

CHAPTER 1. Introduction

In the mid-18th Century, the microscope was employed widely by naturalists to view a great variety of small objects. Among those investigating the world of minute things was one M.F. Ledermüeller. One object which he drew (1760-61: pl. 49, fig. 2) and described was “eine schwimmende Pfifferinsel” -- a hypha-encircled gnat that had fallen into a container of water. To be sure, the organism in his illustrations cannot be identified precisely, but it is certain that he saw filamentous fungi in this “mushroom island;” one such fungus (evidently growing in the water) may have been a watermold.

Citing Ledermüeller as the first to note a member of the Saprolegniaceae -- as did Humphrey (1893) and later (1916) Ramsbottom -- is to give credit where it is not due. Twelve years prior to Ledermüeller’s paper, Arderon (1748) described and illustrated filaments growing from the tail of a roach (*Leuciscus rutilus*). Arderon periodically cut off the infected portions of this fish, but the “distemper” spread anteriorly to the animal’s viscera until it finally “submitted”. The moldiness could not be washed off, Arderon reported, and when he examined some of the filaments with the lens, he found them to be filled with a brownish liquid. His illustrations of this “mortification”, as he termed it, show coenocytic hyphae, and are certainly far more convincing evidence of a saprolegniaceous fungus than Wrisberg (1765) later depicted.

The next verifiable mention of a watermold is that by Spallanzani in 1776 (a French printing of his “Opuscoli...” appeared in 1777, and is the most frequently cited edition). He remarked that minnows and leeches dying in water often became covered with mold. Schrank (1798), like Spallanzani, saw colorless threads on dead fish, but thought they were plants of a “*Conferva*,” and named them *C. piscium* (Kützing, 1849, merged this name with *Saprolegnia ferax*). Meyen (1835), too, saw hyphae on dead animals (flies), and concluded that although they resembled species of *Vaucheria*, they probably were filaments of a water fungus. A part of the “Micrographic Dictionary” published by Griffith and Henfrey (1875) discusses the watermolds known at the time, and echoes the confusion over the precise nature and affinities of these fungi.

The concept of the Saprolegniaceae as a taxonomic unit accumulated gradually through the publications by de Bary, beginning in 1852 and culminating in 1881 (this paper also was issued as a separate, coauthored with Woronin). Humphrey (1893) enlarged to some extent on the circumscriptions emerging from de Bary’s studies, and Coker (1923) further expanded it with the addition of new taxa and detailed accounts of species variability. In a 70 year period, 1823-1893, beginning with Nees von Esenbeck’s establishment of *Saprolegnia* and *Achlya*, eight genera were admitted to what was to become, with Kützing’s (1843) and Pringsheim’s (1858) publications, a recognizable family. A surge of activity, promoted by Coker, in the years from 1921 to 1927 saw the incorporation of seven more genera into the family. In the span of approximately 20 years --1948-1969 -- only two additional genera were proposed for inclusion in the Saprolegniaceae.

Through the years of research on members of the family mycologists were largely preoccupied with the discovery and description of new taxa (general account by

Das-Gupta, 1982, for instance), but it is easily forgotten that over a century and a half of work on the water molds has left a legacy of more than taxonomy. A surprisingly large number of investigators troubled themselves with these fungi as tools for cytological and ultrastructural investigations, as subjects for nutritional and biochemical studies, and as organisms occupying ecological niches. A few members of the family have yielded bits and pieces of genetic information, though certainly not to the extent revealed by some of the higher fungi. The only steroid sex hormones (Chapter 21) known outside the animal kingdom are antheridiol ("hormone A") and the oogoniols ("hormone B") of the dioecious *Achlyas*. In the chapters to follow we explore the diversity (and in a few instances the uniqueness) of the water molds as some of the tools of mycology.

GENERAL CHARACTERISTICS

A definition of the family must emphasize that its members display especially strong oogamy as well as dimorphism of the asexual spores (planonts, zoospores). All members are filamentous, their hyphae being nonseptate save where crosswalls delimit reproductive cells (not organs: these are generally recognized as multicellular entities), and which characteristically display an unlimited capacity for growth. In common with other fungi, the hyphae of water molds elongate by apical growth involving wall vesicle formation (Heath, 1976). The cytoplasm of the mycelium is equipped with all the essential functional and structural appurtenances of any eucaryotic cell: vesicles, endoplasmic reticulum, microtubules, Golgi or dictyosome bodies, mitochondria, and the like.

Mitosis in the somatic nuclei (and meiosis in the reproductive cells of some species, at least) is intranuclear, involving replicating and migrating extranuclear centrioles and radiating kinetochore microtubules (Beakes, 1981a; Heath and Greenwood, 1970c; Heath, 1978b; Tanaka and Heath, 1984). There is a growing body of evidence, largely from ultrastructural studies, that meiosis in the Saprolegniaceae takes place in the gametangia and not during germination of the zygote as has long been thought. This being the case, the somatic nuclei are diploid.

Early literature on the chemistry of the hyphal wall pointed to its cellulosic nature. This of course appeared to set the Saprolegniaceae aside from other fungi in which chitin is the predominating wall constituent, and led to considerable speculation on relationship of this family to others (see Chapter 25). The discovery and confirmation of cellulose in the hyphal wall of the water molds strengthened the arguments of those who held to an algal ancestry and affinity for these fungi. Evidence from the application of refined analytical methods demonstrate that the hyphal wall in all representatives of the family tested is largely glucan: the noncellulosic polysaccharide fraction in several water mold species accounts for more than 85% of the wall constituents (Parker *et al*, 1963). The glucans, it appears (Bartnicki-Garcia, 1968), are β 1, 3- and β 1,6-linked (Chapter 6). Dietrich (1975), however, reasoned that the ratio of

acetate to hexosamine in the hyphal wall of seven species of water molds pointed to the presence of some chitin.

Asexual reproduction in members of the Saprolegniaceae is initiated by the cleavage in a multinucleate, typically terminal, sporangium of an indefinite number of spores (corresponding, presumably, to the xenospores as defined by P.H. Gregory, 1966). The pattern of spore release from the sporangium traditionally has been the chief feature on which genera are established in the family. However, with the exception of two or three groups (for example, *Geolegnia* and *Leptolegnia*), it is now known that members of a given genus sometimes display discharge behavior characteristic of other genera as well. Although the pattern of spore discharge varies, the manner in which these cells are cleaved from the cytoplasm seems to be universal, at least in the early stages, among the members of the various genera. Spore cleavage begins with the invagination of the central vacuole tonoplast between peripheral nuclei and segments of cytoplasm in the sporangium to delimit polygonal cells, then the sudden dissolution of these initials, followed in a short time by their reappearance and subsequent final delimitation (Chapters 8, 14).

Spore discharge in the water molds is effected by three principal mechanisms: the development of an apical (sometimes subapical or lateral) pore in the sporangium wall, the dissolution of a single escape orifice for each spore (dictyocoid sporangium), or the rupture of a large portion of the sporangial wall itself, simply allowing the spores to float free. The precise mechanism of release has never been adequately explained (see Chapter 8, 14), but for members of the two largest genera, the traditional view has been that an endogenous expanding substance swells to push the spores out of the exit orifice. Borkowski's explanation (1968a) is diametrically opposed to this classical view, and does not admit to active motility of the emerging spores as the mechanism of discharge. He theorizes that discharge in *Saprolegnia* species results from differences in electrical charge between the wall of the spore and that of the sporangium. There is substantial evidence (Harold *et al.*, 1987; Korpff, 1986) that transhyphal electric currents are involved in hyphal tip growth, whereas osmotic mechanisms appear to function in spore discharge (Money and Webster, 1985, 1989).

Except for the members of the genus *Geolegnia* (J.V. Harvey, 1925b) and one species of *Aplanopsis* (where no asexual spores of any kind have been discovered; Höhnk, 1952a, b; Dick, 1960a) the planonts emerging from the sporangia or cysts are biflagellate. The primary spore (it is the first to emerge in *Pythiopsis* and *Saprolegnia* but is suppressed in some other genera) is apically or subapically biflagellate and generally pyriform. Schussnig (1948, 1949) coined new terms to designate nonpolar flagellum attachment: subakrokont flagella are attached to the spore body subapically, while flagella laterally attached in a groove are pleurokont. After a period of motility the released primary spore encysts (Crump and Branton, 1966, say that encystment is accompanied by flagellar retraction), and after a period of time a planont emerges again from the cyst. This secondary planont (zoospore) is laterally biflagellate, reniform, and is the strongest, most persisting swimmer of the two types. The secondary spore likewise subsequently encysts -- Crump and Branton (1966) maintain that the flagella of the reniform spore are shed, not absorbed or retracted -- and then, in time, this cell

ordinarily forms a germ hypha that subsequently grows into a mycelial system. One of the pair of flagella on each primary and secondary planont is anteriorly directed and of the tinsel type, the second trails, and is of the whiplash type. Transmission electron microscopy (Heath, 1976; Heath *et al.*, 1982) shows that among other features, the organelle of motility consists of the flagellum proper and, endogenously, a flagellar root or kinetosome. The spores of the Saprolegniaceae are dimorphic or monomorphic (in those cases where the primary flagellate stage is suppressed). The early literature refers to the spores of these fungi as diplanetic or dicystic. Inasmuch as cases of repeated encystments and excystments are well documented (Weston, 1919; Salvin, 1940), these terms are not applicable in a strict, etymological sense (but see Dick, 1973: 117).

Following discharge, the sporangia of most water molds are renewed by a continuation of hyphal growth or by successive, basipetalous or cymose cleavage of additional ones. Renewed hyphal tip growth may be internal through one or more previously discharged sporangia --percurrent (S. J. Hughes, 1971b) -- or lateral by branching from below the delimiting septum of a terminal sporangium. The subject of hyphal branching as an expression of growth together with an analysis of causal factors appears in a series of publications by Bret (1971, in particular) and Larpent (1966; a review and general account).

Some water molds produce densely cytoplasmic hyphal segments of a diversity of shapes and arrangements. These have been variously named: gemmae, chlamydospores, or resistant spores. Gemmae are generally held to be resistant structures, although this has not been proven experimentally. They approximate oogonia and sporangia in arrangement at least, and their content may become functionally transformed into oospores or spores, or the entire structure may germinate directly into a new hypha without internal cleavage.

Members of the Saprolegniaceae are oogamous, with the delimitation from somatic hyphae of specialized gametangia, the oogonium and antheridium. Some species are partially or entirely without antheridia, in which case sexual reproduction is generally thought to be parthenogenetic. Sharp controversy developed in the early years of the 20th Century over whether or not fertilization actually was effected by antheridia (Chapter 12). De Bary, for instance, thought not, while Pringsheim (1882a,b) described sperm-like cells emerging from the antheridia and bringing about fertilization (he based his observations on parasitized material). In any event, the contents of the oogonium segment into one or more oospheres in a fashion recalling very strikingly the cleavage of spores: evagination of a central vacuole tonoplast between aggregating clumps of cytoplasm positioned peripherally in the oogonial cell. Subsequently, the uninucleate oospheres (J. Fletcher, 1979b, reports oospheres with no nuclei) devoid of any periplasm mature into oospores (analogous to the memnospires defined by P. H. Gregory, 1966) that are thick-walled and usually contain a lipid reserve disposed in a particular fashion outside the cytoplasm proper. Howard (1971) has explored oospore type as a function of the location of the ooplast; the superbly conceived ultrastructure analysis by Beakes and Gay (1978a, b) of oospore cleavage and oospore maturation in *Saprolegnia furcata* has revealed much that has been previously unknown about the

zygotic products and incidentally brought into question time-honored terminology. Their evidence, too, points to gametic meiosis in members of the family.

Oospore germination is known for a few species, but the percentage of these cells that actually perform is relatively low. There are four patterns of zygote germination among the water molds involving the production of hyphae alone or hyphae terminating in sporangia (A.W. Ziegler, 1948a, b). Some early investigators described oospore germination as a process of endogenous cleavage directly into planonts, but later studies have not confirmed such a pattern.

In a series of review papers, E. Müller (1970, 1972, 1974, 1976) has recapitulated much of the information on water mold structure coming from accounts of the less classical approaches to morphology. He has also given a precis of taxonomic accounts of these fungi above the familial level.

BIOLOGICAL IMPLICATIONS

Pringsheim (1851, 1858) first recognized the sexual significance of the oogonia, but was less than clear initially about the functional role of antheridial branches. In a classical paper on *Saprolegnia mixta*¹ Klebs (1899) laid the foundation for study of the physiology of reproduction. He found that as long as the fungus was well supplied with nutrients it remained vegetative, but when the quality and quantity of the culture milieu was modified or became limiting to growth reproduction commenced. While Klebs obviously established the base for subsequent studies on morphogenesis, he made no fruitful attempt to analyze his observations. Kauffman (1926) described Klebs' findings as a dictum which said that a given species would react in a particular way in a specifically defined environment each time it was subjected to those conditions.

Another species would respond differently in that environment.

Later studies have borne out Klebs' concept that the developmental phase and form of water molds can be altered by manipulating the environment. He did not, of course, appreciate the fact that the potential form a fungus can take is also determined genetically (Hawker, 1956). Moreover, it has been shown that as a general rule the range of environmental factors influencing the expression of the sexual stage is narrower than those encouraging vegetative growth or even asexual reproduction (Hawker, 1956). Refined experimentation since Klebs' time demonstrates that simply starving a water mold colony does not necessarily induce it to reproduce, but transferring a well-nourished specimen to a dilute medium is likely to promote the

¹ The evolution of taxonomic viewpoints has resulted in a number of nomenclatural changes. Where a correction in the name of any taxon, as we recognize it, is necessary, we append to that name a dagger (†) to indicate that the epithet, as used, has been changed, is excluded, or is synonymous with another name. The assignments of such names are made clear in the taxonomic account.

formation of some reproductive unit, sexual or asexual. It has also been found (Schlösser, 1929) that the delimitation of reproductive cells in certain saprolegniaceous fungi does not necessarily establish an irreversible progressive morphogenetic development. Up to a certain point in their maturation, the sex cells of some species can be induced to revert to vegetative or asexual functions simply by proper manipulation of the environment.

A few years before Klebs had begun to explore the interplay between nutrition and reproduction, de Bary (1881) theorized that chemical substances secreted by the oogonial initials induced antheridial hyphae to form, and exerted on them a chemotropic response. Klebs, too (1899), believed that the presence of oogonia stimulated antheridial formation, and Kauffman (1908) reported that he had caused antheridial branches to appear on the mycelium of a species of watermold normally lacking them simply by adjusting the mineral content of the medium. He concluded that nutrients permitted the synthesis of chemicals which elicited antheridial hyphae and influenced their direction of growth.

Working with matings in "sterile" strains of *Dictyuchus* J. N. Couch (1926b) assembled evidence for some specific diffusing substances implicated in oogonium and antheridium production. It remained for J. R. Raper (1936-1970), however, to demonstrate conclusively that a hormonal mechanism controlled initiation and differentiation of gametangia in some *Achlya* species. He postulated that there existed in heterothallic (dioecious) *Achlyas* a series of four hormones having to do with antheridial hypha stimulation, another triggering oogonium initial formation, a sixth acting to attract and direct the growth of antheridial hyphae and to delimit the antheridial cell, and yet a seventh that induced delimitation of the oogonial initials and subsequently the differentiation of the oogonial cytoplasm into oospheres. The initiating hormone, antheridiol, has since been synthesized. Other steroids -- the oogoniols -- have been identified chemically or synthesized (McMorris *et al.* 1983) and the biosynthetic pathways explored (McMorris and White, 1977; Riehl and Toft, 1985b; see Chapter 21).

The studies by J. R. Raper took the phenomenon of sexuality in the Saprolegniaceae out of the realm of speculation and controversy engendered by the early students of the group. Similarly, the work of Beakes and Gay (1977, 1978a, b), Heath (1974a-c, 1976), Heath and Greenwood (1968-1971), Holloway and Heath (1974; 1977a, b), and others, employing modern methods of ultrastructure research have clarified and expanded tremendously on the earlier poorly refined and often controversial cytological work on watermolds by P.-A. Dangeard (1890-91) and Guilliermond (1941), notably.

Much of the published work on the physiology of the Saprolegniaceae is little more than an exposé of nutritional requirements. Important as such information has proven to be, it falls short of explaining precisely how the watermolds metabolize and function in their environment. Horgen (1977a, b) and associates have taken requisite steps to explain from the biochemical viewpoint some factors operating in the mechanism of sexual reproduction in the watermolds. From a similar base the biochemistry of reactions -- LéJohn (1971a, b) and colleagues have explored such

functions as enzyme systems, ionic control of metabolite flow, and regulatory processes in a representative of *Achlya*. These studies, among others, have opened meaningful new paths for exploration of the metabolic processes operating in species of the Saprolegniaceae.

While the water molds have not attained any distinction as ecological tools, the literature on these fungi is not devoid of various aspects of their distribution and occurrence that would qualify for an ecological flavor. European mycologists (Dick, 1981; Perrott, 1960; R. E. Roberts, 1963; Ristanović, 1970a; Stpiczyńska, 1962; Willoughby, 1962) have been more active generally in exploring the ecology of water molds than have the mycologists of the Western Hemisphere. The more prominent studies of an ecological nature began to appear about 1958, hence our knowledge of this facet of the family is relatively recent. Certainly A. Lund (1934) in Denmark must be singled out as a pioneer in ecological work with these fungi. His analysis of species occurrence was related fundamentally to pH of the water in which he found the organisms, and others have since explored exhaustively this aspect in additional geographical areas. There has also been pioneering work by G. C. Hughes (1962) emphasizing seasonal occurrence with respect to temperature. TeStrake (1958), on the other hand, explored water salinity as a controlling factor in occurrence and frequency of water molds. Quantitative data, so necessary to formulating conclusions on distribution, occurrence, and frequency are scanty; Suzuki (1960a, *et seq.*), Dick (1971c, 1976), Willoughby (1962), and especially Hallett and Dick (1981) have devised or applied quantitative analytical methods having greater or lesser degrees of dependability. Universally acceptable quantitative methods for analyzing the water mold population in soil or water are still wanting.

Until Minden (1916) employed baiting techniques for the capture of zoosporic fungi, the recovery of water molds lay largely in the realm of fortuitous collection on natural substrates in water: dead fish and insects predominantly. From such a humble beginning knowledge of the pathological aspects of members of the Saprolegniaceae developed. Five species share a position of notoriety as causal agents of disease. Historically, the troublesome *Saprolegnia parasitica*[†] is the most widely known of the five. This species (and a host of nonsexual individuals in the same genus) are implicated in what is now generally known as saprolegniosis (Neish, 1976, 1977) of various scaly and non-scaly fish and their eggs (Chapter 29). On the European continent, *Aphanomyces astaci* is a serious pest on the edible crayfish, *Astacus astacus* L. (Unestam, 1965a, *et seq.*; Polglase and Alderman, 1984; S. J. Smith and Söderhall, 1986b). The fungus and the accompanying disease, "krebsspest" or "kräftpest" (crayfish plague), has spread from southern Europe eastward into the Soviet Union, and thence westward into the Scandinavian Peninsula within about a century (Chapter 30).

Water molds have been found to attack a variety of vascular and nonvascular plants, but two -- the last of the aforementioned notorious five -- stand out. *Aphanomyces euteiches* is a serious pathogen of various cultivars of *Pisum sativum* L., but it has been reported to attack some 80 other hosts, though certainly not with the damage that is caused in the roots of peas (Chapter 27). *Beta vulgaris* L. suffers from blackroot (Chapter 28) in almost all regions of the world where it is grown (Papavizas and Ayers, 1974).

Aphanomyces cochlioides is the major pathogen, but it enjoys the company of equally notorious companions in some cases: *Pythium* species, *Phoma betae* Frank, and *Rhizoctonia solani* Kühn. The *Aphanomyces* species attacking sugar beets has been reported also in roots of more than 25 other plant species.

Each of these aspects of the biology of the Saprolegniaceae -- general morphology and development, cytology, ultrastructure, physiology, biochemistry, ecology, pathology, and phylogeny -- are treated in detail in the chapters to follow.

OCCURRENCE AND DISTRIBUTION

Although no specifically directed efforts to analyze and record the distribution of the Saprolegniaceae on a global basis are extant, the literature is not mute on the subject. Published accounts, particularly those of a floristic nature (B. Liu, 1984, for example) leave no doubt that many species of the family are ubiquitous. Certain species, to be sure, appear very infrequently, but whether this is due to natural rarity or simply to the collector's failure to provide the precise conditions for their capture is unknown. In any case, from a reading of the records of distribution, one can propose an honest conjecture that absence of water molds from a particular geopolitical area reflects primarily a paucity of collection and culturing. Both continental and insular regions have mycofloras that include water molds, but insofar as it is possible to judge from existing published records, there are no incontestable cases of endemism. Certainly the very few studies of occurrence over broad geographical areas (such as that by Gaertner, 1954) do not reveal endemic species, even though it must be admitted that some species are less widely distributed than others.

It has been suggested that the frequency of occurrence of species (and concomitantly the variety of taxa) of zoosporic fungi decreases in relation to increasing degrees of latitude in a northerly direction. Our experience with saprolegniaceous forms in Iceland and in the Scandinavian Peninsula does not reflect this conclusion, and the reason seems to lie in frequency of collection. When easily definable natural habitats are visited repeatedly and samples taken, a diverse and generous flora is found to exist. So few studies have been done on the occurrence of water molds in relation to altitudinal differences (and accompanying environmental changes) that nothing substantial emerges (Chapter 3). We are inclined to believe that paucity of collections provide data pointing to altitudinal distribution for the water molds, but which in fact does not occur.

There seems to be little if any evidence that geographical distribution of individual species of Saprolegniaceae is related either to soil type or to the nature of the aquatic habitat, lentic or lotic. In one of the first studies of the occurrence of water molds Waterhouse (1942) observed that a river habitat (lotic) harbored a more diversified flora than did ponds, but the richness of the yield in the river was less. If one examines the results of a variety of studies on rivers and lakes (for example, Willoughby and Collins, 1966; Dick, 1971c) looking simply for species diversity and abundance, Waterhouse's conclusion is supported. If anything can be said about soil type and its relation to species distribution it is that organically-rich soils have a more

diversified and abundant saprolegniaceous flora than, for example, sand or predominantly sandy soils. Muck soils, with their concomitant low oxygen content, are less likely to harbor a rich watermold flora than are loam or agricultural soils. In our experience, if a diversity of species of Saprolegniaceae is to be realized from a single set of samples, collecting and baiting soils from intermittently wetted areas is more likely to result in diversity than is a site that is almost constantly wet or dry.

Although watermolds occur in both terrestrial and aquatic habitats, some appear to show "preferences", as it were, if a sufficient number of samples are taken. Members of *Dictyuchus*, *Brevilegnia*, *Thraustotheca*, and *Geolegnia* are primarily inhabitants of soil. Perhaps this preponderance of their occurrence in soil may be explained, at least in part, by Höhnk's (1935a, 1968) concept of sporulation patterns in the family.

While there has been too little work done to validate the postulate convincingly, there is a gathering body of evidence (Sörgel, 1941; Alabi, 1971a, b) that members of the genus *Saprolegnia* may be somewhat limited geographically. We have only collected one species of the genus in a strictly humid tropical area. If, in fact, this is a real rather than an imagined distributional pattern the reason(s) for it remain to be discovered.

Prior to the discovery by E. J. Butler (1907) that pythiaceae fungi could be collected from soil by baiting, water was thought to be the only habitat for the Saprolegniaceae. Thus, the literature of the 19th and early 20th Centuries records watermolds chiefly as inhabitants of submerged plant or animal parts. Saprolegniaceous fungi have been reported as saprophytic (saprotrophic) on many diverse substrates -- cadavers, eggs, embryos, and adults of various aquatic animals; submerged roots, culms, leaves, and twigs of emergent vascular plants; algal filaments; keratinized materials -- and as parasitic (biotrophic or necrotrophic) forms on roots of some crop plants, and on freshwater fish, to name a few substrates. It seems clear that members of the family do not display any striking substrate preferences (with the exception of the parasitic ones, of course). Although species of Saprolegniaceae are now almost exclusively obtained by baiting techniques, the serious collector will not ignore naturally-occurring submerged plant and animal remains as a source of these fungi.

As will be apparent in the chapters on ecology, the Saprolegniaceae are not limited to freshwater; estuarine or coastal brackish water seems to support a flora of these fungi, though it is by no means rich and diverse. Seashore and desert soils and even windblown silt in depressions on barren lava fields (Iceland) harbor watermolds. The habitats likely to give the greatest yield are those in which organic matter has accumulated. The paper by Sörgel (1941), a model of detailed analysis of insular, peninsular, and continental soil samples, bears out this observation. Four of his conclusions (based on his analysis of the occurrence of various zoosporic fungi in addition to watermolds) are revealing: soils disturbed by man or domesticated animals yield more fungi than undisturbed ones; there are more zoosporic species in wet than in dry habitats; distribution of species is relatively uniform and some fungi previously thought to be rare are not so. Although these conclusions are not universal with regard

to the Saprolegniaceae they are generally indicative of their occurrence and distribution.

SUPRAFAMILIAL CLASSIFICATIONS

In conformity with prevailing thought at the time, cryptogamic botanists of the mid-1800's included the saprolegniaceous fungi among the algae, although some investigators like Thuret (1850) at least recognized that the nongreen, filamentous organisms had some fungus-like characteristics. Pringsheim (1857, 1858) put the known water molds in the Siphonales as colorless, parasitic algae, and elevated the family (with three genera, *Saprolegnia*, *Achlya*, and *Pythium*) to equal status with the Oedogoniaceae. These same genera plus *Hydronema* were put by Endlicher (1841) in a tribe of confervaceous algae, and merged into a single genus *Leptomitus*. The early 19th Century mycologists were, of course, struck by the gross morphological similarity of the water molds to the siphonaceous algae; the undeniable resemblance of the sex cells of *Vaucheria* species and those of the water molds was simply too strong to ignore.

De Bary (1884) recognized the fungal nature of the representatives of the Saprolegniaceae, and assigned them (together with some other fungi) to the Phycomycetes because they had a structural similarity to algae. Most mycologists immediately following de Bary (A. Fischer, 1892; Schröter, 1889, 1893) included the family among the fungi, but in recent times others have reassigned it (as a member of the Oomycetes, usually) to a position within the algae.

The Saprolegniaceae appear in Schröter's scheme (1893) as an assemblage (within the Oomycetes) coequal with the Monoblepharidinae in a subgroup, Eusporangiae, of the Sporangiae. Schröter recognized only two major "classes" of fungi, the Phycomycetes and Eumycetes. He placed three families into the order "Saprolegniinae:" Saprolegniaceae, Leptomitaceae, and Pythiaceae. According to Sorokin[a] (1874), the aquatic and terrestrial Phycomycetes were of equal rank in the "Syphomycetes."

Somewhat less conventional schemes appeared near the beginning of the 20th Century. Petersen (1909a, b; 1910) regarded the water molds as representatives of a group he termed Macro-oomycetes (as distinct from the Micro-oomycetes to which he assigned the chytridiaceous fungi). In the Saprolegniinae, he recognized three families: Saprolegniaceae, Rhipidiaceae, and Pythiomorphaceae. The term Archimycetes, Cavers (1915) believed, could be reasonably expanded to include all "lower" fungi, among them the Oomycetes (of which the Saprolegniaceae were a part). Along with the Vaucheriaceae, Chytridiaceae, Peronosporaceae (and others) Webber (1889) included the Saprolegniaceae, and at the same time assigned all these families to the class Coeloblasteae of the Oophyta.

In the period roughly between 1915 and 1955 the water molds as a group were essentially left at rest among the "Phycomycetes." Schussnig's system (1948) of classification, for instance, certainly conformed to tradition; he merely raised the families of zoosporic fungi to ordinal or class rank. Beginning perhaps most strikingly with Moreau's (1953) system, the Saprolegniaceae (included either in ordinal, class or subclass groupings) underwent a series of less traditional reassignments. Moreau

placed the order Saprolegniales into the subclass Dimastigomycetes of the class Mastigomycetes. Somewhat more recognizable, but still disregarding obvious morphological divergence, was Domjan's (1936) inclusion of the water molds in the same subclass with the chytrids. Chaudefaud's (1960) suprafamilial classification scheme set the water molds aside from the chytrids in a group "Phycomycetes dimastigues" (Phycomycophytes), characterized in part by a haploid thallus.

A rather radical assignment befell the water molds when in 1956 Copeland placed the family Saprolegnia (order Saprolegnina) in Winter's class Oomycetes which he then assigned to the phylum Phaeophyta Wettstein, a group relegated to Hogg's Kingdom Protocista. Copeland's scheme excluded the fungi (together with some other organisms) as nucleated organisms from both the Kingdom Plantae and Animalia. There is certainly little support from mycologists of the zoosporic fungi for including the families Leptomitae and Rhipidiaceae in the same order as the saprolegniaceous fungi, as Copeland clearly did. Strange bedfellows were created when Copeland placed the fungi in the same group with the marine algae and the protozoans.

In a somewhat less radical move than Copeland's, Whittaker (1969) proposed that five kingdoms of organisms be recognized, one being that of the fungi and in which the "oosphere fungi" had a position in a phylum of the subkingdom Dimastigomycota. While Whittaker retained the water molds among the fungi (he placed them in a compartment separate from the true fungi), Kreisel in the same year (1969) did not. He believed that the Oomycetes were one of five classes of fungus-like organisms, but regarded them as heterotrophic members of the Chrysophyta and in this sense brought the water molds back among the algae where they had been placed more than a century before. Consistent with an algal ancestry for the water molds, von Arx (1967) regarded the Oomycota as a group analogous to the Chlorophyceae, and forming, together with the Siphonales, a natural grouping (Einheit).

Surely, the present day systems that discard the Saprolegniaceae into obscurity among the algae have precedent. As early as 1903, Bessey broke with tradition and included the family as hysterochytes in the Siphonales along with such organisms as the chytrids, Cladochytrium, *Vaucheria* species, mucors, and the peronosporaceous "fungi." Recognizing two kingdoms, Protista and Mycota, von Arx (1970) raised the Oomycetes to phylum status coequal with recognized algal groups in the Protista. Thus, he effectively excluded the water molds from the fungi. Shaffer (1975) very explicitly did so as well. In Olive's (1975) system of classification, the class Oomycetes (including the Saprolegniaceae) is retained in the fungal kingdom, but in a phylum -- Pantonomycota -- separate from that of the true fungi. That same class (Oomycetes) Dick (1976) placed in a new subkingdom, the Heterokontimycotina. This taxon embraced those fungi having heterokont flagellation or which were thought to be derived from some heterokont ancestral form. Later, but still retaining the class name Oomycetes, Dick (in Dick *et al.*, 1984) created a subclass - Saprolegniomycetidae - for the "Saprolegnian galaxy" concept proposed by Sparrow (1976). On the basis of a study of the genus *Pachymetra* Croft and Dick, Dick concluded (Chapter 25) that this subclass admitted three orders, Saprolegniales, Leptomitales, and Sclerosporales. This decision revised the earlier concept (Dick *et al.*, 1984) of the Saprolegniomycetidae.

Sparrow, who seems not to have questioned that the water molds were fungi, regarded spore flagellation as a fundamental criterion of relationships, and for this reason advocated (1942) the recognition of uniflagellate and biflagellate series. His review paper of 1976 in essence reverts to conventional, traditional thinking with regard to the Saprolegniales and the families to be included in it. He objected (Sparrow, 1976) to the use of the class designation Oomycetes (he used the term Mastigomycotina in 1973), maintaining that only the monoblepharids truly exhibited the oogamous pattern of reproduction. Nonetheless, the class name seems to have become deeply embedded into mycological writings since the 1950's, and cannot be easily dismissed.

The various schemes to assign the Saprolegniaceae into a proper niche among organisms have not been made facetiously. Each proposal is based on some stated or implied belief or conclusion that has phylogenetic implications. These will be considered in Chapter 25.

THE GENERA OF SAPROLEGNACEAE

The genera assigned to the family seem to have been viewed over the years as relatively stable and recognizable entities. It is in any case true that almost all new genera proposed since the 1937 compilation by Coker and Matthews either have not survived as valid taxa, or have been assigned to other families. Separation of genera still depends largely on the particular pattern of spore release displayed by the organisms and to lesser extent on sporangial renewal, but as has been mentioned, differences in these characteristics are not necessarily exclusive to any one genus.

Table 1 is a listing of the genera recognized in four authoritative accounts that deal exclusively or in part with the Saprolegniaceae. Genera considered as synonyms (*Cladolegnia*, for example) are retained in Table 1 solely for comparative purposes. The year in which the genus was first defined (but not necessarily validated) is included. Generic changes proposed by us appear in the systematic account and are not reflected in the table.