

SYSTEMATIC
ACCOUNT

CHAPTER 31

THE SAPROLEGNIACEAE

Kützing (1843) appears to have been perceptive enough to recognize that Gruithuisen's (1821) "*Conferva ferax*," Agardh's (1824) species of *Leptomitus*, and Nees von Esenbeck's (1823, 1831) *Achlya prolifera* and *Saprolegnia molluscorum* distorted the prevailing concept of existing algal families. Nevertheless, Kützing conformed to the view that the organisms described under these names were algae, although he segregated them into a new family, Saprolegnieae. The description of this family was brief indeed, since Kützing saw (or perhaps only recognized) just the hyphal stage of the species of *Saprolegnia* assigned to this new family. The genus *Mycocoelium*, with its single species, *M. rivulare*, Kützing also placed into the family. The description of this genus is so vague and incomplete that it is impossible to recognize it as a taxon. Kützing's later description (1845) of *Mycocoelium* provided no additional information.

In accord with prevailing thought, Pringsheim (1858) retained the "Saprolegnieen" in the algae, but provided the first reasonably complete description of the family. His chief contribution was to include a characterization of the oogonia and antheridia in the circumscription, and to refer to flagellation of the emerging spores (he believed these had either one or two "cilia"). Humphrey (1893), who erroneously attributed the family name to Pringsheim, essentially corrected the earlier description by the latter, and incorporated into it the concept of chlamydospores (Gemmae). Curiously, Coker (1923) did not include a formal description of the Saprolegniaceae in his monograph, although he did record the essential features of the taxon in a synoptic key. What may be taken as the modern circumscription of the family was provided in 1937 by Coker and Matthews. As has been noted (Chapter 26), Elias (1965) emended the order Saprolegniales to include fossil forms. None of these elements is assignable to the Saprolegniaceae, and the emendments themselves are questionable.

One of the chief characteristics of the family is the expression by most of its members of one or two motile spore (planont) types. Indeed, the separation of genera is based in large measure on this feature. In 1935, Coker introduced the terms monocystic and dicystic to designate the spore types, and to serve in place of two terms which had proven to be inadequate, namely, monoplanetic and diplanetic. Like the terms they were designed to replace, Coker's introductions failed to describe the most basic character of watermold spores, that of their shape and flagellar insertion, a far more stable feature than the number of times the cells encyst or reemerge and swim. In the family, two morphological types of spores are encountered, the pyriform, anteriorly biflagellate primary ones, and the reniform, laterally biflagellate secondary ones. These differences are best reflected in the terms monomorphic (for those individuals with but one spore type), and dimorphic (for, those producing both primary and secondary spores).

A few authors have commented extensively on such aspects of the Saprolegniaceae as terminology and general taxonomic concepts. These paper's --

Moreau and Moreau (1935a, 1938), Coker (1935), Dick (1969b, 1972, 1978), Miller and Ristanović (1975) -- in general point to variability among members of the family, and taxonomic problems likely to be encountered.

The subjective uncertainties of using only visual structural and spore behavior patterns in the taxonomy of the Saprolegniaceae is starkly evident in existing efforts to establish generic limits. The realization of limitations brought about through characterization by traditional observations has prompted some investigators to explore approaches that might augment descriptive morphologies. One such approach is that of phenetic analysis, a quantitative and presumably unbiased similarity and dissimilarity scheme applied to the descriptive delimitation of extant taxa. Powell and Blackwell (1998) used a phenetic approach in a comparative analysis of selected structural features of actual specimens or information from the literature representing twenty genera of the family. Not all of the genera included in their data are necessarily accepted taxa according to some investigators.

From a data set of twenty four characteristics Powell and Blackwell constructed similarity and distance matrices. Of the twenty four morphological markers, only one sexual reproductive feature, namely, oospore/oosphere number, was used. The remaining morphological character determinations were made from sporangial features (for example, proliferation, shape, and persistence of the wall), spore morphology or behavior (cyst germination, distribution in the sporangium, and planetism, for instance), and hyphal features (among others, hyphal tip shape, hyphal diameter, and shape or "texture"). Plotting the character selections against knowledge of representatives of the genera yielded a numerical series assignable to each genus. From these data a table of three phenetic groupings was constructed: (1) *Pythiopsis* to *Achlya* grouping, (2) *Leptolegnia* to *Brevilegniella* (not included in the family, in our view), and (3) *Aplanes* (clearly assignable to *Achlya*, we believe) to *Calyptralegnia*.

Phenetically, the groupings proposed by Powell and Blackwell show that various connections exist among the genera whose representatives were characterized morphologically. A few examples suffice to emphasize the substantial contribution made toward numerical taxonomic analyses in their study of saprolegniaceous fungi. *Isoachlya* appears to be a distinct and valid genus, separable from *Saprolegnia*. *Protoachlya* is, as well, a recognizable member of the family, in good standing. *Couchia* is an intermediate genus between *Pythiopsis* and *Saprolegnia*. *Plectospora* and *Sommerstorffia* are phenetically close, and *Brevilegnia* is in a cluster with *Thraustotheca*. The generic subgroupings proposed by Powell and Blackwell point to a possible more detailed evaluation of genera in the family. Additionally, numerical analyses perhaps also are applicable productively at the species level as well.

As has been noted in Chapter 25, some interrelationships of and within the family may be found likewise in data from biochemical and ultrastructural analyses. The use of nutritional characteristics in the taxonomy of the Saprolegniaceae has been commented upon most extensively by Sorenson (1964). There are some indications from his very thorough nutritional study (and from data of a like nature in some prior accounts by other authors) that the presence or absence of certain nutritional

capabilities would be useful taxonomic adjuvants. For example, species of *Achlya* and *Thraustotheca* utilize sucrose readily, while members of *Saprolegnia*, *Dictyuchus*, and *Aphanomyces* do not. Sorenson concluded that whether or not species used certain inorganic sources of nitrogen and sulfur was probably of little taxonomic value, but amino acid utilization perhaps would prove to be useful. Earlier, Whiffen (1945) had reported that species of *Achlya*, *Aphanomyces*, *Saprolegnia*, and *Thraustotheca* utilized *d*-histidine, while *Dictyuchus monosporus* did not. Isolates of *Saprolegnia* and *Thraustotheca* could use glycine, but those of *Achlya*, *Aphanomyces*, and *Dictyuchus* failed to do so. Storck and Alexopoulos (1970) noted an apparent correlation between GC content and centric oospore production in *Achlya*, *Isoachlya*, and *Protoachlya*. No correlation was evident among the species of *Saprolegnia* with this oospore type. Taxonomic implications of wall-bound amino acids in water molds are touched upon by Vaziri-Tehrani and Dick (1980a, b).

Inasmuch as individual isolates of particular species are known to vary in their nutritional responses (as Sorenson, for example, reported in 1964 for *Thraustotheca*), much more work must be done on nutritional requirements of a variety of species (and numbers of isolates of them) before these parameters can be depended upon in taxonomic application. Many of the comments in Emerson's (1950) essay on the fundamental nature of research problems in aquatic fungi are neither out of date nor inapplicable to the systematics of the Saprolegniaceae.

INFRAFAMILIAL TAXA

From time to time, the family has been subjected to tinkering at the suprageneric level. Often this has been done to accommodate particular genera or to emphasize what are essentially theories of phylogeny.

Linstedt's (1872) synopsis of the Saprolegniaceae divided the family into two subfamilies, the Leptomiteae and the Saprolegnoideae. He then split the latter into two groups, Saprolegnieae and Achlyeae (including *Achlya*, *Aphanomyces*, *Diplanes*, *Dictyuchus*, and *Achlyogeton*). The same two subfamilies (with one orthographic change) were recognized by Humphrey (1893).

That three subfamilies should be accorded status was proposed by Apinis (1929a), all three taxa being derived from some *Aphanomycopsis*/*Sommerstorffia* stock. These were Achlyeae, Saprolegnieae, and Geolegnieae. The latter subfamily included representatives of three genera -- *Geolegnia*, *Brevilegnia*, and *Dictyuchus* -- all having single oospores in the oogonia, and a predominantly terrestrial (as opposed to aquatic) existence. In 1933(a, b), Apinis proposed that his new genus, *Archilegnia*, be assigned to another subfamily, the Archilegnieae. As the genus *Archilegnia* has since been excluded (*see* section on excluded and synonymous genera) such an assignment is unwarranted. The most recent designation of subfamilies was that adopted in 1959(a) by Cejp (1913,1931). He recognized Nemeč *Jaraia* as a valid genus, and included it as the sole representative of the subfamily Jaraieae. The second sub-family, embracing the remaining genera ordinarily assigned to the family, was the Saprolegnieae.

Save largely for the foregoing accounts, there has been little lasting tendency to utilize family subunits (other than genera) in taxonomic studies. In conformity, we follow that practice here.

SAPROLEGNIACEAE

Thallus mycelial, hyphae not constricted; eucarpic, monoecious or dioecious. Gemmae present or absent. Asexual reproduction by means of monomorphic or dimorphic, biflagellate planonts, or by aplanetic spores, in terminal, subterminal, or intercalary sporangia. Sexual apparatus, when present, consisting of morphologically distinct gametangia. Oogonia terminal, lateral, or intercalary; wall smooth or ornamented or merely irregular, pitted or unpitted. Antheridial branches, when present, androgynous, monoclinal, declinal, or exigynous, or limited to a hypogynous or hemihypogynous cell; functional or apparently nonfunctional. Oospores without periplasm, formed from the entire content of the oogonium; one to many produced; when mature, containing an oil reserve distributed within the ooplast; germinating to form mycelium directly, or to produce a hyphal segment bearing a terminal sporangium. Saprophytic (saprotrophic) or parasitic members.

In the following key to the genera of the Saprolegniaceae considerable emphasis is accorded the nature of sporangium renewal and the endogenous and exogenous behavior of the spores. It is necessary to isolate and culture specimens to stimulate or at least favor sporangium production. A suitable method is described in Chapter 2. It is mandatory also to distinguish between primary and secondary sporangia. Primary sporangia are those which appear first in very young cultures, and it is therefore important that mycelium 1-3 days old be examined routinely. In somewhat older colonies, primary sporangia are ones having no internal proliferation, or, if not deciduous, are lowermost on a sympodially branched hypha or a basipetalous-renewed one. Multiple spore discharge patterns occur in members of nearly all genera, but are particularly prevalent in *Achlya*, *Brevilegnia*, *Dictyuchus*, *Protoachlya*, and *Pythiopsis*.

The formal descriptions of taxa necessarily include subjective descriptive terms applied to the frequency of occurrence of certain structural features, for example, oogonial shape and antheridial branch origin. We have arbitrarily assigned percent frequency figures to most commonly used terms, and have drafted the descriptions of specimens accordingly. "Predominantly" means that a particular feature occurs in 85% or more of the cases observed (25 to over 150 observations or measurements). A character appearing in 45-84% of the cases is referred to as occurring frequently, generally, usually, or often. Other terms and their equivalent percentages follow: occasionally or sometimes, 20-44%; infrequently, seldom, or sparsely, 10-19%, rarely 1-9%, and very or extremely rarely, less than 1%.

Unidentified specimens have been described or reported in most genera. Citations to the descriptions, illustrations, or records of these individuals are included in the generic treatment following the recognized, valid taxa. For the most part, these

unidentified specimens were ones lacking the morphological stages necessary for complete identification.

KEY TO THE GENERA OF THE SAPROLEGNIACEAE

1. Parasitic in egg masses and eggs of various Chironomidae; producing appressorial complexes of various forms; or occurring in microscopic animals and forming hyphae or cells that have a capturing function 2
1. Not parasitic, but if so having neither appressorial complexes nor cells or hyphae that perform a capturing function 3
 2. Mycelium developing in eggs and egg masses of Chironomids; appressorial complexes produced *Couchia* (p. 461)
 2. Mycelium limited to an endobiotic, lobulate thallus; producing rigid, spiciform, extramatrical branches modified for capturing function, or forming spores that produce cells having such a function *Sommerstorffia* (p. 465)
3. Primary or primary and secondary sporangia abundant or sparse, but not absent in water culture 5
3. Primary or secondary sporangia absent in ordinary water culture, or extremely rarely produced, and then only on earliest formed hyphae when induced by acidifying the culture water 4
 4. Sporangia not known to occur; oogonia not intercalary or dolioform; wall smooth or sparsely papillate or crenulate, occasionally surrounded by a hyaline envelope; oogonia almost always with a single oospore; hypogynous antheridial cells absent *Aplanopsis* (p. 469)
 4. Sporangia extremely rare, or induced sparingly in acidified culture water; some oogonia intercalary and dolioform wall densely ornamented or smooth, but

if the latter generally having eight or more oospores; no hyaline envelope around oogonia; hypogynous antheridial cells sometimes present	<i>Achlya</i> (p. 473)
5. Spores monomorphic, and of the primary type (pyriform, apically biflagellate); may undergo repeated encystments, but only primary planonts released at excystment	<i>Pythiopsis</i> (p. 576)
5. Spores dimorphic, monomorphic, or nonmotile; if monomorphic are of the secondary type (reniform, laterally biflagellate)	6
6. Spores emerging from primary sporangia without prior encystment; secondary sporangia usually behaving as primary ones, but some may retain encysted spores that excyst and escape as secondary planonts; wall of primary and usually of secondary sporangia remaining intact after spore release	7
6. Spores encysting within primary sporangia and then escaping as secondary planonts, or not becoming motile; secondary sporangia usually behaving in the same manner as primary ones, buy some may actively discharge spores without their prior encystment; wall of primary or secondary sporangia, or both, may disintegrate in part or entirely following or during spore release	13
7. Most or all primary spores emerging as planonts from primary sporangia and generally from secondary ones, and some or all swimming away sluggishly or actively form the exit orifice	8
7. Most or all primary spores nonflagellate upon emerging from primary sporangia and generally from secondary ones, but on exiting from the sporangium some or all encysting immediately at the exit orifice or in its vicinity	10
8. Primary spores swimming away slowly from exit orifice, and encysting a short distance from it; sporangia usually renewed in a cymose fashion, but if renewed internally, secondary ones	

- formed entirely outside the empty ones *Protoachlya* (p. 586)
8. Primary spores swimming away actively from exit orifice; at least some sporangia renewed internally, with all or part of the secondary ones enclosed by the primary sporangium; other sporangia renewed in a sympodial, cymose, or basipetalous fashion 9
9. Spores in more than one row in the sporangium, and not elongate upon emergence; oogonia usually producing more than one oospore, but not producing only a single oospore in every oogonium throughout the colony *Saprolegnia* (p. 599)
9. Spores in a single row in the sporangium, and elongate on emergence then changing shape to pyriform; each mature oogonium containing only one oospore *Leptolegnia* (p. 661)
10. Some primary spores motile at discharge, and in part encysting near the exit orifice loosely aggregated in clusters, and in part swimming away to encyst at a distance from the exit pore *Protoachlya* (p. 586)
10. No primary spores motile at discharge; encysting immediately in a distinct, compact clump, or a hollow sphere 11
11. Sporangium consisting of a compact, lobed and branched irregular system basally, and a slender, elongate evacuation tube *Plectospira* (p. 673)
11. Sporangium commonly cylindrical, fusiform, clavate, naviculate, or filamentous throughout its length 12
12. Sporangium filamentous, spores in a single row *Aphanomyces* (p. 676)
12. Sporangia not filamentous, but commonly cylindrical, fusiform, clavate, or naviculate; spores in more than one row, at least in apical portion of the sporangium *Achlya* (p. 473)
13. Primary sporangia releasing primary spore cysts passively by disintegration or dissolution of the sporangium wall, or upon dehiscence of an apical segment of the wall; secondary sporangia releasing cysts in same manner as primary ones, but with some spores escaping individually and leaving a network of empty cysts from which the sporangium

- wall dissolves, or escaping through an apical pore and clustering in a compact or hollow sphere at the orifice 14
13. Primary sporangia releasing motile secondary spores individually from the primary spore cysts, the cysts remaining within the sporangium and leaving a network of wall material; sporangium wall may or may not disintegrate in part or entirely; secondary sporangia releasing spores in the same manner as the primary ones 17
14. Primary and secondary sporangia releasing primary spore cysts intermittently in groups upon dehiscence of the apical portion of the sporangium *Calyptralegnia* (p. 731)
14. Primary and secondary sporangia releasing primary spore cysts upon dissolution of sporangium wall at one or more areas, but not by the dehiscence of the apical portion alone 15
15. Oogonia predominantly with more than one oospore *Thraustotheca* (p. 734)
15. Oogonia containing only one oospore each 16
16. Planonts not produced, all spores germinating directly into new hyphae; spores generally ovoid or ellipsoid; always in a single row in the sporangium; wall of the sporangium sometimes constricted at intervals between spores; secondary sporangia behaving like primary ones in spore release *Geolegnia* (p. 740)
16. Planonts released individually from primary spore cysts that generally are spherical; spores in one or more rows in the sporangium; wall of sporangium not constricted at intervals; secondary sporangia behaving in spore release like the primary ones, but some also releasing spores individually from cysts in an intact sporangium, leaving a network of cyst walls (dictyuchoid), or discharging spores through an apical pore, these then encysting in a compact clump or hollow sphere (achlyoid) *Brevilegnia* (p. 744)
17. Sporangia long, filamentous, simple or branched, one spore wide, fragmenting into branched or

- unbranched segments; planonts released individually from cysts, leaving a catenulate series of intact cyst walls; entire hypha may convert into a sporangium *Phragmosporangium* (p. 769)
- 17. Sporangia cylindrical, fusiform, or clavate, or globose to subglobose or obpyriform, but not filamentous; spores in more than one row in the sporangium 18
 - 18. Sporangia cylindrical, fusiform, or clavate; oogonia smooth-walled, containing only one oospore each *Dictyuchus* (p. 771)
 - 18. Sporangia globose, subglobose or obpyriform; oogonia ornamented, containing one or more oospores each *Aphanodictyon* (p. 786)