THE MYCETOZOA: A REVISED CLASSIFICATION[1]

LINDSAY S. OLIVE[2]
Department of Botany
University of North Carolina
Chapel Hill, N. C. 27514

INTRODUCTION

The name Mycetozoa was proposed by de Bary in 1859 to accommodate the plasmodial slime molds or myxomycetes and the cellular slime molds. He later (1887) included such forms as *Plasmodiophora* and the Proteomyxida as uncertain affiliates. De Bary (1887) made it clear that he did not consider the mycetozoans to be directly related to the fungi but thought that both groups were derived independently from the flagellates. In addition, it was his conclusion that the Mycetozoa should be considered outside the limits of the plant kingdom. Though a number of subsequent investigators have held the same view, mycetozoans have been studied primarily by mycologists, who have generally preferred to treat them as fungi (e.g., Martin, 1960; Alexopoulos, 1962) or as a closely allied group. In view of the increased interest in the taxonomy, phylogeny, and biology of these organisms, this appears to be a propitious time for a re-examination of their classification.

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De Bary was among the earliest to point out that the resemblances between mycetozoans and fungi are of a superficial nature, a cell wall being absent in the trophic stage of the former and present in the latter. The nutrition of mycetozoans is primarily holozoic, while that of fungi is osmotrophic. In addition, the flagellar apparatus of mycetozoans differs significantly from that of any known fungus with flagellate cells.

On the other hand, the plant-like appearance of the fruiting bodies of many mycetozoans and the demonstration that some of them contain cellulose in the spore wall or other structures have been primary factors influencing some authors to place these organisms in the plant kingdom, and these are valid considerations. However, the claim by Martin (1960) that the ability of a myxomycete plasmodium to grow osmotrophically in a liquid medium in the laboratory is a plant-like characteristic is diminished by the knowledge that animal cells from protozoans to man may be thus maintained. Furthermore, his comparison of the sheath around plasmodial veins with the hyphal walls of fungi cannot be considered seriously in the absence of comparative developmental and chemical studies and in view of the striking morphological and developmental differences between a plasmodium and a mycelium. The sheath of mycetozoans (Olive, 1967) is more likely to prove analogous to the protective sheath-like layer that commonly surrounds the aerial hyphae and sporulating structures of fungi.

From the time of de Bary, students of these organisms have debated the question of relationships among groups of Mycetozoa, de Bary himself believing that the myxomycetes and cellular slime molds might be related. The main trophic stage of myxomycetes is a multinucleate plasmodium which eventually gives rise to fruiting bodies that are generally visible to the unaided eye. At least in some species, meiosis and plasmogamy occur in the life cycle. Motile cells, each with a pair of closely associated kinetosomes that give rise to one or two flagella, are also present. In cellular slime molds no flagellate cells are found, and the trophic stage consists of phagotrophic, uninucleate amoeboid cells. At the onset of fruiting, the cells gather into aggregates in which they retain their individuality. The aggregates then give rise to fruiting bodies, mostly microscopic or very small in size, in which some of the cells develop directly into spores. A regular sexual process is probably absent.

Recently, an entirely new order of relatively simple microscopic mycetozoans, the Protosteliida Olive & Stoianovitch (1966b), has been described. As the order continues to be enlarged by subsequent collections, it is becoming apparent that the group has most likely had a monophyletic origin from free-living flagellates and that they have diverged along unique lines that lead into the cellular slime molds on one hand and into the myxomycetes on the other. The fruiting body of the protostelids most often consists of a single spore, but sometimes two or more, borne on a slender stalk. The trophic stage varies from uninucleate amoeboid cells to reticulate plasmodia, and flagellate cells similar to those of myxomycetes are present in some genera. Sexuality has not been demonstrated.

Further discussions of group characteristics and possible interrelationships will be found in the following sections. There are several other groups that have sometimes been placed tentatively among the Mycetozoa, but whose relationships are obscure. The Plasmodiophorida, which are obligate parasites with endobiotic plasmodia, zoosporangia, and clusters of resting spores, are such a group. There is no clear-cut evidence that they are related to any of the mycetozoans. Recent studies by Amon & Perkins (1968) and Porter (1969) show that the labyrinthulids cannot be accommodated here. The biflagellate zoospores with anteriorly oriented tinsel flagellum and posteriorly oriented whiplash flagellum, as well as an eyespot, are very unlike the flagellate cells of mycetozoans. Perkins & Amon (1969) have discovered synaptonemal complexes—the indicators of meiosis—in the uninucleate sporangia of *Labyrinthula*. The group has probably had an independent origin from the phytoflagellates. Other small groups whose relationships to mycetozoans are questionable are discussed, along with the Plasmodiophorida, under "Groups of Uncertain Affinity."

In a forthcoming publication, *Protozoology Guidebook* (in press), the Mycetozoa (or Mycetozoea) are recognized as a class of the Sarcodina, which includes both strictly amoeboid forms and forms predominantly amoeboid but with flagellate cells at certain stages of development. The same treatment is followed here (See classification outlined in "Conclusions"). Somewhat more detailed keys to the various groups of mycetozoans, along with more numerous illustrations, will be found in the *Guidebook*. The major purpose of this paper is to review the present system of classification in the light of recent discoveries and make the changes indicated by these findings. The class as a whole has hardly received adequate treatment since the time of de Bary (1887). Except for the myxomycetes, a group treated in excellent taxonomic detail by Martin & Alexopoulos (1969), keys to taxa down to the genera will be given and references to more detailed treatments will be noted. The system of nomenclature recommended for major taxa by Honigberg et al. (1964) is adopted. Authorship of taxa formerly included in the plant kingdom and transferred to positions of similar rank in the Protozoa is left unchanged. For the convenience of those who prefer to classify these organisms as plants, the equivalent botanical taxa are given in parentheses. Those who may not wish to be confined to the recognition of only two kingdoms of living organisms are referred to the recent proposal of Whittaker (1969), and a recommended modification of it (Olive, 1969) in which the mycetozoans are classified as Protista (essentially Protozoa).

CLASS MYCETOZOA DE BARY, 1859

Flagella present or absent, when present, anterior and 1 or 2 in number, devoid of mastigonemata; trophic stage holozoic, uninucleate and amoeba-like to multinucleate and plasmodial, with contractile vacuoles; sexual reproduction present or absent; sporulation by any of the following means: (1) differentiation of single amoeboid cells (which may or may not be the products of plasmodial segmentation) to form simple, stalked, 1-several-spored

sporocarps (Protostelia), (2) aggregation of simple amoebae to form multicellular pseudoplasmodia that give rise to stalked multispored sorocarps (Dictyostelia and Acrasia), or (3) development of multispored fruiting bodies from a multinucleate plasmodium (Myxogastria).

Four subclasses are recognized: Protostelia, Dictyostelia, Acrasia and Myxogastria. The Dictyostelia and Acrasia, which formerly comprised the Acrasida (Acrasiales), commonly known as cellular slime molds, are here treated as separate subclasses, the Acrasida now becoming the sole order of the Acrasia. The latter have probably had a phylogenetic origin independent of other groups of Mycetozoa, but since only two species have been investigated in any detail, they are tentatively being retained in the class until their relationships are better understood. In view of recent evidence that both the Dictyostelia and Myxogastria have evolved from the Protostelia, it appears likely that the Mycetozoa, with the exception of the Acrasia, are of monophyletic origin.

The Mycetozoa are of wide distribution, occurring in terrestrial habitats on such substrates as soil, dung, tree bark, and dead vegetation, where they feed on other microorganisms, particularly bacteria and fungi. Only a few have been grown in axenic culture. The Myxogastria, or myxomycetes, constitute the largest group and are the only mycetozoans with fruiting bodies large enough to be readily detected in nature.

KEY TO SUBCLASSES OF MYCETOZOA

Fruiting bodies commonly minute, the spores not delimited endogenously by cleavage; trophic stage uninucleate to multinucleate and plasmodial; flagellate states present or absent.

- Sporulation not preceded by aggregation of amoebae; sporocarps 1-few-spored; trophic stage amoeba-like to plasmodial, with filose pseudopodia; flagellate stage present or absent ..... Protostelia I.
- Sporulation preceded by aggregation of amoebae to form a pseudoplasmodium; sorocarps multispored; trophic stage amoeba-like; flagellate stage absent.
  - Amoebae with filose pseudopodia; stalks of fruiting bodies provided with a stalk tube ..... Dictyostelia II.
  - Amoebae of the limax type, typically without filose pseudopodia; stalk tube lacking ..... Acrasia III.

Fruiting bodies generally (but not always) macroscopic, multispored, the spores formed endogenously by cleavage; trophic stage a multinucleate plasmodium, flagellate stage present ..... Myxogastria IV.

I. SUBCLASS **PROTOSTELIA** L. OLIVE, SUBCL. NOV. (PROTOSTELIIDAE).

The trophic stage varies from uninucleate or plurinucleate amoeboid cells to multinucleate reticulate plasmodia, the latter differing from those of myxomycetes in lacking the rhythmic ebb and flow of protoplasm. Filose pseudopodia are characteristic of all species. Flagellate cells may be present or absent. The 1-few-spored fruiting bodies arise from single uninucleate or plurinucleate prespore cells. Contractile vacuoles are present in all active protoplasts. The

nuclei have a single, usually centrally positioned nucleolus. Just after nuclear division in most species studied several nucleolar bodies appear and fuse into one, though the coalescence is sometimes delayed, thus giving the nucleus a plurinucleolate appearance as in the Dictyostelia. It is common to find striking variations in size of nuclei within a single culture of the same species, which would indicate that polyploidy (probably endopolyploidy) is common. The occurrence of a regular sexual process in the life cycle has not been substantiated for any member of the subclass. Anastomoses and fusions between protoplasts appear to be common among the Protostelia, thus providing an opportunity for heterokaryosis and possibly parasexuality.

Ontogeny of the protostelid sporocarp is diagrammatically illustrated in Fig. 1. The prespore cell at first becomes hemispherical, then hat-shaped as its protoplasm concentrates in the center, leaving a thinner margin. A thin protective sheath, which begins to develop over the protoplast at this time, surrounds the sporocarp throughout its ontogeny. A steliogen appears in the lower part of the protoplast and begins to secrete the stalk. A narrow portion of the steliogen extends into the upper part of the stalk during its development, keeping the stalk tube hollow. At the end of the process of sporogenesis, which may require little more than half an hour, the protoplast secretes a wall and develops into a spore at the tip of the stalk (Olive & Stoianovitch, 1966b). The spores may be round, oval, pyriform, or elongate.

The occurrence of flagellate cells in what are considered to be the more primitive protostelids indicates that the group has evolved from simpler free-living flagellates. It is difficult to imagine a species simpler than *Cavostelium apophysatum* L. Olive which could still be classified as a mycetozoan. As will be brought out more fully below, there is now convincing evidence for considering the protostelids as ancestral to both the Dictyostelia and the Myxogastria.

The protostelids are of widespread occurrence throughout the world and

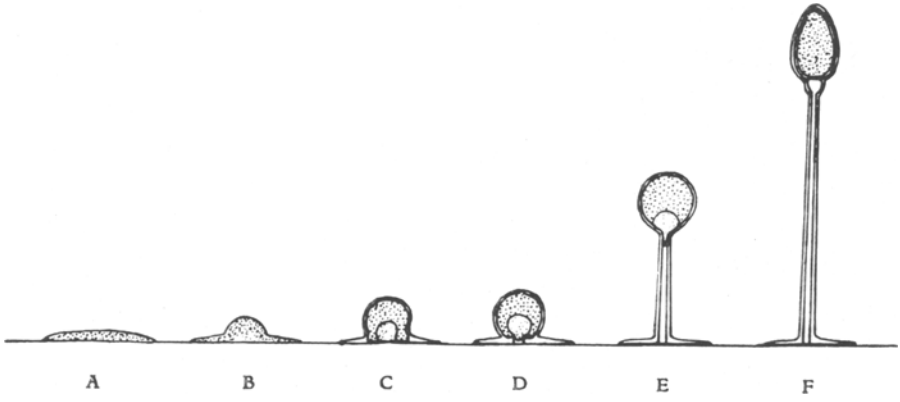

FIG. 1. Diagrammatic illustration of sporogenesis in *Nematostelium ovatum*. *A*, prespore cell; *B*, hat-shaped stage; *C*, delimitation of steliogen and sheath; *D*, beginning of stalk development; *E*, intermediate stage in stalk development, with steliogen extending into stalk tube; *F*, mature sporocarp. (From Jour. Protozool. **13**: 168; 1966)

are readily isolated from dead wood, tree bark, humus, soil, dung, and especially from moribund but still attached plant structures (pods, capsules, berries, etc.). Further information on isolation and culture, with additional bibliographical references, may be found in a recent monographic treatment (Olive, 1967). A single order is recognized.

ORDER PROTOSTELIIDA OLIVE & STOIANOVITCH, 1966b (PROTOSTELIALES).

The order has the characteristics of the subclass. For reasons discussed below, the Ceratiomyxidae, formerly included in the myxomycetes, are being transferred to the Protosteliida.

Key to Families of Protosteliida

Sporocarps produced directly on the substrate
Flagellate cells present ..... Cavosteliidae A.
Flagellate cells absent ..... Protosteliidae B.
Sporocarps produced on gelatinous spore horns; flagellate cells present
Ceratiomyxidae C.

A. Cavosteliidae L. Olive, 1964 (Cavosteliaceae)

When the undescribed isolates are taken into consideration, the family may be described as including those forms with flagellate cells, a trophic stage ranging from uninucleate amoebae to reticulate plasmodia, and 1-several-spored sporocarps produced directly on the substrate (and not on spore horns). Recent fine structure studies (Furtado & Olive, in press) show that, as in the myxomycetes, there are two closely associated kinetosomes in the anterior end of the flagellate cell, with one or two flagella attached. Thus far, only one genus has been formally described, but representatives of three new genera have been isolated.

Cavostelium L. Olive, 1964.

The trophic stage in this genus is comprised mainly of uninucleate amoeboid cells, though occasional plurinucleate but non-reticulate protoplasts may also be produced. The sporocarps are short-stalked, and there is an apophysis at the apex of the stalk. The spores are nondeciduous. Two species have been described: *C. apophysatum* L. Olive (1964) with 1-2-spored sporocarps, and *C. bisporum* Olive & Stoianovitch (1966c) with consistently 2-spored ones.

An undescribed new form from Tahiti (and a similar isolate from Brazil), which will be referred to here by its collection number, *Ta* 67-7[3] (Fig. 2), is especially remarkable in its resemblance to the genus *Ceratiomyxa* (below), which, until now, has generally been included in the myxomycetes. Its sporocarps have slender stalks that bear the spores singly. Under suitable conditions of germination, the spores produce protoplasts that round up and cut out 4-8 uninucleate cells, each of which produces one or sometimes two flagella. Eventually, reticulate plasmodia develop in the cultures, and some of them

[3]Because of previous commitments, the author is constrained to avoid publication of this and certain other new genera at this time.—Ed.

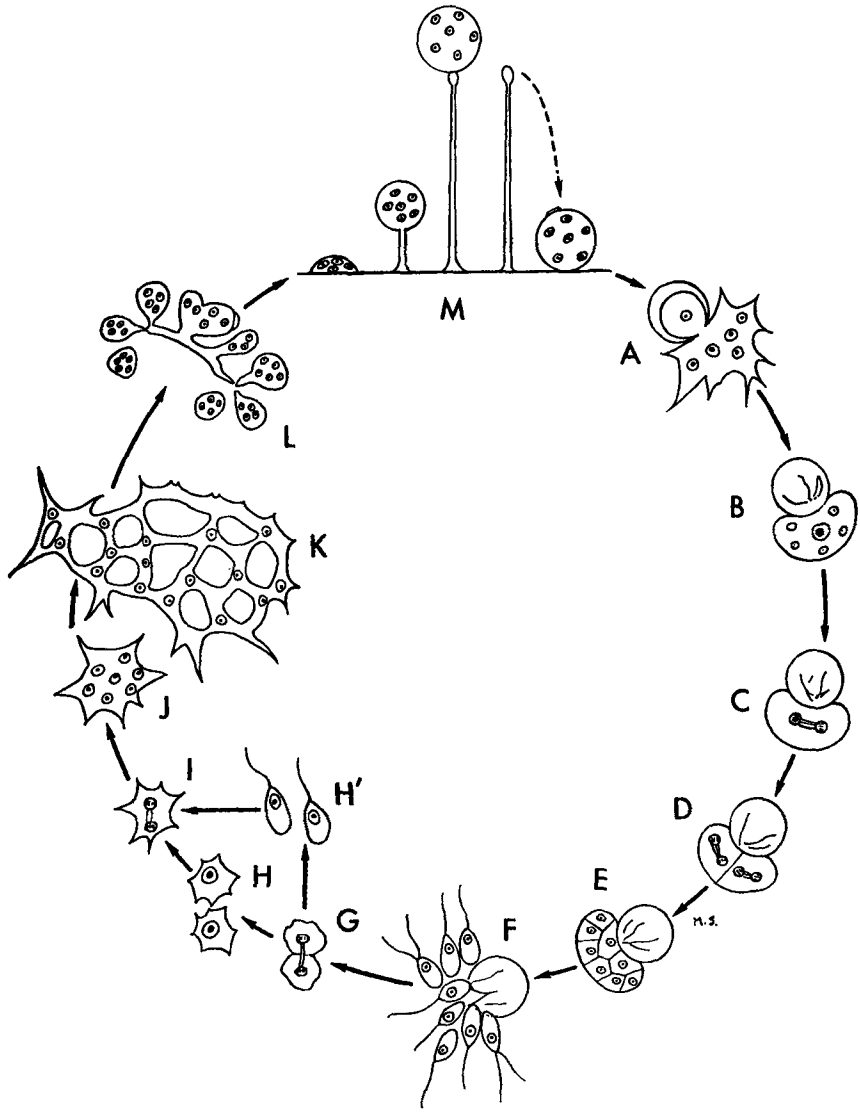

FIG. 2. Life cycle of protostelid isolate *Ta 67-7*. *A*, spore germination; *B*, cyst formation *C*, *D*, two successive divisions of the single surviving nucleus; *E*, delimitation of 8 cells following third mitosis; *F*, release of flagellate cells; *G*, cell division; *H*, amoeboid cells formed; *H'*, flagellate cells formed; *I*, *J*, early stages in plasmodial development by nuclear division without cell division; *K*, mature reticulate plasmodium; *L*, prespore cell formation; *M*, sporogenesis.

segment into prespore cells that give rise to the individual stalked sporocarps. Except for the fact that sporulation does not occur on upright columns formed by the plasmodia, the entire process closely resembles that of *Ceratiomyxa*

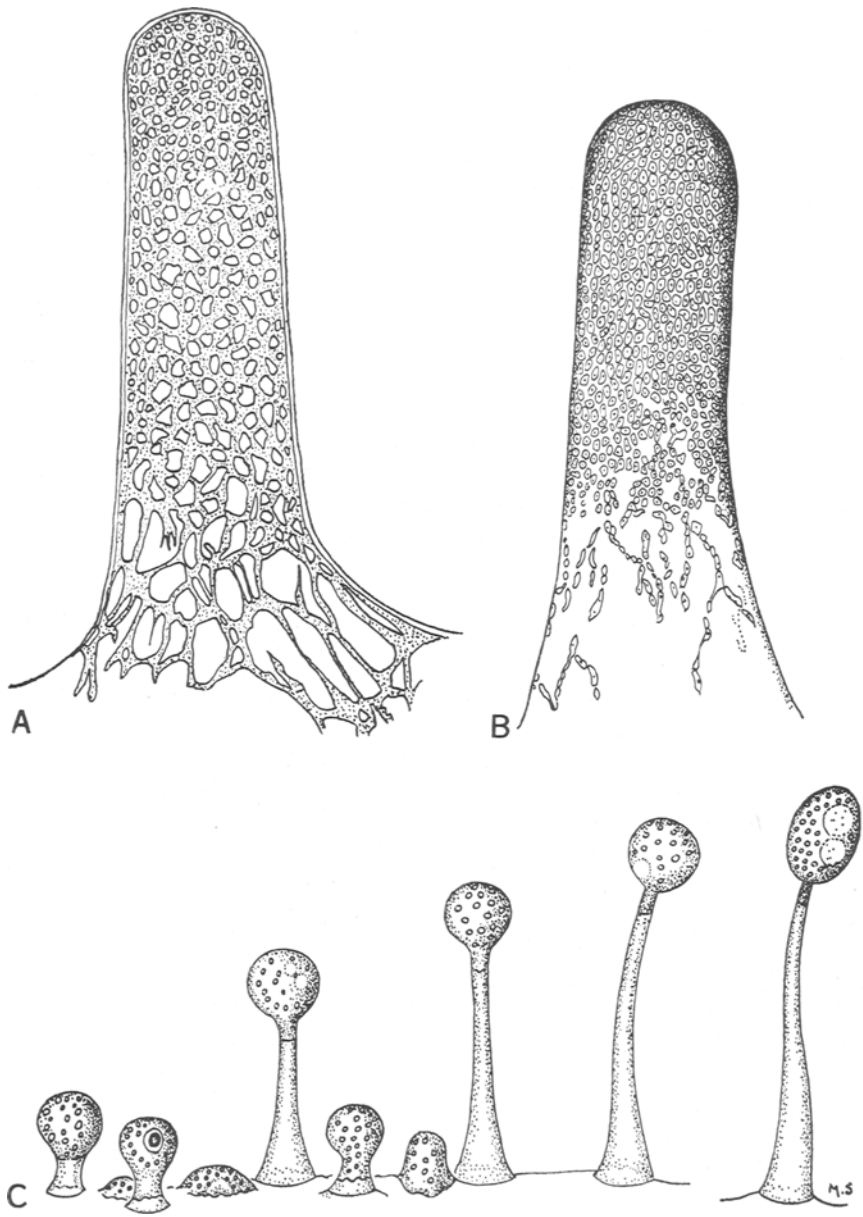

FIG. 3. *Ceratiomyxa fruticulosa. A,* fruiting horn in plasmodial stage; *B,* fruiting horn with uninucleate prespore cells delimited; *C,* sporogenesis. (Redrawn from Famintzin & Woronin, 1873).

(Fig. 3). We believe that this is indicative of the phylogenetic origin of *Ceratiomyxa* from a protostelid such as *Ta 67-7*

Another undescribed flagellate protostelid, isolated from oak bark in Chapel Hill and tentatively referred to here as *NC 69-27*, produces very slender-stalked sporocarps with 2 to several spores. Its trophic stage is an amoeboid protoplast with one to perhaps 20 or more nuclei that looks like a diminutive form of the protoplasmodium of *Echinostelium* (Alexopoulos, 1960b), a genus that contains the smallest known myxomycetes. The smallest described species of *Echinostelium* is *E. roseum* Ing (1965), which produces stipitate fruiting bodies with sporangia devoid of capillitium and containing 20-24 spores. Sexuality has not been demonstrated in either *Echinostelium* or *NC 69-27*. The more difficult question may prove to be, not whether protostelids are phylogenetically related to myxomycetes, but where to draw the line between them. Dr. Travis Brooks (personal communication), of Southeast Missouri State College, has reported finding on bark *Echinostelium*-like forms smaller than *E. roseum*, but he has not yet succeeded in culturing them.

We have isolated a third undescribed flagellate protostelid (*Br 67-33*) that closely resembles *Protostelium mycophaga* Olive & Stoianovitch, even to the orange pigmentation of the protoplasts, but the latter is distinguished by its inability to produce flagellate cells. This new isolate demonstrates the close relationship between the Cavosteliidae and the next family.

B. Protosteliidae Olive & Stoian., 1966b (Protosteliaceae)

This is a group of non-flagellate forms with primarily 1-spored (1-2-spored in one species) sporocarps with stalks that range from short and subulate to long and slender. In one series the spores are apophysate and deciduous, while in the other they are non-apophysate and non-deciduous. Since the spores have an adhesive surface, those of the latter group are probably disseminated largely by small forms of animal life such as mites, thrips, and nematodes. The trophic stage may be in the form of uninucleate amoebae, or both uninucleate and plurinucleate protoplasts, or reticulate plasmodia. Four genera have been described. However, recent investigations in our laboratory indicate that two species placed in one of these genera (*Schizoplasmodium*) are not directly related to the type species. They are hereby segregated into a new genus (*Nematostelium*), described in this review for the first time.

Key to Genera of Protosteliidae

Spores typically deciduous, subspore apophysis present
- Trophic stage a reticulate plasmodium
  - Spores discharged forcibly from short-stalked sporocarps ..... *Schizoplasmodium* a.
  - Spores deciduous but not forcibly discharged, borne on long stalks *Nematostelium* b.
- Trophic stage comprised of uninucleate to plurinucleate amoeboid protoplasts *Protostelium* c.

Spores non-deciduous, non-apophysate
- Trophic stage a reticulate plasmodium ..... *Schizoplasmodiopsis* d.
- Trophic stage comprised of uninucleate to plurinucleate amoeboid protoplasts *Protosteliopsis* e.

a. *Schizoplasmodium* Olive & Stoianovitch, 1966a.

The sporocarp consists of a short stalk bearing a single plurinucleate spore with subtending apophysis. The spore is forcibly discharged by means of a gas bubble that develops between spore wall and surrounding sheath and bursts, thus expelling the spore from the stalk. The germinating spore gives rise to a plurinucleate protoplast with filose pseudopodia that develops into a reticulate plasmodium. Eventually some of the plasmodia fragment into plurinucleate prespore cells that produce the sporocarps. The striking resemblance of the sporocarps of *S. cavostelioides* Olive & Stoianovitch (1966a) to those of *Cavostelium apophysatum* indicates a close phylogenetic relationship between the two genera. Both species are of widespread occurrence, and both are sometimes isolated from the same collection.

The removal of two long-stalked species formerly included in *Schizoplasmodium* to the following genus leaves only the types species, *S. cavostelioides.*

b. **Nematostelium** Olive & Stoianovitch, gen. nov.

Sporocarpium e spora unica apophysata et decidua; stipitibus gracilibus; plasmodiis reticulum proferentibus, postea fractis in presporas quae directe in sporocarpia simplicia evolvent.

Trophic stage a thin, reticulate, multinucleate plasmodium, which produces filopodia or reticulopodia, segmenting into plurinucleate prespore cells that develop directly into slender-stalked, 1-spored sporocarps; spores plurinucleate, provided with distinct hilum, germinating to produce a plasmodial protoplast. Type species: **Nematostelium ovatum** (Olive & Stoianovitch) Olive & Stoianovitch, comb. nov. (Syn. *Schizoplasmodium ovatum* Olive & Stoianovitch, 1966b) (Fig. 1).

A second, similar but round-spored species is known, for which a new combination is also required: **Nematostelium gracile** (Olive & Stoianovitch) Olive and Stoianovitch, comb, nov. (Syn. *Schizoplasmodium gracile* Olive & Stoianovitch, 1966b).

The recent discovery of isolate *Ta* 67-7 (see Cavosteliidae) is the major factor that has led to the segregation of these two species into a separate genus. The striking similarities between the plasmodia and sporocarps of *Ta* 67-7 and those of *Nematostelium* indicate the origin of the latter genus from a form such as *Ta* 67-7, which is considered the more primitive because of its flagellate cells (see Fig. 6).

c. *Protostelium* Olive & Stoianovitch, 1960.

The sporocarps are typically slender-stalked and 1-spored, and the spores are deciduous. There is a reduced apophysis at the base of the spore. Flagellate cells are lacking. The trophic stage is commonly made up of uninucleate amoeboid cells, but in some species plurinucleate cells are also common. The genus, which contains 5 known species, has recently been monographed (Olive & Stoianovitch, 1969).

Two species have globose spores. The most common of these is *P. mycophaga* Olive & Stoianovitch, with three known varieties, all of which have orange protoplasts. *P. irregularis* Olive & Stoianovitch has larger sporocarps

and non-pigmented protoplasts that vary from uninucleate to plurinucleate but do not become reticulate. The sporocarps are sometimes 2-spored. Three species have non-spherical spores. *P. zonatum* Olive & Stoianovitch, whose stalk contains a series of minute vesicles rather than a stalk tube, and the smaller *P. pyriformis* Olive & Stoianovitch have bell-shaped to pyriform spores. They differ from other protostelids in having the stalk generated within a cylindric steliogen. *P. arachisporum* Olive & Stoianovitch has oval to peanut-shaped spores.

d. *Schizoplasmodiopsis* Olive, 1967.

The reticulate plasmodia, which resemble those of *Schizoplasmodium,* segment in similar manner to form prespore cells that give rise to the sporocarps. The genus differs primarily in having non-apophysate spores that remain attached to the stalk. The single known species is *S. pseudoendospora* Olive, Martin & Stoianovitch (Olive, 1967), which has uninucleate prespore cells and spores and stalks that are relatively short and subulate. The specific name refers to the frequent appearance of enucleate sporoid bodies in the encysted protoplasts.

e. *Protosteliopsis* Olive & Stoian., 1966d.

The genus resembles *Protostelium* in some ways, but its spores are non-apophysate and non-deciduous. In the single described species, *P. fimicola* (Olive) Olive & Stoianovitch, the trophic stage is comprised predominantly of uninucleate amoebae. However, several undescribed forms that we have isolated produce both uninucleate and plurinucleate protoplasts.

C. Ceratiomyxidae Schröter, 1889 (Ceratiomyxaceae)

This family is transferred here for the first time to the Protosteliida. It is distinguished from the other two families by the extensive development of the plasmodial stage with its accompanying copious production of mucus, and the development of what at first appear to be fructifications of macroscopic size. In fact, however, the reticulate plasmodium with its mucus layer is thrown up into simple or branched columns on which sporulation occurs. The plasmodium segments into prespore cells that develop directly into slender-stalked, single-spored sporocarps of microscopic size, just as in other plasmodial protostelids (Fig. 3). The single known genus *Ceratiomyxa* contains only 3 species, of which only *C. fruticulosa* (Müll.) Macbride is common and widespread. A number of authors, including Martin & Alexopoulos (1969), have placed the Ceratiomyxidae in the myxomycetes, but there seems little reason to consider them closely related to that group.

C. fruticulosa has been studied extensively in the laboratory. The observations of Famintzin & Woronin (1873), which remain the most detailed thus far reported (Fig. 3), and of E. W. Olive (1907) make it clear that the stalk is produced in the manner characteristic of protostelids (Fig. 1). They note that the protoplast partly extends into the narrow stalk, leaving the stalk, according to Olive, "a slender, apparently empty filament." Our own observations on sporulation in *C. fruticulosa* tend to confirm this and reveal, in

addition, that there is a thin sheath around the entire developing sporocarp. Also, we find that the spores are deciduous. Several investigators have shown that the single nucleus in each spore undergoes two successive divisions, producing 4 nuclei. On germination of the spore, the 4-nucleate protoplast emerges, a third nuclear division occurs, and the protoplast divides into 8 uninucleate cells, each of which develops a single conspicuous flagellum. A second smaller flagellum has also been reported by some investigators.

Although there are claims that the two nuclear divisions in the spore are meiotic (E. W. Olive, 1907; Wilson & Ross, 1955; Sansome & Dixon, 1965), conclusive evidence of this is lacking. Most cytological studies have reported a chromosome number of 8. Gilbert (1935), McManus (1958), and Sansome & Sansome (1961) have reported plasmogamy between flagellate cells, but these observations have generally failed to distinguish clearly between plasmogamy and what might be the results of incomplete cleavage following the 8-nucleate stage or the occurrence of plasmotomy. Only Gilbert seems actually to have reported seeing nuclear fusion, while McManus was unable to confirm its occurrence. Electron microscope studies of the spore just prior to nuclear division, with the object of establishing the presence or absence of synaptonemal complexes, should be helpful in determining whether there is a sexual process in the life cycle of *Ceratiomyxa.*

Since well developed reticulate plasmodia of true myxomycetes always appear to be characterized by a rhythmic ebb and flow of protoplasm in their veins, we have examined plasmodia of *C. fruticulosa* from this standpoint. In no case have we observed this type of movement. On the contrary, the movement is more sporadic and limited, sometimes occurring in two directions within one vein at the same time, as in other plasmodial protostelids. If a portion of the plasmodium is placed in water on a slide or on the surface of an agar plate, the injury caused by detachment, or the change in osmotic relationships, usually induces a surge of protoplasm in one direction for a time, but no rhythmic ebb and flow has been seen. Thus it appears that both sporocarp and plasmodium of *Ceratiomyxa* have much more in common with those of other protostelids (e.g. *Ta* 67-7. Fig. 2) than with those of true myxomycetes.

II. SUBCLASS **DICTYOSTELIA** L. OLIVE SUBCL. NOV. (DICTYOSTELIIDAE)

The trophic stage consists of uninucleate amoebae with filose pseudopodia. The nuclei commonly contain 2-4 peripheral nucleoli instead of the single central one found in most other mycetozoans, including protostelids. A basic chromosome number of 7 was found by Wilson (1953) in *Dictyostelium discoideum* Raper, and Ross (1960) reported the existence of haploid and diploid strains in this species. Electron microscopy (Mercer & Shaffer, 1960) has revealed a fairly typical fine cell structure in *Dictyostelium.*

When the dividing myxamoebae have reached a certain critical density on the substrate, they begin to be drawn towards centers of aggregation originating around "initiator cells" in response to the production of a substance called *acrasin.* Konijn et al. (1967) have presented evidence that the chemical

attractant in *D. discoideum* is 3′, 5′-cyclic adenosine monophosphate (AMP) and that it is active at very low concentrations. The cells move into the centers in continuous streams. The mature aggregate is a *pseudoplasmodium,* in which the cells maintain their individuality. In some species the pseudoplasmodium migrates in slug-like fashion prior to sorogenesis. Finally, each pseudoplasmodium produces one or sometimes several long-stalked multispored sorocarps.

It is generally thought that a regular sexual process does not occur in the dictyostelids (L. S. Olive, 1963), though cannibalistic engulfment and cell anastomosis may be mistaken for plasmogamy (See Huffman & Olive, 1964). The apparent rare occurrence of nuclear fusion and the very low yield of genetic recombinants from mixed cultures of mutant phenotypes (Sussman, 1961; Sinha & Ashworth, 1969) indicate that a parasexual process similar to that reported in *Aspergillus* occurs in this group.

Synergism between mutants of cellular slime molds has been demonstrated by Sussman and others. For example, Sussman (1954) was able to obtain normal fruiting bodies in *D. discoideum* from a mixture of "fruitless" and "aggregateless" mutants. It was not demonstrated whether complementation occurred between intact membranes or through cell anastomoses, but genetic recombination was not involved.

The morphology of sorogenesis has been worked out in great detail by Dr. Kenneth Raper and others. These and other aspects of the biology of cellular slime molds are covered in excellent detail in *The Cellular Slime Molds* by J. T. Bonner (1967), to which the reader is referred for further information, including an extensive bibliography. The monograph of E. W. Olive (1902) remains the only general taxonomic treatment of the cellular slime molds up to the present time. A single order is recognized.

ORDER Dictyosteliida J. J. Lister in Lankester, 1909, emend. L. Olive (DICTYOSTELIALES).

The order has the characteristics of the subclass.

Two families, distinguished primarily on the basis of stalk characteristics, are recognized. The stalk tube is thought to be homologous with that of protostelids (Olive, 1967).

Key to Families of Dictyosteliida

Stalk tube narrow and hollow ..... Acytosteliidae A.
Stalk tube broader and filled with a framework of empty cells ..... Dictyosteliidae B.

A. Acytosteliidae Raper (Raper & Quinlan, 1958) (Acytosteliaceae)

The family has the characteristics of the single known genus and species, *Acytostelium leptosomum* Raper (1956), which is occasionally isolated from soil and humus. It is the only member of the Dictyosteliida that, like many protostelids, is known to thrive on yeasts as well as bacteria. In sorogenesis, typically several pseudoplasmodia arise from a single aggregate of amoebae, and each gives rise to a sorocarp consisting of a sorus of numerous round spores borne at the tip of a long, narrow, hollow stalk. The developing sorocarp is

surrounded by a thin sheath, which later disintegrates around the mature sorus. Gezelius (1959), in her ultrastructure studies of the sorocarp, described this layer as a slime envelope. She also demonstrated that the stalk is composed of cellulose fibrils of the same size as in *Dictyostelium,* laid down longitudinally in bundles as in that genus and arranged longitudinally in almost concentric layers. Her failure to observe a lumen in the stalk can probably be traced to the tendency of the stalk tube to swell in water (Olive, 1967).

The stalk of *A. leptosomum* resembles that of a number of protostelids, both in diameter and in the presence of the narrow lumen. Dr. Brian Shaffer (personal communication) has found that when the organism is grown on pure water agar, occasional single-spored fruiting bodies are produced; and under similar conditions we have found 2-spored ones. These are indistinguishable from protostelid-type sporocarps. Furthermore, the nucleus of *A. leptosomum* is of a type intermediate between those of protostelids and the Dictyosteliidae in having most often 2, fairly frequently only 1, and only occasionally 3 peripheral nucleoli. Even in protostelids a plurinucleolate condition is common just after nuclear division, the uninucleolate condition being restored sometimes belatedly, by fusion of the several nucleolar bodies into one. For these reasons, *Acytostelium* is considered intermediate in the evolution of the Dictyosteliida from the protostelids (Olive, 1967).

B. Dictyosteliidae Rostafinski, 1875 (Dictyosteliaceae)

The sorocarp is characterized by a multispored sorus of round to bean-shaped spores borne on a stalk that consists of a stalk tube stuffed with empty cells. The fine structure studies of Gezelius (1959) have demonstrated an outer "slime envelope," probably homologous with the sheath of protostelids and *Acytostelium,* which surrounds the entire developing sorocarp but breaks down around the mature sorus. In addition there is an inner layer, probably homologous with the stalk tube of the foregoing groups, that contains parallel, longitudinally oriented cellulose fibrils and which extends from the apex of the stalk within the sorogen or sorus to the stalk base. From the base of the sorogen or sorus to the base of the stalk, the stalk tube is double layered, apparently as a result of additional deposition of cellulose fibrils by the cells that have entered the stalk tube. These cells also secrete cellulose walls around themselves before becoming highly vacuolate and then empty, thus giving added support to the stalk. It appears, therefore, that the stalk has evolved into a more elaborate complex structure in the Dictyosteliidae than in the Acytosteliidae, another point in favor of considering the latter more primitive.

Members of this family have been found primarily in soil, humus, and dung. Three genera are known.

Key to Genera of Dictyosteliidae

Apex of sorocarp not expanded into a denticulate spore-bearing cupule
  Sorocarp typically with terminal sorus only, sometimes with small irregularly distributed lateral sorogens ..... *Dictyostelium* a.
  Sorocarp with both terminal sorus and whorls of smaller, stalked secondary sori ..... *Polysphondylium* b.
Apex of sorocarp expanded into a denticulate spore-bearing cupule ..... *Coenonia* c.

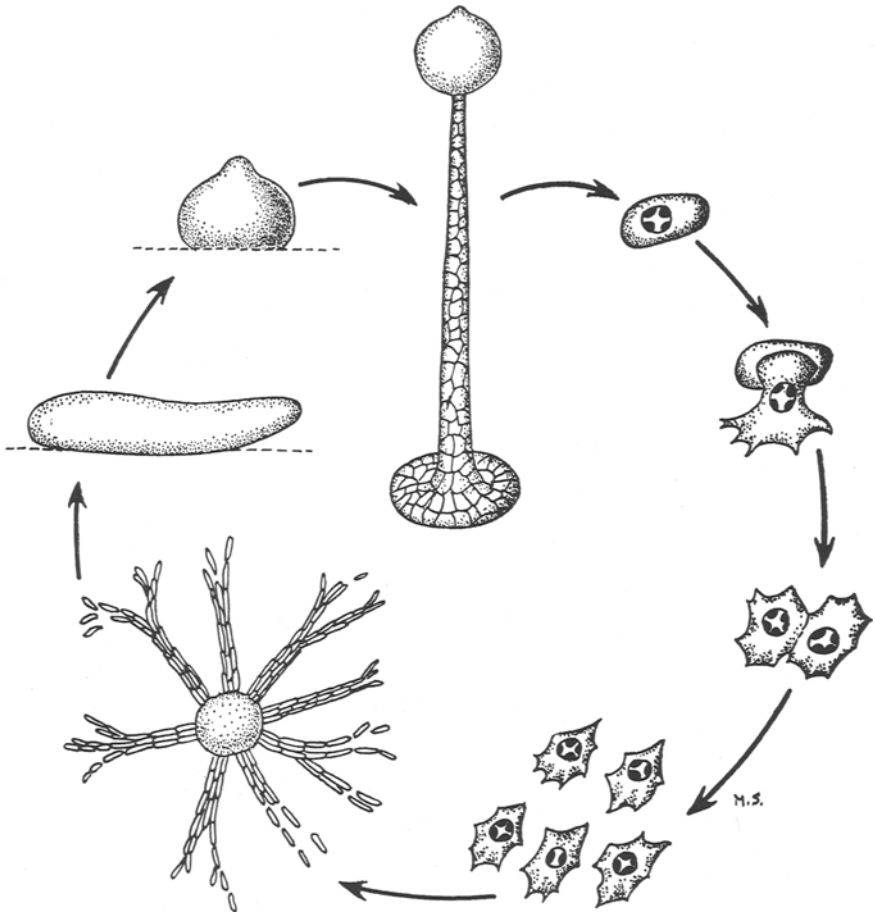

FIG. 4. Life cycle of *Dictyostelium discoideum*.

a. Dictyostelium Brefeld, 1869.

This genus is the largest of the three and contains some of the most commonly encountered cellular slime molds. The most extensive studies of morphogenesis in this remarkable group have been made by Raper (1956, 1960), Bonner (1967), and their co-workers. A great deal of variation exists among the 13 known species. *D. mucoroides* Brefeld, probably the most common and widespread of the dictyostelids, and the purple-spored *D. purpureum* E. W. Olive have sorogens that deposit a stalk horizontally on the substrate during migration and later produce an aerial stalk. *D. discoideum,* the most intensively investigated species (Fig. 4), and *D. polycephalum* Raper have pseudoplasmodia that migrate without stalk formation on the substrate. Pseudoplasmodia of the latter are long and worm-like, and each gives rise to a fascicle of sorocarps. *D. minutum* Raper is more or less a smaller version of *D. mucoroides* but lacks a migrating stage. *D. lacteum* van Tieghem has small sorocarps with round

spores and stalks that sometimes taper apically into a narrow acellular filament (tube?). *D. deminutivum* Anderson, Fennell & Raper (1968), the species with the smallest sorocarps, has unusually narrow, reniform spores and a stalk containing a single tier of cells. Other species described since the appearance of Bonner's text will be found in the publications of Nelson, Olive, & Stoianovitch (1967), Raper & Fennell (1967), and Raper & Cavender (1968).

Evidence of diploidy in *D. discoideum* has been discussed by Bonner (1967). More recently, Ashworth & Sackin (1969) have reported that cell volume in this species is related directly to the number of chromosomes present, and they have presented evidence for a wide range of aneuploidy. They have also given what may be the most logical explanation of the "initiator cells" described by Ennis & Sussman (1958) as initiators of cell aggregation. It is thought that n+1 cells with 8 instead of the normal haploid complement of 7 are the most likely initiators when the extra chromosome is a duplicate of the chromosome that carries a gene specifying some component essential for production of aggregation centers. In other words, dosage effect is the decisive factor. Their discovery that about 1/2,000 cells are of this type agrees very well with the report of Ennis & Sussman that initiator cells occur at a frequency of 1/2,200.

b. *Polysphondylium* Brefeld, 1884.

The two known members of this genus are among the most attractive of the cellular slime molds. They are distinguished by their long, often recumbent stalks, cellular in structure, terminated by a relatively large sorus, and with regular whorls of smaller stalked sori dispersed at intervals below. The sorocarps of *P. violaceum* Brefeld are relatively large and have violet-colored sori, while the smaller and more delicate ones of *P. pallidum* E. W. Olive have whitish sori. These species can sometimes be detected in nature with the aid of a hand lens. *P. pallidum* has been cultured on a defined medium by Goldstone et al. (1966).

c. *Coenonia* van Tieghem, 1884.

The single described species, *C. denticulata* van Tieghem, has sporocarps of an unusual nature. The stalk is expanded above into a cup-like structure with marginal teeth, with the sorus of round spores seated in the cup. Each peripheral stalk cell also has a small tooth or papilla. Sorocarps sometimes have a whorl of secondary stalked sori, which may be indicative of a phylogenetic relationship to *Polysphondylium.* The species has not been reported since its original discovery by van Tieghem on decaying beans in France.

III. SUBCLASS **ACRASIA** L. OLIVE, SUBCL. NOV. (ACRASIDAE)

The limax-type amoebae, which move by means of lobose extensions of the protoplast that develop typically as sudden hyaloplasmic outbursts (especially in the direction of cell movement), and the lack of a stalk tube in the sorocarp distinguish this subclass from other cellular slime molds (Dictyostelia). In species such as *Acrasis rosea* Olive & Stoianovitch, filose extensions may be

present in the posterior uroid region, but the amoebae still move by means of lobose expansions of the cell periphery. These differences are considered of basic importance in indicating a separate phylogenetic origin of this group from simpler protozoans. Although sorogenesis is preceded by cell aggregation, as in dictyostelids, there is no reason to believe that this has resulted from other than parallel evolution. Loose aggregates of cells are also known to form in free-living soil amoebae and in protostelids (Raper, 1960; Olive & Stoianovitch, 1969). Thus, even though the conventional procedure is followed (tentatively, at least) in placing the Acrasia in the Mycetozoa, there is no evidence that they are related to the remainder of that class.

The acrasian amoeba typically contains a contractile vacuole and a single nucleus with central nucleolus, though fine structure studies have shown that the nucleolus of *Acrasis rosea* is considerably more complex than it appears to be under the light microscope (Hohl & Hamamoto, 1968; D. J. Reinhardt, unpublished data). In older cultures individual amoebae frequently round up and secrete walls around themselves, thus becoming microcysts. Cell aggregation leading to sorogenesis differs from that characteristic of dictyostelids in that the amoebae move into the aggregation center not in streams, but singly or in small groups, and they do not elongate in the direction of movement. Also, in *A. rosea* at least, aggregating cells fail to respond to cyclic AMP (T. M. Konijn, personal communication). In the few species thus far investigated the stalks of the sorocarps contain viable cells. Since only two species have been studied in any detail, little may be said regarding possible relationships among the organisms now placed in the subclass. Tentatively, a single order with two families is recognized.

Order Acrasida Schröter, 1886, emend. L. Olive (Acrasiales).

The order has the characteristics of the subclass.

Key to Families of Acrasida

Spores in membranous compartments of the sorocarp ..... Guttulinopsidae A.
Spores not compartmentalized ..... Acrasidae B.

A. Family **Guttulinopsidae** L. Olive, fam. nov. (Guttulinopsidaceae)

Myxamoebae pseudopodiis lobatis praeditae; pseudoplasmodia complanata, non migrantia; sorocarpi stipitati, cum soris terminalibus; sporae in loculis membranaceis dispositi.

The family is characterized by flattened, non-migrating pseudoplasmodia, stalked fruiting bodies bearing mucilaginous sori, and spores produced within membranous compartments of the sorocarp. The thin membranes break down readily in the upper part of the maturing sorocarp, thus freeing the spores, which collect in a capitate mucilaginous mass.

Guttulinopisis. E. W. Olive (1901) is the only genus thus far described. It is here being separated from close association with the next genus, with which Olive originally allied it. *G. vulgaris* E. W. Olive, a common species on dung of horse and cow, is the only member of the genus that has been

studied in detail (L. S. Olive, 1965), and it has been designated the type species. The whitish sorocarps appear within two days on fresh dung placed in a moist chamber. The organism can be cultured on agar media in the presence of a suitable bacterium and will sporulate in culture. However, isolates soon cease normal sporulation unless maintained on sterile dung or dung agar. Sorocarps are often compound, with one to several smaller, lateral sori. The compartments are more persistent in the relatively thick stalk region, where some spores may also be found. Sorocarps most often appear to arise singly from flat plaque-like aggregates of amoebae, which, at least by analogy, may be called pseudoplasmodia. In sporulating cultures some spores may also be found within these plaques. The spores of *G. vulgaris* are distinguished by their peculiar irregularities—they tend to be round but with indentations here and there. Too little is known about the two other species described by E. W. Olive (1901, 1902) to determine whether they actually belong in the same genus with *G. vulgaris.* They were found on dog dung. An unnamed new species discovered by K. B. Raper (1960) and tentatively referred by him to the genus *Guttulina* (= *Pocheina*) probably belongs here, as it seems to have compartmentalized sorocarps.

B. Family Acrasidae van Tieghem, 1880, emend. L. Olive (Acrasiaceae).

There is no evidence of compartmentalization of spores in members of this family. The amoebae aggregate in a manner similar to that described for *Guttulinopsis.* The stalk cells of mature sorocarps remain viable. In two undescribed species being investigated by K. B. Raper (1960) and tentatively placed by him in the genus *Guttulinopsis,* there appears to be little or no distinction between stalk cells and spores, and any cell of the sporocarp may function as a spore. These two species have not yet been assigned to a genus, though they probably belong in the Acrasidae. Thus far, the family contains only two known genera.

Key to Genera of Acrasidae

Spores produced in a terminal spherical sorus ..... *Pocheina* a.
Spores in simple or branched chains ..... *Acrasis* b.

a. *Pocheina* Loeblich & Tappan, 1961 (syn. *Guttulina* Cienkowsky, 1873)

The genus is poorly undertsood, since the type species *P. rosea (Cienk.)* Loebl. & Tapp., discovered on dead wood in Russia, has never been isolated and cultured. Recently, Kenneth Raper (personal communication) has observed and photographed the sorocarps of what must certainly be this or a closely related form on tree bark from Holland, but he has not yet been able to culture it. The rather short-stalked sorocarp is rose-colored and has a terminal sorus of round, minutely punctate spores, as well as a stalk with wedge-shaped cells. The species may prove to be related to *Acrasis rosea,* which also has rose-colored fruiting bodies and which sometimes produces spores in a terminal sorus as well as in the usual catenulate arrangement. Three other species described by E. W. Olive

(1902) are too poorly understood to be adequately discussed here. They need to be studied carefully in culture before their natural affinities can be determined.

b. *Acrasis* van Tieghem, 1880.

The sorocarp is variable, consisting of a single series of stalk cells and a single simple or branched spore chain, or a compact cluster of stalks with separate spore chains, or a trunk-like stalk two to many cells in thickness with branching spore chains. Only two species are known. The type species, *A. granulata* van Tieghem, is known only from its original description. It was found on a culture of beer yeast in France. The sorocarps consist of a single row of stalk cells terminated by a single chain of spores, but sometimes several sorocarps are united into a compact fascicle. The spores are deep violet in color. The pigment is confined to the spore walls, which are minutely warty.

A second species, *A. rosea* Olive & Stoianovitch (1960), was described 80 years after the first. Its spore walls are smooth and non-pigmented, but the protoplasts are rose-colored, the pigments having been identified as carotenoids (Fuller & Rakatansky, 1966). The pink sorocarps vary greatly in size and complexity, the simplest having a single series of stalk cells and a single simple or branched spore chain, while the larger ones have thick trunk-like stalks and many branching spore chains. In some isolates, the sorocarps often appear as though compounded of several simpler ones, a feature which tends further to ally this species with *A. granulata.* A thin sheath surrounds the entire sorocarp. Spores are distinguishable from stalk cells by the presence of a hilum in the spore wall at each point of contact with another spore.

Reinhardt (1968a) has shown that a period of light followed by a period of darkness is required for sporulation in a number of *A. rosea* isolates that he studied, and that the time of fruiting may be shifted to any desired hour by regulation of these periods. Although there is no evidence of a sexual process in *A. rosea,* there is reason to believe that heteroplasmons may result from cell anastomoses (Olive, Dutta, & Stoianovitch, 1961). The species is a common one in various parts of the world and may be readily isolated from dead attached plant structures such as pods, capsules, flowers, small fleshy fruits, etc.

IV. SUBCLASS MYXOGASTRIA Macbride, 1899 (MYXOGASTRIDAE)

The myxomycetes or true slime molds constitute by far the largest subclass of mycetozoans. They commonly occur on dead wood and humus, and their fruiting bodies are usually large enough to be seen with the unaided eye, though some are not apparent without a lens. Sporocarps of the various genera and species show much diversity in form, size, shape, and color. Three major types have been distinguished. The *sporangium* is relatively small, stalked or sessile, and contains a mass of spores surrounded by a fragile layer called the peridium. The *plasmodiocarp* is generally net-like or irregular and without a stalk. It is derived from the main veins of the plasmodium. The *aethalium* is relatively large and cushion-shaped and is derived from all or a major portion of the plasmodium. In all types capillitial or pseudo-

capillitial threads are generally found intermingled with the spores, which are typically uninucleate but may also be plurinucleate in some species. Granules or crystals of calcium carbonate are commonly deposited in or on the fruiting bodies of many species and may be of diagnostic value.

The smallest and simplest sporangia of myxomycetes are found in the genus *Echinostelium,* which contains five known species. The simplest of these is *E. roseum* Ing (1965), which has stalked sporangia of microscopic size with no capillitium and only 20-24 spores. The previously discussed hypothesis that myxomycetes may have evolved from protostelids through *Echinostelium*-like forms emphasizes the primitive nature of the small sporangial type of sporocarp. Myxomycetes with plasmodiocarps or aethalia are probably derived from sporangiate forms through such intermediates as *Reticularia* and *Enteridium,* whose aethalia are composed of confluent but still partially discernable sporangia.

The major trophic stage of a myxomycete is a free-living, holozoic plasmodium. The plasmodia also show much variation in form, size, and color (Alexopoulos, 1960a). The simplest type—the *protoplasmodium*—is a multinucleate amoeba-like protoplast that does not show the rhythmic ebb and flow of protoplasm characteristic of the other two types. It is found in *Echinostelium* and several other genera and is probably the most primitive type. The *aphanoplasmodium* is a thin and relatively inconspicuous reticulate type, while the *phaneroplasmodium* is a coarser and thicker reticulate kind that is also the most commonly observed in nature. Phaneroplasmodia of *Physarum polycephalum* Schw. have been grown in axenic culture on a chemically defined medium (Daniel, Kelly, & Rusch, 1962). The sheath-like layer that covers the plasmodia and probably the developing fruiting bodies may be homologous with that of protostelids and dictyostelids.

A number of myxomycetes have been shown to be heterothallic, and those studied in greatest detail have proved to have a mating type system controlled by multiple alleles at a single locus (Collins, 1963), as in many of the higher club fungi. Except for *Perichaena vermicularis* (Schw.) Rost. (Ross, 1967), those described as being homothallic have never been shown to have a sexual process, and it is therefore not known which of these may be apomictic.

A representative life cycle of a heterothallic myxomycete is diagrammed in Fig. 5. Germinating spores give rise to uninucleate planonts with one or two apical flagella, often two unequal ones, without mastigonemata. Perhaps the most important point here is not whether the number of flagella is one or two but that the basal apparatus is a pair of closely associated kinetosomes (Schuster, 1965; Aldrich, 1968), emphasizing the potentially biflagellate nature of the planonts (as is now proving to be the case with flagellate protostelids). The flagellate cells or similar amoeboid cells lacking flagella function as gametes, fusing in pairs. Plasmogamy is followed by karyogamy and the resultant zygote, which is also the first cell of the diploid or plasmodial phase, develops by enlargement and successive mitoses without cell division into a coenocytic plasmodium. Mitosis in the amoeba is accompanied by break-

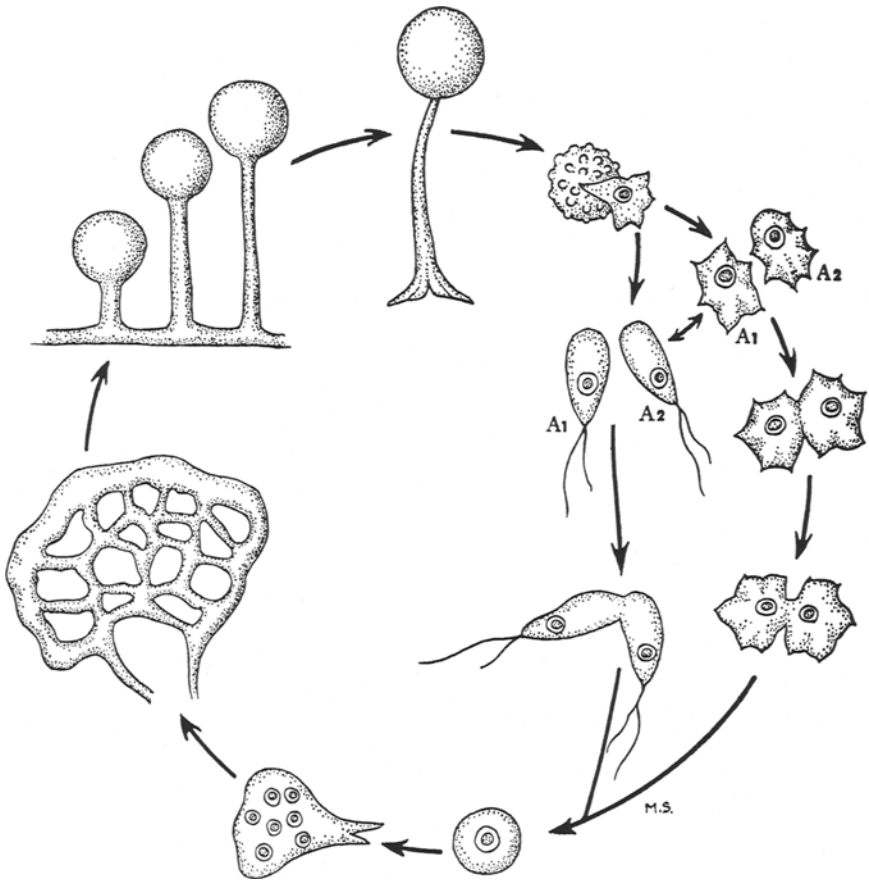

FIG. 5. Life cycle of a myxomycete. A_1 and A_2 denote compatible mating types. Meiosis may occur in the sporangium just prior to spore cleavage or in the germinating spore.

down of the nuclear membrane; whereas, in the plasmodium the membrane persists (Kerr, 1967; Aldrich, 1969). Kerr has noted that the nucleolar material first reappears as 3-5 small bodies that fuse into one, very much like that described earlier in protostelids. Chromosome numbers are generally quite high in myxomycetes, and polyploidy appears to be fairly common. In *P. polycephalum,* the most intensively studied species, chromosome counts in plasmodial nuclei by various investigators range from 20 to more than 100, indicating the occurrence of endopolyploidy.

As the plasmodium creeps about in or on the substrate, it feeds by ingesting bacteria, fungal spores and hyphae, and other microorganisms. A clearly observable alternating ebb and flow of protoplasm is evident in the veins and advanc-

ing front. Just prior to fruiting the plasmodium flows out onto an exposed surface and gives rise to sporocarps characteristic of the particular species. In species such as *Didymium nigripes* (Link) Fr. it has been observed that, just before sporangial development, the plasmodium segments into a number of small, rather regularly spaced presporangial masses, very much resembling prespore cell formation in plasmodial protostelids. The rhythmic ebb and flow movements continue in the developing sporangia until they approach maturation.[4]

For many years there has been considerable debate over where meiosis occurs in myxomycetes, whether in the sporangium or in the spore. Using the occurrence of synaptonemal complexes (as seen in the electron microscope) as an indicator of meiotic prophase, Carroll & Dykstra (1966) found that meiosis takes place in the sporangium of *Didymium iridis* Fr. just prior to spore cleavage, while Aldrich (1967), in a study of three species of *Physarum*, located it in the spores. As Ross (1967) has suggested, this may reflect upon a lack of stabilization on the site of meiosis in the life cycle of a myxomycete.

For a more detailed treatment of the biology of myxomycetes, the text of Gray & Alexopoulos (1968) is recommended, and for taxonomic purposes the illustrated monograph of Martin & Alexopoulos (1969) is indispensable. Though Alexopoulos (1962) has preferred to treat the myxomycetes as a subdivision of the division Mycota (fungi), there appears to be no convincing evidence for considering them directly related to the fungi. Since the true slime molds are such a large group and have already been treated in great detail systematically, no keys to taxa lower than orders will be included here. The five orders of endosporous myxomycetes recognized by Martin & Alexopoulos (1969) are adopted in this review. The major departure from their system of classification, as already noted, is in the transfer of the Ceratiomyxidae to the Protosteliida.

Key to the Orders of Myxogastria

Sporangia stalked, minute, globose or ovate, rarely attaining 0.1 mm diam., often much smaller; plasmodia small, amoeba-like and non-reticulate ..... Echinosteliida (Echinosteliales).
One family: Echinosteliidae (Echinosteliaceae).

Sporangia various, very rarely under 0.1 mm diam., usually much larger and often complex; plasmodia generally but not always reticulate

Spore mass pale to bright-colored or dingy olivaceous, rarely darker; lime usually absent from sporocarps

True capillitium lacking, pseudocapillitium often present ..... Liceida (Liceales).
Three families: Liceidae (Liceaceae), Reticulariidae (Reticulariaceae), and Cribrariidae (Cribrariaceae).

[4]This information is from a film by Dr. Norman S. Kerr, listed as No. E 1569 (1968 and 1969) by the Institut für den Wissenschaftlichen Film, 3400 Göttingen, Nonnensteig 72, West Germany.

True capillitium present, thread-like and sculptured ..... Trichiida (Trichiales).
Two families: Trichiidae (Trichiaceae) and Dianemidae (Dianemaceae).

Spore mass black or deep violaceous to ferruginous, rarely colorless, lime present or absent in sporocarps
Neither peridium nor capillitium calcareous; lime when present restricted to substrate, stipe, and columella ..... Stemonitida (Stemonitales).
One family: Stemonitidae (Stemonitaceae).

Peridium and/or capillitium calcareous ..... Physarida (Physarales).
Two families: Physaridae (Physaraceae) and Didymiidae (Didymiaceae).

GROUPS OF UNCERTAIN AFFINITY

The Plasmodiophorida Cooke, 1928 (Plasmodiophorales), which contain the single family Plasmodiophoridae Zopf, 1884 (Plasmodiophoraceae) with nine genera, are probably not directly related to any of the foregoing three subclasses. Since all are obligate parasites within living cells of plants (including fungi) and are consequently difficult to study in the laboratory, their life cycles are not well understood. Their nutrition is considered primarily osmotrophic, but Karling (1968) has summarized the evidence for their being at least partly phagotrophic, a premise that has received some support from the recent ultrastructure studies of Williams & McNabola (1967).

Although plasmogamy between motile gametes has been claimed by some investigators, these reports are fragmentary and unconvincing, and it must be concluded that demonstration of a sexual process is lacking. The small plasmodia are confined to the host cells. Their nuclei undergo a form of mitosis that has been called promitosis or "cruciform division," during which the nucleolus elongates and constricts while a ring of chromosomes around the nucleolus splits into two rings, one of which passes with a daughter nucleolus into each newly formed nucleus. The daughter nuclei are formed by constriction of the persistent nuclear membrane around the middle. Although promitosis was described earlier in free-living amoebae (Nägler, 1909), it is not found in any of the previously described groups of mycetozoans. Nuclear divisions in the plasmodium just prior to the delimitation of small uninucleate resting spores are reported to be typically mitotic in appearance (i.e., with spindle but without persistent nuclear membrane), and some investigators have considered them to be meiotic. However, there is still no convincing evidence that meiosis occurs in the life cycle.

At germination each resting spore produces an anteriorly biflagellate zoospore that is able to infect the host plant. Zoosporangia may develop early in the life cycle and produce similar zoospores, which some think may function as gametes. The flagella lack mastigonemata (See Karling, 1968). There is little information on how they swim, but a few reports (e.g., Kole, 1954; Keskin, 1964) state that the shorter flagellum extends forward and the longer one backward during swimming. What others have called plasmogamy Keskin has considered "vegetative fusion."

The two most important species of plasmodiophorids economically are *Plasmodiophora brassicae* Woronin, the cause of "club root" of cabbage and other cruciferous plants, and *Spongospora subterranea* (Wallr.) Lagerh., which causes "powdery scab" of white potato. In spite of the fact that these have also been among the most frequently investigated species, accurate information on several crucial stages in the life cycle is lacking.

The Plasmodiophorida are treated in great detail from all aspects of their biology and taxonomy in the monograph of Karling (1968), who is inclined towards the theory that the group has originated from the Proteomyxida. Honigberg et al. (1964) place the latter in the class Actinopodia of the Sarcodina. There are a number of proteomyxids that enter algal cells and feed by ingesting bits of the algal protoplasts. They form "zoocysts" that resemble the zoosporangia of some plasmodiophorids, and these give rise to biflagellate zoospores. Resting cysts are also produced. However, further comparison with the plasmodiophorids is hampered by even less information on their life cycles, with very little known about their cytology. Karling (1944) described a new genus and species, *Phagomyxa algarum,* on the marine alga *Ectocarpus,* which he considered intermediate between the Proteomyxida and Plasmodiophorida. The plasmodia ingest bits of the algal protoplast and, as in the plasmodiophorids, are characterized by synchronous nuclear division, though little evidence of promitosis was found. Zoosporangia with heterocont zoospores were present, but no resting spores were seen.

The Heimerliaceae Arnaud (1949) are a little known and seldom mentioned group that Arnaud thought might be related to the cellular slime molds. He found them on humus and rotting wood during wet periods. The fructifications were described as hyaline and consisting of a slender stalk bearing a mucilaginous globule of spores at the apex. However, further studies were hampered by failure of the spores to germinate. Arnaud recognized six genera, but they seem generally to have been ignored by others. We have recently isolated two organisms from dead vegetation that may belong to this group. They are parasites of ciliates and produce small, multinucleate plasmodium-like protoplasts within the host cells. The "stalk" is an aerial exit tube for the spores of the parasite and may be produced by the ciliate instead of the parasite (G. W. Erdos, unpublished data). The spores collect in a glutinuous mass at the tip of the exit tube. In the presence of healthy host cells in a drop of water they develop two unequal flagella lacking mastigonemes and penetrate the pellicle of the ciliate cells to cause new infections. Whether these two species are valid members of the Heimerliaceae is not known, since this family is so poorly understood. Their relationships to other groups are also obscure, though certain similarities to plasmodiophorids and proteomyxids are apparent. They clearly do not show affinities with the cellular slime molds. Our isolates are under investigation, and it is hoped that more information on their relationships will soon be forthcoming.

Echinosteliopsis oligospora Reinhardt & Olive (1966), found on dead plant structures in various parts of the world, superficially resembles a minute *Echinostelium* but differs markedly from that genus in several important

details. It is a holozoic organism that, on the natural substrate, produces mostly 4-8-spored stalked sporangia. Each sporangium is derived from a protoplasmodium-like amoeboid cell. The spores are formed by progressive segmentation of the sporangial protoplast (Reinhardt, 1968b). On germinating, the spore produces a protoplast with filose pseudopodia. During the trophic phase the protoplasts contain from one to several nuclei, and the largest ones may show occasional reticulations. No sexual process has been observed. The organism is distinguished from a myxomycete by its large nucleus with numerous peripheral nucleolar bodies and by the absence of a flagellate stage. Since it does not fit into any known group, a new family and order are proposed for it. The subclass in which it belongs is also uncertain, as it may have evolved independently of other known groups of mycetozoans.

ECHINOSTELIOPSIDA L. OLIVE, ORD. NOV. (ECHINOSTELIOPSIDALES)

Echinosteliopsidae L. Olive, fam. nov. (Echinosteliopsidaceae)

Sporocarpia minuta, simplicia, stipitata; sporangia plurispora; myxamoebae filopodiis praedita, non-flagellatae; nuclei multinucleolati.

Sporocarps small, simple, stipitate; sporangia several-spored, spores formed by cleavage; myxamoebae with filose pseudopodia, non-flagellate, 1-several-nucleate; nuclei miltinucleolate.

The single known species is *Echinosteliopsis oligospora.* Many years ago, Sorokin (1876) described an unusual organism from horse dung which he named *Bursulla crystallina* but which does not seem to have been encountered since. It is described as having small stalked sporangia with 8 spores. However, the latter lack surrounding walls and are, therefore, released from the sporangium as naked protoplasts. These protoplasts have conspicuous filose pseudopodia and appear to be uninucleate. No flagellate stage was found. The vagueness of the nucleus in the cell indicates that it may be of the plurinucleolate type, a kind that is less conspicuous than the uninucleolate nucleus. Although the organism was thought to have a sexual stage, the evidence is unconvincing. Both Sorokin and Zopf (1884) considered the organism a simple myxomycete, and Zopf placed it in a separate family, the Bursullineae. It seems more likely related to *Echinosteliopsis* and is tentatively placed in the Echinosteliopsidae. Since the relationship is uncertain, Zopf's family is not adopted for *Echinosteliopsis.* There is much need for re-isolation and detailed study of *Bursulla crystallina* before a meaningful classification can be made.

CONCLUSIONS

Whittaker (1969) has published one of the most useful classifications of living organisms, in which he recognizes five kingdoms: Monera (prokaryotes), Protista (chiefly protozoa), Fungi, Plantae (multicellular plants), and Animalia (multicellular animals). Serious consideration of this proposal was recommended by Olive (1969), who transferred Whittaker's subkingdom Gymnomycota—equivalent to Mycetozoa of the present treatment—from Fungi to Protista. However, until the system of taxonomic hierarchies has been worked

out in greater detail for the Protista, the following conventional system based on that of Honigberg et al. (1964) is tentatively adopted:

PHYLUM PROTOZOA

SUBPHYLUM SARCOMASTIGOPHORA

SUPERCLASS SARCODINA

CLASS MYCETOZOA

SUBCLASS I. PROTOSTELIA (PROTOSTELIIDAE)

ORDER PROTOSTELIIDA (PROTOSTELIALES)

Family A. Cavosteliidae (Cavosteliaceae)
Family B. Protosteliidae (Protosteliaceae)
Family C. Ceratiomyxidae (Ceratiomyxaceae)

SUBCLASS II. DICTYOSTELIA (DICTYOSTELIIDAE)

ORDER DICTYOSTELIIDA (DICTYOSTELIALES)

Family A. Acytosteliidae (Acytosteliaceae)
Family B. Dictyosteliidae (Dictyosteliaceae)

SUBCLASS III. ACRASIA (ACRASIDAE)

ORDER ACRASIDA (ACRASIALES)

Family A. Guttulinopsidae (Guttulinopsidaceae)
Family B. Acrasidae (Acrasiaceae)

SUBCLASS IV. MYXOGASTRIA (MYXOGASTRIDAE)

ORDER 1. ECHINOSTELIIDA (ECHINOSTELIALES)
ORDER 2. LICEIDA (LICEALES)
ORDER 3. TRICHIIDA (TRICHIALES)
ORDER 4. STEMONITIDA (STEMONITALES)
ORDER 5. PHYSARIDA (PHYSARALES)

Groups of uncertain affinity discussed in this review are Plasmodiophorida (Plasmodiophorales), Heimerliaceae, and Echinosteliopsida (Echinosteliopsidales).

A tentative phylogenetic scheme is presented in Fig. 6. Alterations are certain to be required as further information is obtained on known forms and as new mycetozoans are discovered.

This review obviously raises more questions than it answers. One of its chief purposes is to make the reader aware of what has been done and of the variety of interesting research problems that need solving. Intriguing ideas on potential research projects will undoubtedly occur to each reader in relationship to his own interests and background. Several that occur to the author are listed below:

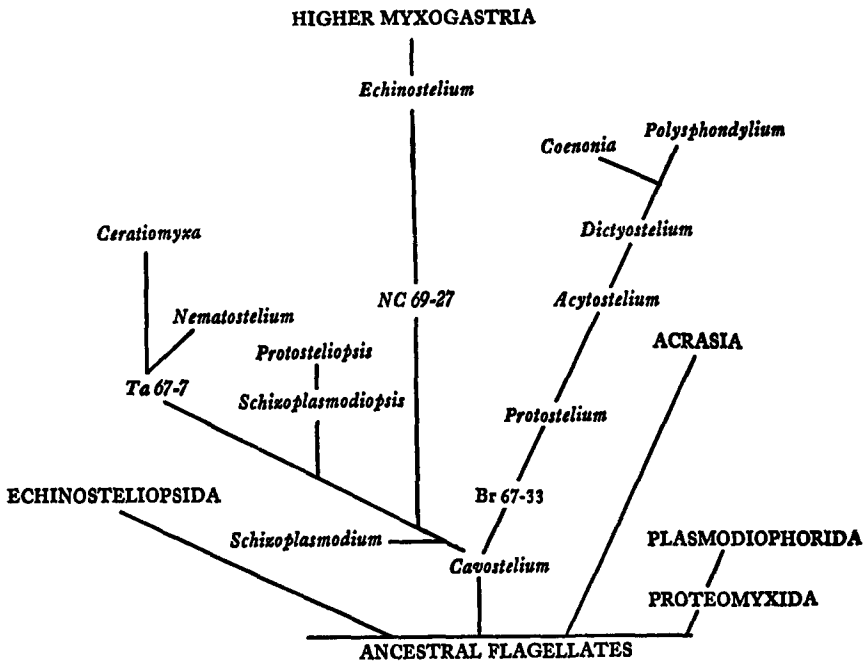

FIG. 6. Tentative phylogenetic scheme for Mycetozoa and groups of doubtful affinity. The Myxogastria may have had more than one protostelid ancestor.

(1) *Taxonomy and phylogeny.* Undoubtedly, numerous interesting taxa remain to be discovered, especially in the Protostelia and Acrasia, and rarely reported species need to be rediscovered and isolated for detailed study.

(2) *Morphology.* Additional morphological studies are needed in all groups, but particularly in the Acrasia. Further ultrastructure studies in all major groups would also be of great value.

(3) *Cytology and genetics.*

(*a*) Mitosis. Details of the nature of mitotic division have not been worked out for protostelids, dictyostelids, and acrasids. Comparative mitotic studies would throw more light on interrelationships.

(*b*) Meiosis. Genetic and ultrastructure studies are needed to help reveal which mycetozoans have a sexual phase and which do not. For example, it is not known whether most of the so-called homothallic myxomycetes are truly homothallic or are apomictic. Use of electron microscopy to determine whether synaptonemal complexes are present in the sporangia or spores would help solve this problem. Similar studies applied to other groups would also be helpful.

(*c*) Parasexuality. Evidence for the occurrence of a parasexual process has been obtained in *Dictyostelium,* and it will probably be found in other groups. The possibility that sexuality in mycetozoans has evolved from parasexuality as a result of localization and regularization of the attendant processes should be considered.

(*d*) Ploidy. Variations in ploidy are known to occur in *Dictyostelium* and myxomycetes, and there is evidence that they occur also in other groups, including protostelids. As already noted, aneuploidy appears to have an important function in aggregation in dictyostelids. Its possible significance in other mycetozoans needs investigation. It should be kept in mind that polyploids may originate either from parasexual nuclear fusion or from endopolyploidy, either of which could be followed by aneuploidy resulting from gradual chromosomal elimination.

(*e*) Heterokaryons and heteroplasmons. Little attention has been given to the occurrence of heterokaryosis or to the influence of mixed cytoplasmic organelles upon phenotype. Preliminary studies of this type in *Acrasis rosea* (Olive et al., 1961) indicate that this line of investigation would be profitable.

(*f*) DNA characteristics. Comparative studies on base ratios and DNA homologies would be an important adjunct to studies on group interrelationships and phylogeny.

(4) *Nutrition.* Only a few dictyostelids and myxomycetes, but no protostelids or acrasids, have been cultured axenically. The ability to culture these organisms axenically would facilitate several of the research projects listed above. It would also permit much needed investigations on biosynthetic pathways. This would, in turn, add much to our understanding of group relationships among mycetozoans and possible relationships of the class to other protozoans (e.g., Vogel, 1964).

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