

AQUATIC MYXOMYCETES

Mitsunori Tamayama

Morioka Chuo High School, 4-26-1 Mitake
Morioka City, Iwate Prefecture 020-0122, Japan

and

Harold W. Keller

Botanical Research Institute of Texas, 1700 University Drive, Fort Worth, Texas 76107-3400 and University of
Central Missouri, Department of Biology and Earth Science, Warrensburg, Missouri 64093, U.S.A.

Correspondence to: haroldkeller@hotmail.com

Abstract

Phaneroplasmodia of *Diderma effusum* were observed feeding on green algae and diatoms submerged in water in an aquarium. This is the first recorded description of this species submerged in water and growing on agar culture. Portions of the plasmodium were also observed adhering to the skin surface of an eel-like fish swimming in the aquarium, suggesting that accidental contact may serve as an agent of dispersal in aquatic habitats. Collectors are encouraged to explore aquatic habitats that include the margins of lakes, ponds, and in *Sphagnum* bogs, swamps, and wetland areas. Species of the Physaraceae are noted and discussed as occurring more frequently in aquaria and in aquatic habitats. Field observations are described for collections of a *Trichia* sp. on cattails and *Badhamia lilacina* on *Sphagnum* moss. Examples of taxa found in aquaria are *Didymium difforme*, *D. iridis*, and *D. nigripes*. Color images document the development of the plasmodia in the aquarium and on the agar surface.

Introduction

Myxomycetes are typically found in moist terrestrial habitats as plasmodia or fruiting bodies on decaying logs or among forest litter of decaying leaves,

twigs, or woody fragments. Ground sites attract most myxomycete collectors but aquatic habitats may also harbor all life cycle stages, especially the microscopic swimming swarm cells, the amoeboid myxamoebae and the microscopic or macroscopic plasmodia and possibly the fruiting bodies. Water, either in the temporary form of a thin film on the surface of water-soaked bark of living trees, or on decaying wood or leaves found on ground sites, or submerged vegetation under standing water, or in natural or artificial wetland areas, are potential sites for life cycle myxomycete stages. This includes the margins of lakes and ponds and self-contained bodies of water in cement ponds, stock tanks, roof eaves, and fish aquaria that may support aquatic myxomycetes.

Review of Past Literature

There are scattered reports of aquatic myxomycetes, the earliest being that of Ward (1886). He observed the growth of a myxomycete identified as *Diderma difforme* on roots of hyacinths cultured in nutrient solutions. Apparently the plasmodia grew in size and developed fruiting bodies completely submerged in the water. Plants were grown vertically with the roots hanging down in water where tiny black spots thought to be sporangia of a myxomycete appeared on the surface of the submerged roots and on the leaves exposed to dry air outside. Description of sessile sporangia included a capillitial network with nodes that had deposits of granules or crystals of calcium carbonate. Sporangia that developed at the water-air interface

had a grayish peridium with calcium carbonate. The sessile sporangia had deposits of calcium carbonate that Ward (1886) described as being amorphous, granules, or crystals that clearly places this taxon in the Physarales and Didymiaceae. This taxon was assigned to *Diderma difforme* (now considered a synonym of *Didymium difforme*) with the cautionary statement that "... it seems very likely to belong to the genus *Diderma*, having several of the characters of that genus well marked" (Ward, 1886). There are discrepancies here, however, based on the presence of calcareous nodes that interconnect a network of capillitial threads more typical of the Physaraceae and the genus *Physarum*. The presence of calcareous granules and crystals raises questions about assignment to the genus *Physarum*, *Diderma*, or *Didymium*. The presence of "calcareous nodes" in the capillitium would rule out the genera *Diderma* and *Didymium* since both genera typically lack calcium carbonate in the capillitium that follows current classification. This may be a species of *Physarum* – possibly *Physarum cinereum*.

Additional species of myxomycetes identified as *Physarum gyrosum*, *P. nutans*, *Fuligo cinerea*, and *F. septica* were grown submerged in water and the plasmodial stage observed by Parker (1946). All of these taxa are members of the family Physaraceae in the order Physarales.

There are few reports of plasmodia or fruiting bodies in natural aquatic habitats but noteworthy is *Didymium aquatile*

described by Gottsberger and Nannenga-Bremekamp (1971). The plasmodium was observed as a greenish-yellow phaneroplasmodium growing in a stream submerged at a depth of 10-20 cm on leaves and twigs and sometimes floating on the water surface. This stream was in a secondary forest in the district of Botucatu, Sao Paulo state, Brazil. These observations were made several times as the phaneroplasmodium was growing on the sandy bottom and moving against the current, sometimes leaving the water to form fruiting bodies. The advancing and feeding edge of the phaneroplasmodium was "deeply incised" instead of the typical even margin.

It was extrapolated further that "Should future studies reveal that the plasmodium characters of this species are fundamentally different from those found in all other myxomycetes, then it might be desirable to refer *Didymium aquatile* either to a new genus or to a subgenus of its own." This overemphasis of a life cycle growth form known to be highly variable gives little credibility and justification for a new genus; even the status of a new species is questionable. In addition, the new species description is based on highly variable sporangial morphology such as the translucent stalk, hemispherical spore case, scanty capillitium, crystal aggregates irregular in shape, and spores varying from 6.5 to 17 µm in diameter (Gottsberger and Nannenga-Bremekamp, 1971). All of these characters are known to be highly variable in field collections and in cultures of *Didymium* species. Water should be considered along with premature drying as possible causes for this variability (Keller and Schoknecht, 1989).

Myxomycetes (13 identified species) were isolated from substrata submerged in southern Illinois swamps (Shearer and Crane, 1986). One species was new to science, *Diderma diadematum*. Identification to species included the Trichiales (7), Physarales (2), Stemonitales (2), and Liceales (2).

Kappel and Anken (1992) reported a plasmodium growing submerged in water on the inner surface of a zoological aquarium that produced stalked sporangia identified as *Didymium nigripes*.

One of us (HWK) has observed a green phaneroplasmodium growing completely submerged in water on the inner surface

of an aquarium. This plasmodium was carefully removed and maintained in agar culture by feeding it oat flakes. Microscopic observation revealed a unicellular green alga present throughout the protoplasm in the fan and veins. The plasmodium was maintained for several months, and during this time, the alga thrived and became incorporated into the normal rhythmic protoplasmic streaming. Some of the algal cells became enclosed in food vacuoles but the majority were scattered throughout the protoplasm. Attempts to isolate the green alga were successful and it was identified as a species of *Trebouxia* (Keller and Braun, 1999).

The plasmodium continued to increase in size and maintained its green color throughout this period. These cultures were maintained on 2% water agar and the plasmodia were fed crushed and sterilized old-fashioned oat flakes. The plasmodium increased in size and was sub-cultured by transferring portions on agar blocks to additional agar plates until 10 agar cultures were maintained. These cultures continued to grow and were also green in color which suggested the algal cells were capable of surviving in the plasmodial protoplasm.

To our knowledge, this is the first reported record of a myxomycete forming an algal-myxomycete association. Eventually, the plasmodium formed stalked sporangia typical of the genus *Didymium*, but the stalks in this case were bright green instead of dark brown. Apparently most of the green alga cells were deposited in the stalk. The sporangia were identified as *Didymium iridis*. Even though the spores germinated, repeated attempts to continue the life cycle failed because plasmodia never formed (Keller and Braun, 1999).

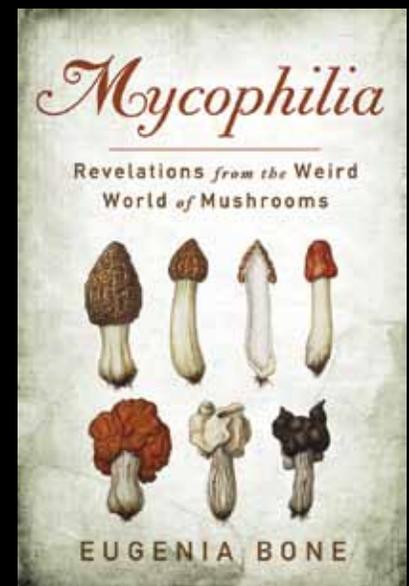
More recently Lindley et al. (2007) isolated 14 myxomycete species from submerged vegetation of aquatic habitats (ponds and lakes). These samples were taken from 5 cm above and below the water level and were cultured in moist chamber cultures. Fruiting bodies were identified to species in the Physarales (7), Trichiales (3), Liceales (3), and Stemonitales (1). It is interesting to note that members of the Physarales predominate in these aquatic habitats.

Another example of a myxomycete that developed in an aquarium was described by Müller et al. (2008).

Color pictures illustrate a yellow phaneroplasmodium changing to white that eventually formed stalked sporangia typical of *Didymium nigripes*. The myxomycete species observed growing thus far in submerged aquatic environments are: *Didymium aquatile*, *D. iridis*, *D. nigripes*, *Fuligo cinerea*, *F. septica*, *Physarum gyrosum*, and *P. nutans*. These species are all members of the Physarales.

White plasmodia of *Physarum didermoides* and *Fuligo cinerea* were grown on sterile oat agar culture free of bacterial contaminants in association with three species of green alga that formed green plasmodia. Direct microscopic observation confirmed the presence of dividing green alga cells of *Chlorella xanthella* apparently establishing an endophytic myxolichen (Lazo, 1961). This suggested that apparently the algal component replaced bacteria as a source of nutrients. In contrast, the yellow plasmodia of *P. polycephalum*, *P. gyrosum* and *F. septica* appear to take the algal cells and digest them and the plasmodia do not become green. Another study using white plasmodia of *Fuligo cinerea* demonstrated the exchange of ³²P radioactive phosphorus between algal cells of *Chlorella xanthella* and the

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plasmodium, reinforcing the notion that this was a symbiotic (mutually beneficial) association (Zabka and Lazo, 1962).

One of the best examples of moist habitats in nature associated with myxomycetes, blue green algae (cyanobacteria), green algae, and diatoms was documented by Smith and Stephenson (2007). Algae and the leafy liverwort *Nowellia curvifolia* were associated with myxomycete sporangia of *Barbeyella minutissima* on decaying decorticated logs of Red Spruce (*Picea rubens*) and Fraser Fir (*Abies fraseri*) at high elevation ground sites in the Appalachian Mountains of West Virginia and Great Smoky Mountains National Park. *Barbeyella minutissima* is restricted to this type of habitat where species of cyanobacteria represented by *Chroococcus tenax*, *Aphanothece saxicola*, and *Aphanocapsa elachista* var. *conferta* and two green algae, *Mesotaenium chlamydosporum* and *Chlorococcum humicola* dominated based on relative density. Evidence was based on myxomycete fruiting bodies collected in the field but unfortunately lacks direct observation of the tiny plasmodia in the field or associations with algae on agar culture.

Field Observations

One of us (HWK) has observed and collected myxomycete fruiting bodies from aquatic habitats. One example is taken from a field foray in 1969 at the annual Mycological Society of America Foray held at the University of Michigan Biological Station, September 9 to 13. Here, Travis E. Brooks and HWK searched for myxomycetes in the shallow areas of the upper part of Douglas Lake where cattails were abundant. We pulled cattails (*Typha latifolia*) and split the stalks at or below water level and found sporangia of a *Trichia* species (BPI 835108). We could not identify this species but there were no distinctive morphological characters to justify description of a new species. Also of note is the observation of Olive (1975) who found that one of the most productive substrata for myxomycetes was old cattail inflorescences. Cattails occur around the edges of ponds, lakes, and in drainage areas, along with emergent macrophytes that may serve as potential aquatic habitats

for myxomycetes. This habitat may fall in the category of being in the right place at the right time in order to find myxomycete fruiting bodies. If conditions are not optimal, their presence will be overlooked.

Wetland myxomycetes were highlighted by Ing (1994). One example found at Douglas Lake (by HWK) was the yellow phaneroplasmodium of *Badhamia lilacina* that thrives in aquatic areas of *Sphagnum* bogs. The distinctive lilac sporangia were restricted to this habitat fruiting on drier sites of the moss phyllidia (personal observations). This species along with *Symphytocarpus trechispora*, *Amaurochaete trechispora*, *Lamproderma columbinum*, *Lepidoderma tigrinum*, and *Diderma simplex*, have also been recorded from bog mosses (Ing, 1994). Lister (1918) also records the development of *Lamproderma scintillans* aphanoplasmodium on stones in a shallow stream. These understudied acid *Sphagnum* bogs appear to have a

top provided with a water circulating aeration and purification system. A fluorescent light was operational during the time course of these observations (Fig.1). The aquarium was put on a table in the corridor of the second floor of the Morioka Daisan High School, located in Morioka City, Iwate Prefecture, Japan. Water volume was maintained at an estimated 45 liters or about ¾ full.

Two high school students and Mitsunori Tamayama, their instructor, recorded plasmodial observations and water temperatures between 16.0°C and 18°C based on readings taken every 3-4 days over a six week period. The pH was tested with Whatman pH indicator paper on 14 March 2009 with a value of pH 4. The quality of the aquarium water and tap water was tested on Thursday 19 February 2009 with a PACKTEST kit of Kyoritsu Chemical-Check Lab., Corp.

This aquarium also contained three fish, Oriental weather loaches (a freshwater eel-like fish, *Misgurnus anguillicaudatus*). Artificial food



Figure 1. Aquarium where myxomycete and fish observations were made.

distinctive array of myxomycete species.

Aquarium Myxomycete Observations

Observations of a white myxomycete plasmodium were made in an aquarium with the approximate dimensions of 40 cm X 30 cm X 25 cm. Four glass walls were supported by a plastic frame and bottom. The aquarium had an open



Figure 2. White plasmodia adhering to skin of fish near head. Note the black charcoal blocks on bottom of aquarium and whitish food particles.



Figure 3. Close-up of fish with pieces of white plasmodia adhering to skin.

This table gives the results of the chemical analysis. (mg/L = ppm)

Chemical compound	Tap water	Aquarium water
Chemical oxygen demand (COD)	0	10
Nitrogen as a form of ammonium (NH ₄)	0.5 (0.64)	10 (13)
Nitrogen as a form of nitrous acid (NO ₂)	<0.005 (0.017)	<0.005 (0.017)
Nitrogen as a form of nitric acid (NO ₃)	0.5 (2.2)	10 (43)
Phosphorus as a form of phosphoric acid (PO ₄)	0.02 (0.06)	>1 (3)

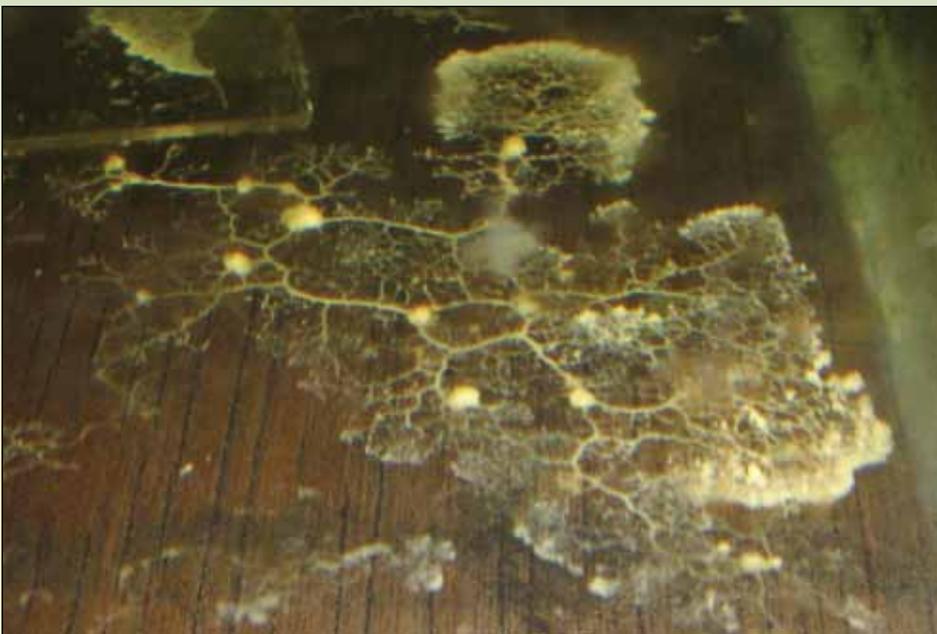


Figure 4. Multiple white plasmodia on bottom of aquarium with well developed anterior advancing fans and trailing veins. Diameter of the thermometer ca.8 mm.

was added for the fish that contained an assortment of nutrients including vitamins, amino acids, wheat flour, beer yeast, gluten, and minerals. These fish moved about the aquarium but were never observed feeding on the plasmodia. Nevertheless, portions of the plasmodium were observed adhering to the heads of the fish suggesting a physical contact reminiscent of the recent description of a lizard and a myxomycete plasmodium and sporangia (Townsend et al., 2005). This is the first report of a mobile fish in an aquatic habitat that could possibly serve as means of dispersal and transfer of a myxomycete plasmodium (Figs. 2 and 3). Plasmodia were not observed floating in the water but adhering only to the aquarium and fish surfaces.

Plasmodial development was first observed in the aquarium on January 14, 2009, and thereafter, continued daily until March 31, 2009. All plasmodia in the aquarium were creamy white and this color did not change over time. These plasmodia were representative of the phaneroplasmodial type which is the largest and often the most colorful type seen in the field. At maturity, seen in Figs. 4, 5, and 6, plasmodia were visible to the unaided eye, extending several centimeters. The phaneroplasmodia seen here exhibited polarity and directional movement, terminating anteriorly as an advancing, fan-shaped feeding edge, and posteriorly, as a trailing network of veins (Figs. 4, 5, and 6) (Keller and Braun, 1999). The entire phaneroplasmodium has a raised three-dimensional appearance with definite margins (Figs. 4, 5, and 6). This type of plasmodium grows best under drier conditions where free-water is absent. Members of the Physarales are the best example of this type of plasmodium. Apparently this plasmodial type is also tolerant in aquatic habitats growing on submerged substrata. It appears that the plasmodia were feeding on green algae identified as *Microthamnion* sp. and diatoms (*Eunotia incisa*) on the inner glass surface of the aquarium (Fig. 6).

There were 18 phaneroplasmodia growing on either the activated charcoal granules (approximately 4 X 5 X 9 mm), on the floor of the aquarium (Fig. 4), or on the glass surface of the aquarium sides submerged under water (Figs. 5 and 6), or above the water level on the glass surface. These plasmodia grew

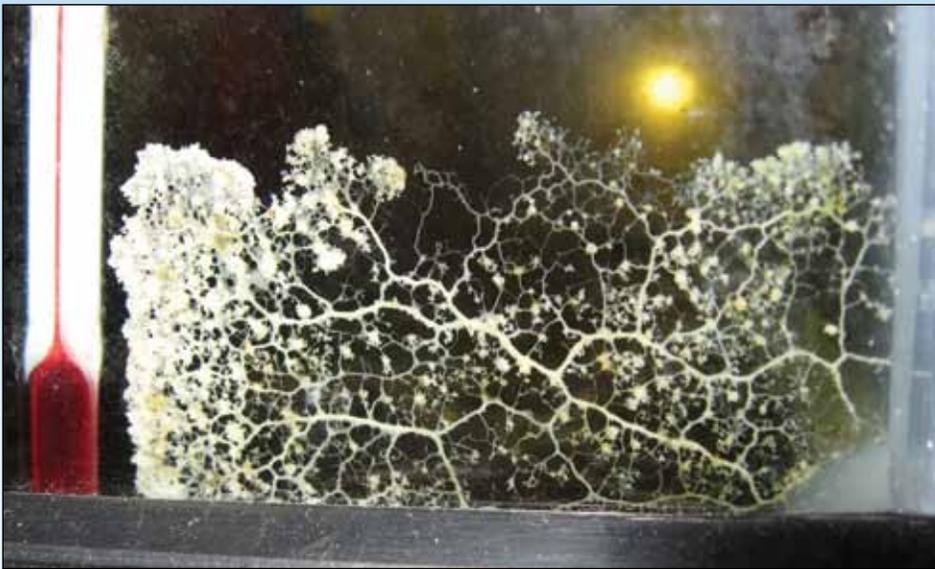


Figure 5. White plasmodium on inner surface of aquarium wall showing an intricate branching network of veins.



Figure 6. Three plasmodia feeding on film of green algae and diatoms on the surface of aquarium glass.



Figure 7. Plasmodium feeding on oat flakes on agar surface



Figure 8. The plasmodium shown here on the agar surface were larger after feeding on oat flakes.

under water for a period of 76 days after which observations stopped. The plasmodia reached a maximum size up to 15 X 20 cm in length and in most cases migrated to the bottom of the aquarium where they became larger and more vigorous (Fig. 4). No fruiting bodies ever developed in the aquarium. Plasmodia were removed from the aquarium using the charcoal blocks and transferred to the surface of 2% water agar in culture dishes. Additional observations were made on the agar surface and sterile old-fashioned oat flakes were added as an additional food source (Fig. 7).

Here the plasmodia actively migrated off the charcoal onto the agar surface eventually feeding on the oat flakes and increasing in size (Fig. 8). Portions of the plasmodia sub-cultured to additional agar plates resulting in larger, thicker, and denser plasmodia that had yellowish or creamy white colors. Rarely these plasmodia fused. These plasmodia often moved some distance eventually forming fruiting bodies on the inner plastic surface of the culture dish lid (Figs. 9 and 10). Phaneroplasmodia often migrate 8 to 16 cm or more to drier sites to form fruiting bodies when cultured on agar. This is in contrast to species of *Perichaena*, such as *Perichaena depressa* and *P. quadrata*, where the mature plasmodium moves more slowly over the agar surface and usually fruits there (Keller and Eliasson, 1992).

Fruiting bodies were obtained 13 times from February 28 to November 1, 2009. The white fructifications formed on the plastic surface of the culture dish lid as effused plasmodiocarps typical of the species *Diderma effusum* (Fig. 10). This was in contrast to the formation of fruiting bodies on the more moist agar surface where atypical sporangia or short plasmodiocarps were present (Fig. 11). This often occurs when excessive water or a film of water is present on the agar or if the fruiting bodies form submerged as shown for *Perichaena depressa* (Keller and Eliasson, 1992; Fig. 2). The peridium of *D. effusum* consisted of amorphous, white calcareous granules (not crystals). The dark purplish brown capillitial threads lacking calcium carbonate are typical of the family Didymiaceae. The spores were dark brown in mass, purplish brown by transmitted light, minutely warted, and 7-8 μm in diameter.



Figure 9. Fruiting body on the inner side of plastic lid.



Figure 10. Pseudo-aethaliate fruiting body (note bumpy surface of individual sporangia) on the surface of the agar dish plastic wall.

Ultrastructural Observations

Study of green plasmodium was a special ultrastructural project of mine while a graduate student at the University of Iowa (HWK 1967-1971). The electron microscope facility prepared the green myxomycete plasmodium of *Didymium iridis* to determine the fate of the algal cells. Direct observation of shuttle protoplasmic streaming showed green algal cells as part of the flowing protoplasm. The green plasmodium also had bacteria and oat granules that were sources of food eventually incorporated into the protoplasm. Preparation followed a modified protocol used by Kazama and Aldrich (1972) for myxamoebae of *Physarum flavicomum*. Staining results of acid phosphatase activity were based on lead deposition around the algal cells inside the vacuolar spaces, indicating that algal cells were being digested by the food vacuoles (unpublished observations). It appears that under certain conditions algal cells can survive and serve as a food source for the plasmodium. This is probably an opportunistic association based on the availability of the predominant food source at any given time.

Conclusions and Future Directions

The aquarium study is the first to show that the plasmodium of *Diderma*



Figure 11. Sporangiate fruiting bodies on agar surface.

effusum can survive submerged in aquarium water, and feed on unicellular green algae and diatoms. This association has been described as being a food source or a myxolichen depending on the degradation or coexistence of the algal component. It appears that algae, under certain conditions, may serve as a food source as well.

Two different forms of *D. effusum* fructifications developed on the surface of the substrata: more pseudo-aethaliate or effused plasmodiocarpous on the plastic surface of the wall and lid of the culture dish, and more sporangiate on

the moist agar surface. The variability in fruiting body habit should be considered when preparing species descriptions, keys to identification, and describing new species.

A survey of published literature lists the following species occurring under aquatic conditions: *Badhamia lilacina*, *Diderma effusum* (this paper), *Didymium aquatile*, *D. difforme*, *D. iridis*, *D. nigripes*, *Physarum gyrosum*, *P. nutans*, *Fuligo cinerea*, and *F. septica*, all members of the Physarales. Members of the Physarales have been cultured from spore to spore more frequently than

any other myxomycete order (Gray and Alexopoulos, 1968). This may account in part for the occurrence of chiefly physaraceous species in submerged aquatic environments or in the presence of free water. Furthermore, species of *Perichaena* (Trichiales) and *Stemonitis* (Stemonitales) when cultured under laboratory conditions on water agar in culture dishes, require the presence of free water in the early stages of plasmodial formation or sclerotization occurs (Keller and Eliasson, 1992, and unpublished observations).

The accidental adherence of plasmodial fragments to the skin of the fish present in the aquarium suggests another way myxomycetes may be transported to other locations. Plasmodia appear to have a fixed dorsal-ventral connection to hard surfaces or more examples of floating plasmodia would occur submerged in water – either in aquaria or agar culture. However, the conditions of an artificial man-made environment such as an aquarium may not be duplicated in natural habitats. Thus, evidence acquired from aquaria should not be taken out of context and applied to broad generalizations.

More potential aquatic habitats must be explored to determine if myxomycetes do indeed complete their life cycle under these conditions. To date, moist chamber cultures of submerged aquatic macrophytes have produced the fruiting body stage of

myxomycetes. In the field a collector must be in the right place at the right time following the right weather conditions to find fruiting bodies. The readership of FUNGI and members of the North American Mycological Association interested in exploring aquatic field habitats, including understudied *Sphagnum* bogs, lakes, or ponds, should keep myxomycete plasmodia and fruiting bodies in mind.

Acknowledgments

The co-author (MT) wishes to thank Mr. Yasuo Ito, his former high school biology colleague who first noticed the aquarium myxomycete. MT also is grateful to his former high school students, Mr. Masato Saito (now at the University of Tokyo) and Mr. Takeru Hanada (now at Iwate University) who helped record aquarium observations and data. Our thanks to Mr. Yukinori Yamamoto for his identification of *Diderma effusum* and Dr. Akihiro Tsuji, National Museum of Nature and Science, Tokyo (TNS) for his identification of the green alga and diatom. Relf Price read multiple drafts of the manuscript and three anonymous reviewers improved the content of the narrative.

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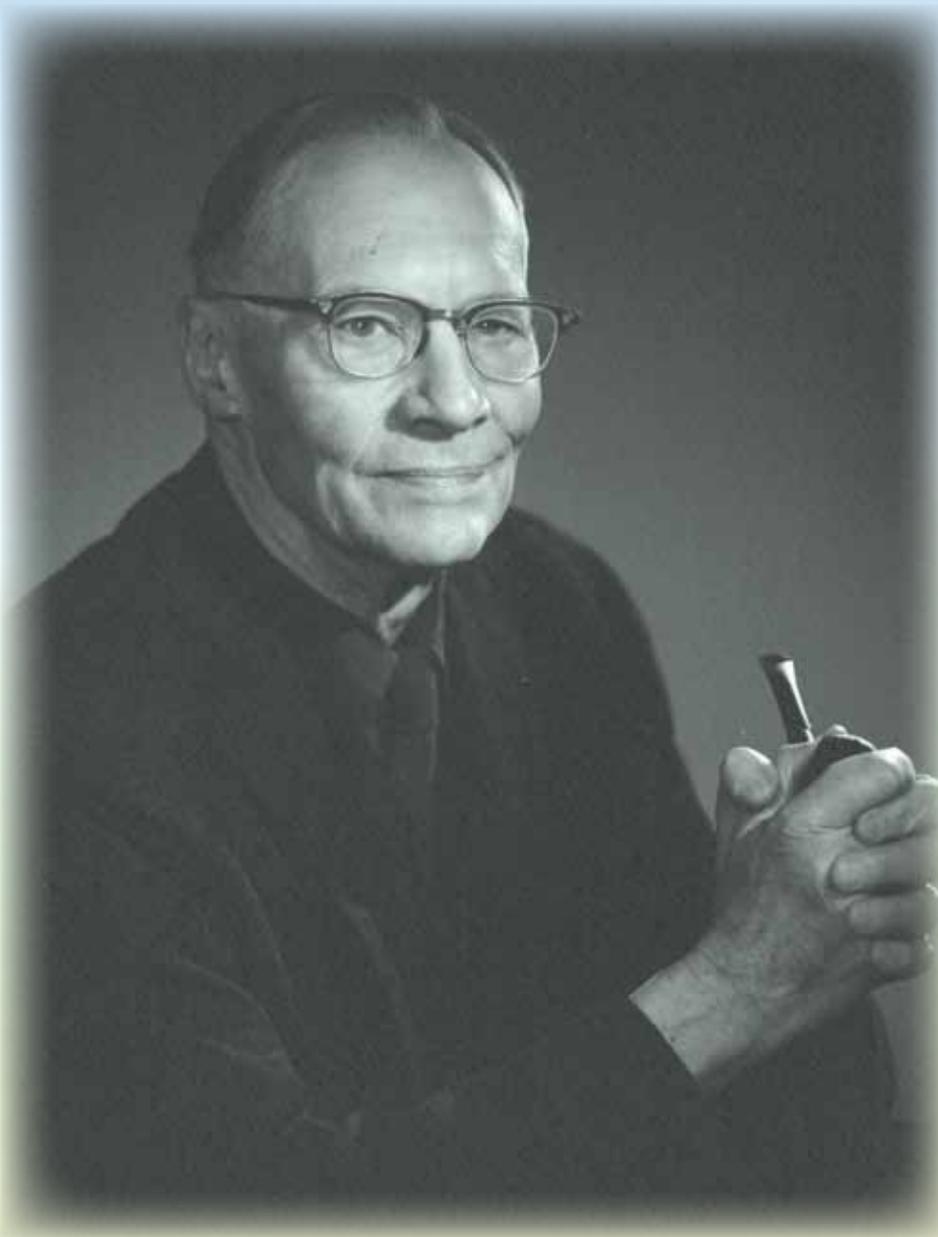
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Professor George Willard Martin, Ph.D.

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This poem, *The Myxomycete*, was found among a stack of papers on a desk in Dr. Martin's office. It was one of the mimeographed handouts for the classes he taught but was never published. I was privileged to be his last student from 1967 to 1971 at the University of Iowa and enjoyed reading this poem. It was published by Keller and Braun in 1999 (see page xvi) and has been used as a handout in many myxomycete workshops. The chain rhyming scheme, and beautiful, sometimes humorous prose, highlight the plasmodial and fruiting body stage of the myxomycete.

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Harold W. Keller ♣

THE MYXOMYCETE

by Professor George W. Martin

I grieve to say the history with scandal will be rife
For every myxo is compelled to lead a double life
At first, in piles of rotten leaves, in sodden logs or stump.
Pretending to be animal, it crawls and creeps and clumps,
Then, as it shifts to fungus form, it seeks the outer air,
And if your eyes are keen enough you're sure to find it there
As animal, the shape it takes we call plasmodium,
Bacteria and yeasts and spores serve as its pabulum;
It eats them all, and goes its wan, and waxes fat and strong,
Nor ever wonders whether such behavior may be wrong.
Its lack of moral scruple is without a doubt complete;
No conscience has been noted in the Myxomycete
Anon its fruiting stage begins. Before our startled eyes
It hastens to transform itself into a fungus guise.
With curious excitement all its veins become suffused,
Its nuclei meiotically divide and are reduced.
Into aethalium, sporange or curved plasmodiocarp
The change is sudden, quick, abrupt, distinct, decisive, sharp.
It gleams as iridescent orbs or waves as feathered plumes,
Or livens up a bit of bark with particolored blooms;
Or turns a dingy fallen leaf into a beauty spot; –
But some of them, I must confess, are not so very hot.
The firm peridium dries and splits and through each tiny tear
Each passing breeze releases spores by clouds into the air,
Until some capitillial tufts, an empty stalk or two,
Are all that's left to mark the place whereon the slime mold grew.
But now the spores have dropped by scores in humid cul-de-sacs;
There each small cell begins to swell and soon the spore wall cracks;
Out slips a protoplasmic globe which squirms a bit and then
Develops a flagellum and thus swims beyond our ken.
It eats, divides and eats again, but soon there comes a time
When food tastes flat, and life like that seems scarcely
Worth a dime.
Each lovely little swarm cell seeks to find a fitting mate,
And round and round they dance in pairs, not ever hesitate.
They closer press, the clasp grows tight, and soon the two are one.
The nuclei fuse, flagella are retracted, and it's done.
This is the new plasmodium. The cycle now repeats;
It joins with others, crawls around, and eats and grows and eats,
And in its time it fruits again, and so the tale is told
Of this, as every living thing, forever new, though old.

The morals of my tale are neither many nor profound,
And since they are the common sort they everywhere abound,
I will not waste your time and mine by trying to expound; –
Just help yourself to what you want and pass the rest around.