plasmodium might absorb the by-products, 3, a normally non-parasitic plasmodium after being allowed to move over a culture of bacteria or of yeasts, which have been found associated with an actively parasitic plasmodium, does not become mycophagous when given the opportunity to digest fungous material.

The process of destruction appears to be of a chemical nature, as is evidenced by observing the individual hyphae in contact with the plasmodium gradually lose their sharp outlines and become dissolved. The time required for the dissolution of the fungous tissue seems to vary with the digestive secretions of the plasmodium, but no special study of this digestive process was made. The nature of the hyphal wall appears to play an important role in susceptibility to plasmodial attack, as is shown by their attack on hyaline hyphae more readily than on colored ones. No microchemical tests of the hyphal walls have been made with which this specificity could be correlated. The thickness of the fungous wall likewise appears to be directly proportional to the length of time necessary for its digestion by the plasmodium, as is shown by thin-walled hyaline hpyhae of the hymenium actually dissolv- away within a few seconds after coming in contact with the advancing margin of the plasmodium, while thick-walled hyphae either may require several minutes for their dissolution and may be found several millimeters behind the advancing margin before they break down, or they are not digested but are left as debris.

In order to dispel any possible idea that digestion occurs in advance of the plasmodium, it is emphasized that the tissues to be digested must lie in close contact with the plasmodium. This contact, however, may be either with the surface membrane or with a vacuolar membrane. Although digestion of hyphae in vacuoles is a possibility, it could not be definitely demonstrated in stained preparations of plasmodia parasitising sporophores, but the hyphal tissues appeared to be digested without engulfment at the ventral surface of the plasmodium (Plate 48, fig. 5).

On the other hand spores appear to be more generally enclosed in vacuoles for digestion. An excellent example of the ingestion of spores was witnessed when sections of the plasmodium of *Physarum polycephalum* attacking the lamellae of *Hypholoma sublateritium* were examined (Plate 48, figs. 6–7). The smooth, oblong-elliptical, purple-brown spores, measuring 3–4 x 6–7 microns, may be clearly seen enclosed in vacuoles in the matrix of the plasmodium. In Plate 48, figs. 6–7, the spores are shown near the ventral surface of the plasmodium and the nuclei near the dorsal surface. The plasmodium is highly vacuolate in its ventral portion where it is assimilating nutrients. Very large, dark-colored, thick-walled spores are many times not ingested but merely pushed aside mechanically by the plasmodium.

Although Lister (8) and others report that fungous tissues, spores, and other solid ingesta are engulfed and move in the protoplasmic currents of the plasmodium, the authors have found that the plasmodium feeding upon a sporophore carries on practically all of its digestion of hyphae and spores close to the advancing margin. Only occasionally what appears to be a bit of hypha or a spore may be seen coursing through the plasmodial strands back of the advancing edge.

A study of sections of the pileus of *Pleurotus serotinus* attacked by the plasmodium of *Physarum flavicomum* shows the gills becoming more and more eroded until there remains only a small shapeless mass of indigestible residue. In Plate 48, fig. 5 the basidial layer has completely disappeared and the tissues underneath the plasmodium are being dissolved. There is a sharp line of demarcation between the plasmodium and the fungus. As soon as the basidial layer is dissolved on one gill, the Myxomycete moves to that of the next.

SUMMARY

Attention is called to the ability of plasmodia of Myxomycetes to parasitise the fruitbodies of common wood-rotting fungi. Some species of Myxomycetes have been shown by field observations and laboratory tests to be very generally parasitic upon Hymenomycetes, while other species are moderately so, or as yet, nonparasitic. In the laboratory about eighty-five species of the Hymeniales, ranging from fragile fleshy Agarics to hard woody Polypores, were inoculated and most of them were found to be attacked by one or more of the thirty-three different plasmodia used in this study.

Plasmodia of the following species are now known to be mycophagous: *Badhamia foliicola, B. magna, B. rubiginosa, B. utricularis, Brefeldia maxima, Fuligo septica, Hemitrichia clavata, Leocarpus fragilis, Lycogala epidendrum, Physarum flavicomum, P. polycephalum, P. rigidum, P. tenerum, P. virescens,* and *Trichia decipiens.* Many other plasmodia, as yet unidentified, exhibited various degrees of parasitism. Unaccounted for preference for some fruitbodies is exhibited by the plasmodia. Mushrooms poisonous to man are readily parasitized by plasmodia, but the maturity of the sporophore does affect the parasitism of the Myxomycete.

The plasmodia bring about the destruction of the sporophores in two ways: 1, by actively digesting the sporophores themselves, and 2, by leaving the moist, slimy, injured fungous tissues, over which they have passed in an ideal condition for infection by bacteria and fungi which carry the destruction further.

The process of destruction of the sporophores is one of digestion, the basidial layer being usually the first tissue attacked. Hyphal tissues are digested at the highly vacuolate ventral surface of the plasmodium without enclosure within the vacuoles, while the spores are usually ingested and then digested within the vacuoles.

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EXPLANATION OF PLATES 48 AND 49

Fig. 1. Fruitbodies of *Collybia succosa* which had been inoculated with *Physarum polycephalum* twelve hours previously. The two sporophores on the left are held erect with pins due to destruction of their stipes by the plasmodium.

Fig. 2. Twenty-four hours later the plasmodium has reduced all of the fruitbodies to moist blue-black masses of tissue.

Fig. 3. Pore surface of *Polyporus Schweinitzii* being attacked by the plasmodium of *Physarum polycephalum*. $\times$ 8.

Fig. 4. The same pore surface after the plasmodium has passed over it. Note the thin pore walls left behind. $\times$ 8.

Fig. 5. Photomicrograph of gills of *Pleurotus serotinus* being attacked by the plasmodium of *Physarum flavicomum*, showing the manner in which the tissues are digested. Observe the sharp line of demarcation between the darkly stained plasmodium and the tramal tissue. Section cut 10 μ thick and stained with Flemming's triple. $\times$ 63.

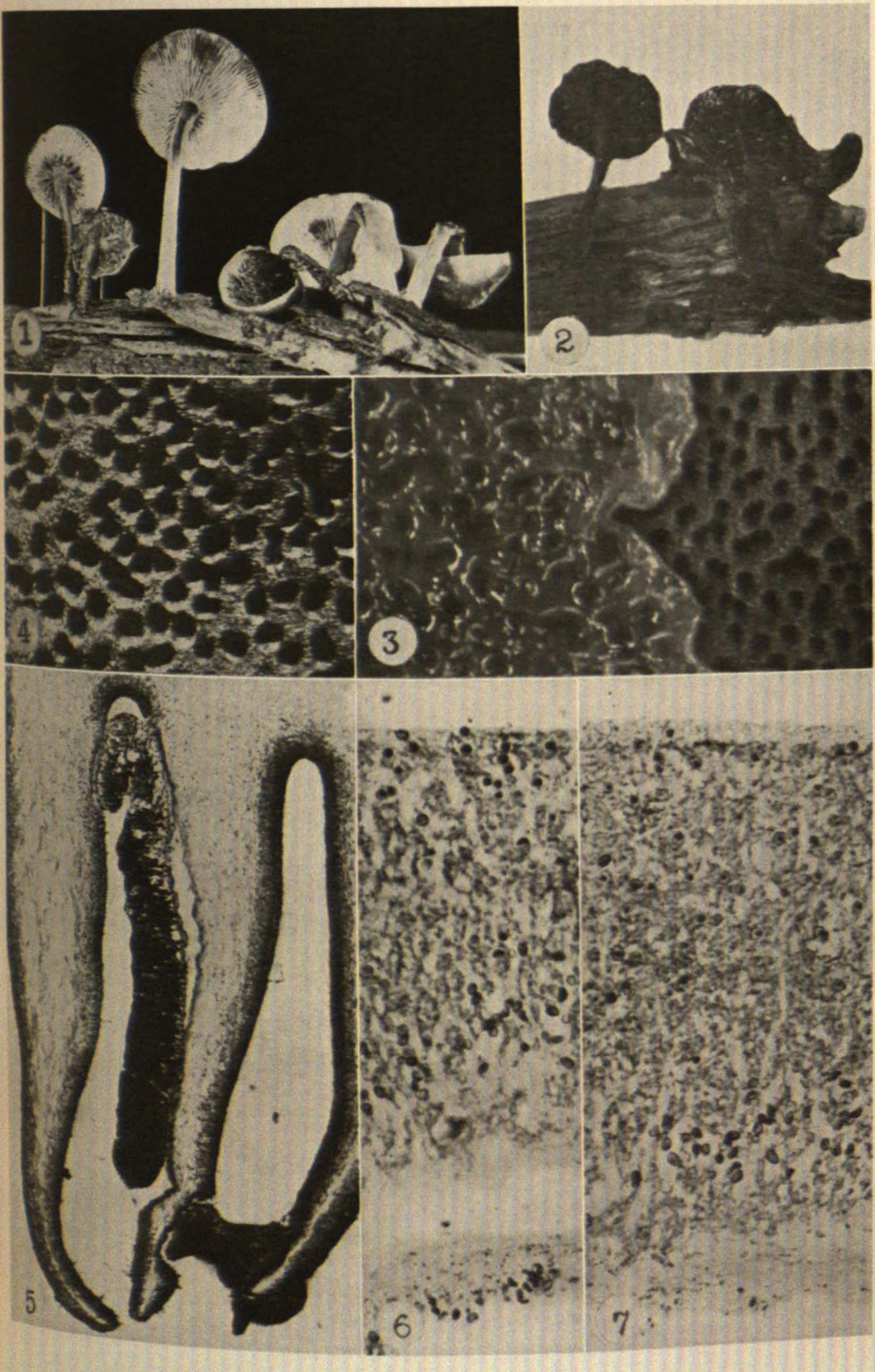
Fig. 6. Photomicrograph of the plasmodium of *Physarum polycephalum* shown digesting the hymenium and ingesting the spores from a gill of *Hypholoma sublateritium*. The trama and hymenial layer on one side of the gill has been digested but the hymenial layer on the other side of the gill is shown at the bottom of the picture. $\times$ 295.

Fig. 7. Photomicrograph of another portion of the plasmodium and gill shown in Fig. 6. Here is shown a bit of the trama at the bottom of the section, the dark colored spores ingested in the vacuolate ventral portion of the plasmodium, and the stained nuclei with their nucleoli which appear as bulls-eyes in the dorsal portion of the plasmodium. Paraffin section cut 3 μ thick and stained with iron-alum-haematoxylin. $\times$ 295.

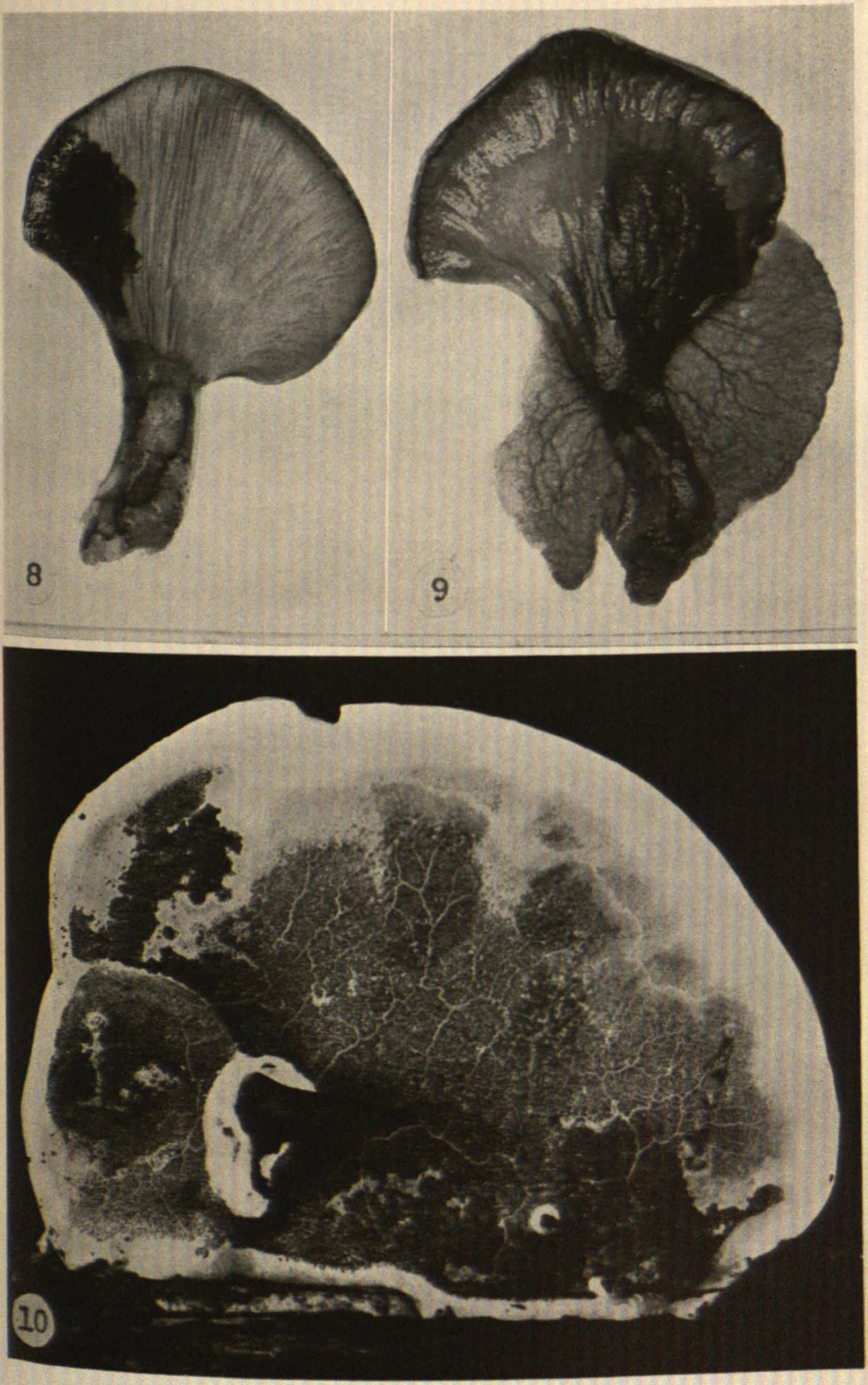
Fig. 8. *Pleurotus serotinus* inoculated with the plasmodium of *Physarum flavicomum*.

Fig. 9. Twenty-four hours later the plasmodium has destroyed the gills, leaving behind a moist, slimy surface ideal for the growth of bacteria and saprophytic fungi.

Fig. 10. A sporophore of *Fomes applanatus* twenty-four hours after being inoculated with the yellow plasmodium of *Physarum polycephalum*. The fluffy white surface layer of hyphae is being removed thus allowing the eroded brown pore surface to show through.



PARASITISM OF PLASMODIA ON SPOROPHORES



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