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Some Observations on the Plasmodia of Myxomycetes

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Some Observations on the Plasmodia of Myxomycetes[1]

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Abstract. Three distinct types of plasmodia are illustrated and compared. The physaraceous type is easily visible when mature, and forms a fleshy fan in the advancing portion. The stemonitoid type is delicate and transparent, macroscopically invisible up to the time of fruiting. The third type always remains microscopic, and never forms a reticulum of veins.

Until recently it was commonly held that in the vegetative stage the various species of Myxomycetes are indistinguishable by plasmodial type. *Physarum polycephalum* has been used for so much of the work done with plasmodia that it has been tacitly accepted as typical of the entire group. This indistinguishability is either stated or implied in all the usual descriptions of Myxomycete plasmodia. In his introduction to *The Mycetozoa of North America*, Hagelstein (1) says, "The plasmodia vary in color and size in different species, and are sometimes confined to a particular habitat; otherwise there is no way of differentiating between various plasmodia."

In 1959, Alexopoulos (2) published a description of the laboratory cultivation of *Stemonitis flavogenita* and pointed out that its plasmodium has a number of characteristics which sharply distinguish it from plasmodia of the physaraceous type. Cultivation of *Stemonitis fusca* was reported soon after by McManus and Richmond (3) and its plasmodium was described as very similar to that of *S. flavogenita*. A more detailed study of the plasmodium of *S. fusca* and a method for its cultivation on glass were published somewhat later (4).

A third type of plasmodium which differs markedly from both the preceding types was found in the laboratory cultivation of *Echinostelium minutum* by Alexopoulos in 1960 (5). It has recently been found by McManus (unpublished data) that *Clastoderma debaryanum* has a plasmodium of a type quite similar to that of *E. minutum*.

The present paper describes further comparative studies of these three types of plasmodia.

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The Stemonitoid Type of Plasmodium

Transparency. The plasmodium of *S. fusca* is very delicate and transparent. In the vegetative stage it is so flattened over its substrate that it is probably totally invisible in its habitat in nature. When growing in agar culture, it can be studied well microscopically under optimum conditions of lighting, but even when well developed it is almost impossible to see macroscopically on the surface of an agar plate. It can be more readily studied in culture when growing on a glass surface, without the obstruction of an agar substrate.

The transparency of the protoplasm seems to be due chiefly to the absence of refractile granules within it. Even in very early stages of development, when reversible streaming is just beginning, the protoplasm of the physaraceous type of plasmodium is filled with such granules. Figure 1 shows a beginning plasmodium of a species of *Physarum* developing from spores on a cover slip in a hanging drop of dilute elm bark extract. The granules are numerous and are distributed throughout the veins, both in the flowing central stream and in the stationary outer cortex. Figure 2 shows the plasmodium of *Stemonitis fusca* in a similar culture at the same stage. The heavy, highly refractile granules are absent, and the protoplasm corresponds to what has usually been described as hyaloplasm (6).

As the *S. fusca* plasmodium continues to enlarge, the veins become wider and thicker, but they remain macroscopically practically invisible up to the time of fruiting. Because of this near-invisibility of the vegetative stage of the stemonitoid type of plasmodium, Alexopoulos (7) has proposed that it be designated an "aphanoplasmodium" and the term "phaneroplasmodium" be used for the easily visible physaraceous type. These terms will be used accordingly in this paper.

The unusual delicacy and transparency of the plasmodium of *S. fusca* was noticed before 1900 by Celakovsky (8) and by Miller (9).

Growth Habit. The aphanoplasmodium, when growing on agar, seems to consist of long main veins which do not tend to anastomose. These have short side branches that do anastomose with each other and then rejoin the main vein (Figure 3). Only in the anterior region and when the plasmodium is actively migrating does it move forward in sheets with confluent pseudopods to form a fan (Figure 4).

The phaneroplasmodium, on the contrary, characteristically forms a large fan (Figure 5) and most of the substance of the plasmodium is included in this part.

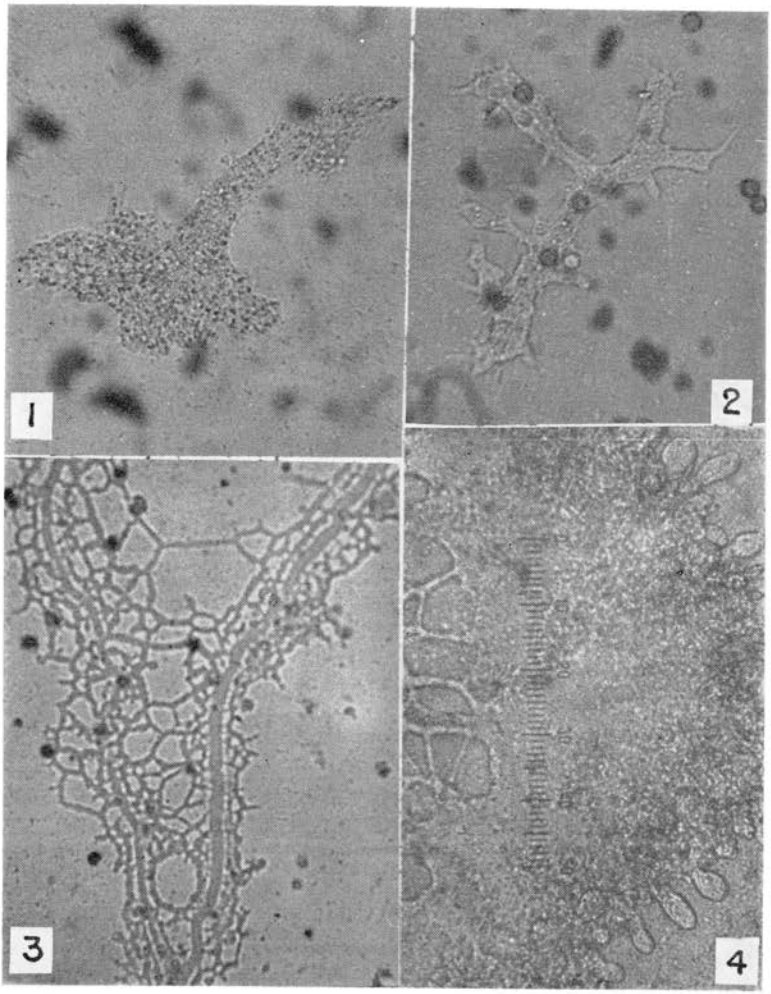

Figure 1. Beginning plasmodium of a species of *Physarum* developing from spores on a cover slip in a hanging drop. Note the presence of dense granules throughout the protoplasm. Unstained. X about 450.

Figure 2. Beginning plasmodium of *Stemonitis fusca* developing from spores on a cover slip in a hanging drop. Unstained. Note absence of dense granules in protoplasm and filiform shape of pseudopod-like extensions. X about 450.

Figure 3. Plasmodium of *Stemonitis fusca* growing on agar. Note long unbranched main veins and short side branches which anastomose with each other. X about 50.

Figure 4. Plasmodium of *Stemonitis fusca* growing on agar. An advancing fan in a confluent sheet is presented on the right side of the photograph, and the pseudopods are lobose. Anastomosing strands are on the left. The plasmodium had just been transferred to fresh agar. 10.4μ between each two gradations on the scale.

This growth habit is not of such constancy as to be a reliable distinguishing characteristic, however, because the activities of the plasmodium at the moment seem at least partly to determine

its gross morphology. When it is feeding, there is no advancing fan in either type. It may remain flattened out in a net, with veins surrounding the particles on which it is feeding, or it may flow over and entirely cover them, so that no net is visible. When it has absorbed sufficient food, it is likely to begin active migration to a cleaner site on the substrate, leaving its slime envelope behind.

Both the phaneroplasmodium and the aphanoplasmodium show this behavior, so the growth habit depends at least to some extent on the physiological conditions of the moment, and the appearance of the veins depends on which part of the plasmodium—anterior or posterior—they occupy.

Streaming. The rhythmic reversible streaming appears to be grossly smilar in the two types as to rate, force, and duration of flow in one direction. There is a difference, however, in the proportion of the vein contents involved in the flow. In the phaneroplasmodium, the moving stream is confined to a central channel, which is apparently not physically separated from a stationary outer cortex. This differentiation into moving central mass and stationary outer layer is evident even in very small veins which have just developed from germinated spores in a hanging drop on a cover slip.

In the aphanoplasmodium, all of the contents of the vein are involved in the streaming. No stationary outer cortex can be seen.

Migration. A hyaline outer layer surrounding the inner granular portion has often been described for the phaneroplasmodium (10). This is difficult to detect except in the area of an advancing vein. Pseudopod-like extensions of hyaline protoplasm are sometimes put out in the direction of migration, or a cap of hyaline protoplasm moves forward and the granular protoplasm then flows into it.

The aphanoplasmodium also advances in this way, but since all of the protoplasm is so nearly hyaline, there is no sharp demarcation between the extensions and the main mass.

There is a difference, too, in the usual shape of the pseudopod which is formed. In the phaneroplasmodium it is typically blunt or lobose, whereas it is more often pointed and filiform in the aphanoplasmodium.

Vacuoles. Vacuoles are present in both types of plasmodia, but are much more evident in the aphanoplasmodium. They tend to be obscured by the granules in the protoplasm in the phaneroplasmodium, but by careful observation of small veins at high

power they can be identified. They are seen most easily as they are carried along in the moving central stream. They are larger than the vacuoles in the aphanoplasmodium, and they often contain visible particles. The vacuoles of the plasmodium of S. *fusca* are small and often appear to be empty of particles, even under high magnification (Figure 6). They are so small and the protoplasm is so transparent that they often make the protoplasm look slightly granular. However, when the veins are much flattened or very small, they can be identified as vacuoles.

Some larger vacuoles, containing spores or cysts, are also pres-

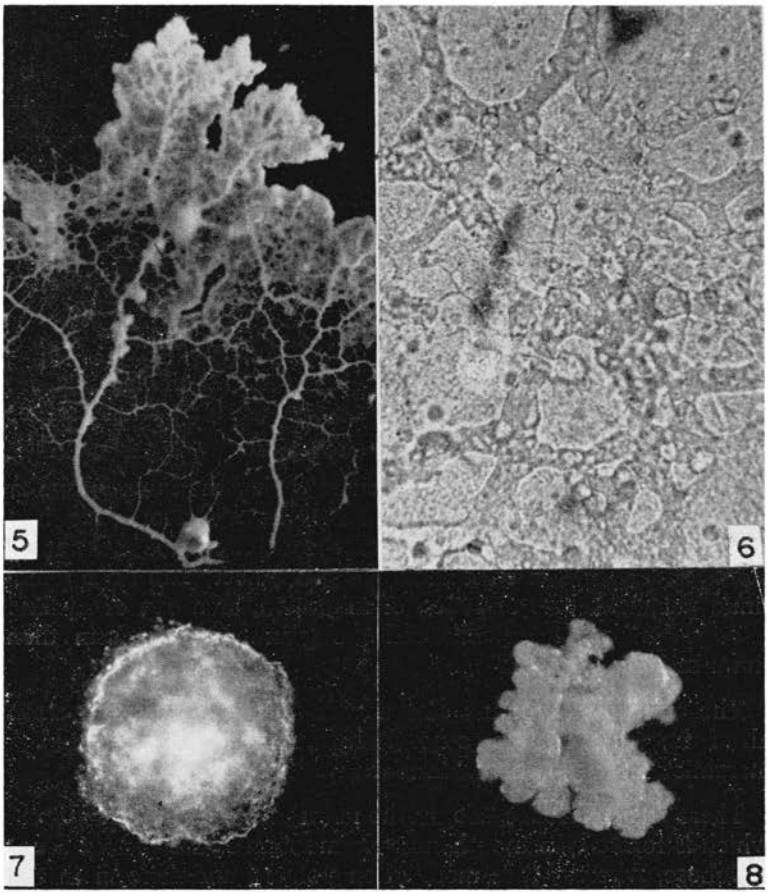

Figure 5. Growth habit of physaraceous type of plasmodium. X about 50.

Figure 6. Plasmodium of *Stemonitis fusca*. Unstained, growing on agar. Note numerous small vacuoles, delicacy and transparency of the veins. X about 450.

Figure 7. Typical appearance of mature plasmodium of *Clastoderma debaryanum* growing on agar. X about 450.

Figure 8. Plasmodium of *Clastoderma debaryanum* suspended in fluid medium. Small lobes have formed over the surface of the plasmodium, but it does not form a network of veins. X about 450.

ent in both types. Living swarm cells have been seen to be ingested by the plasmodium of S. *fusca*, and they remain active for some time within the vacuole.

The Protoplasmodium

Echinostelium minutum. The laboratory cultivation of *Echinostelium minutum* was reported for the first time by Alexopoulos in 1960 (5). He found that this tiny form, whose fruiting body is only 0.5 mm tall, has a third type of plasmodium which differs from both the phaneroplasmodium and the aphanoplasmodium. It always remains microscopic, and never forms a network of veins. Alexopoulos described the streaming within it as irregular. It is not a definite reversible streaming as is present in the other types, and it is so slow as to be imperceptible except at high magnification. He believed that one plasmodium gives rise to one sporangium only.

Clastoderma debaryanum. A similar type of plasmodium was discovered by McManus (unpublished) when *Clastoderma debaryanum* was cultivated on laboratory media for the first time. Figure 7 shows this plasmodium. It remains spherical when growing on agar, never putting out long pseudopods or spreading into nets. It is granular and rather homogeneous and because it tends to enlarge in three dimensions it is difficult to study by transmitted light when mature. Just before fruiting, it usually migrates actively on an agar plate, and at that time it is often flattened sufficiently to see some streaming within the protoplasm. This is probably reversible, but it is hard to make out definite channels. It could best be described as irregular, as Alexopoulos described the streaming of *E. minutum.*

When suspended in a fluid medium, the surface of the plasmodium of *C. debaryanum* pushes out into short, blunt lobules, as shown in Figure 8, but these never become a network of veins.

For this type of plasmodium, which Alexopoulos regards as primitive, he suggests the designation protoplasmodium (7). A similar type of plasmodium was described by Zukal in 1893 (11) for *Licea parasitica.*

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