

## CHAPTER 38

### SAPROLEGNIA Nees von Esenbeck

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*Diplanes* Leitgeb, Jahrb. Wiss. Bot. 7:385. 1869-70.

*Isoachlya* Kauffman, Amer. J. Bot. 8:231. 1921.

*Cladolegnia* Johannes, Feddes Repert. Spec. Nov. Regni. Veg. p. 211. 1955.

*Scoliolegnia* Dick, J. Linn. Soc. Bot. 62:255. 1969.

Monoecious. Sporangia fusiform, clavate, cylindrical, or irregular; renewed by internal proliferation, and also occasionally sympodially, cymosely, or in a basipetalous fashion. Spores dimorphic; sometimes polyplanetic; primary spores swimming away immediately upon release; in older cultures, and regularly in some species, discharge may be aplanoid or dictyuchoid. Gemmae present or absent. Oogonia lateral, terminal, intercalary, or sessile; variously shaped, but predominantly spherical or obpyriform. Oogonial wall pitted or unpitted; smooth or ornamented. Oogonial stalks of various lengths; usually simple. Oospores centric, subcentric, subeccentric, or eccentric; one to many; germinating to form a new mycelium, or to produce a germ hypha bearing a terminal sporangium. Antheridial branches, when present, androgynous, monoclinal, dichlinous, or hypogynous. Antheridial cells predominantly tubular or clavate; attached laterally or apically or in a digitate manner to the oogonial wall.

Type species: *Saprolegnia ferax* (Gruith.) Thuret, Ann. Sci. Nat. Bot. (3<sup>e</sup> sér.) 14:229 et sqq., pl. 22. 1850.

Seymour (1970), reduced *Isoachlya* and *Cladolegnia* to synonymy with *Saprolegnia*, and the justification for that nomenclatural change need not be repeated here. Dick (1969b) seems to have retained *Isoachlya* Kauffman as a valid, genus, but (if we interpret his account correctly) did not accept *Cladolegnia*. Although the reference to Leitgeb's *Diplanes* is usually cited as his 1868 publication, he did not formally describe a species to accompany the generic name. Therefore, his paper of 1869-70 is taken as the proper original record of this genus.

In 1969(a), Dick redefined *Saprolegnia asterophora*, a, species which he had commented upon earlier (1960c), and described (but did not name) two additional forms of the species with ornamented oogonia. These three taxonomic entities he regarded (Dick, 1969a:255) as "...segregate species within an aggregate...", raised the two forms to specific rank, and placed them in the new genus *Scoliolegnia*. In 1979, Mil'ko published a synopsis of the systematics of the genus *Saprolegnia*, and reduced *Scoliolegnia* to synonymy with the earlier taxon. As we agree fully with Mil'ko's decision and basic premise, but recognize that his paper is not in translation, we are including our own analysis of the status of Dick's genus. The priority for the nomenclatural changes in the species rests with Mil'ko.

According to Dick (1969a), the delicate, flexuous mycelium and the “gritty” granular aspect of the hyphae were characteristic of the three species assigned to *Scoliolegnia*. He remarked that this mycelial texture contrasted with the stout, straight hyphae prominent in species of *Saprolegnia* and *Isoachlya*. These characters alone, however, did not form the sole basis on which *Scoliolegnia* was established.

Dick (1969a) concluded that the genera of Saprolegniaceae were defined on too few characters. Accordingly, he compared and contrasted the species of *Scoliolegnia* on twenty structural criteria. The descriptive matter provided by Dick (particularly the characterization in Table 1 of his 1969a account), and the accompanying illustrations permit but one conclusion: there are essentially only two features that could possibly be used to distinguish *Scoliolegnia* species from members of *Saprolegnia*. These are, for *Scoliolegnia*, the flexuous hyphae and the flared aspect of the rather prominent exit papilla after it has opened terminally at spore emergence. The first characteristic (mycelial texture) is, in fact, one by which de Bary's *Saprolegnia asterophora* (one of the species assigned to *Scoliolegnia*) usually can be recognized in water culture; Dick's two new species of *Scoliolegnia* also at times may be made out in gross culture on this feature. The prominently flared, opened exit papilla is not a consistent characteristic of *Saprolegnia asterophora*, and other species of *Saprolegnia* sometimes produce similar ones. Other structural features that Dick used to circumscribe his species, such as mean diameters of the exit papillae and of the oogonial stalks, are in our judgment too variable to be of value at the species level, to say nothing of the generic level. In any event, Dick did not mention the conspicuous nature of the exit papilla remnants in the formal description of *Scoliolegnia*.

We find commendable Dick's (1969a) argument that genera should be defined on the basis of several characters, but his contention falls short with respect to *Scoliolegnia*, since that genus rests in our view on only two criteria. In what we regard as a fundamental morphological characteristic essential for generic delimitation -- spore discharge pattern and sporangial renewal -- *Scoliolegnia* species cannot be distinguished from those of *Saprolegnia*. We interpret Dick's argument favoring the recognition of *Scoliolegnia* basically to be a proposition that generic determinations in the Saprolegniaceae may be made independent of reliance on sporangial renewal method.

Admitting to *Saprolegnia* species with flexuous hyphae does not at all distort that genus into an unrecognizable complex. The same may be said for including species with subeccentric oospores. Indeed the concept of *Saprolegnia* is more firmly and competently established by the admission of Dick's *Scoliolegnia* species.

As with *Achlya*, *Saprolegnia* has been variously divided into infrageneric units. Schröter (1893) accepted three subgenera: *Eusaprolegnia* (the *S. ferax* group), *Desmolegnia* (the *S. monoica* complex), and *Astrolegnia*. Coker (1923) recognized *Eusaprolegnia* with four “Groups” -- *Diclina*, *Ferax*, *Hypogyna*, and *Torulosa* -- and *Pseudosaprolegnia*, with the single species, *S. asterophora*. In 1959(a), Cejp raised Coker's *Hypogyna* and *Diclina* groups to section status (in the subgenus *Eusaprolegnia*, and did likewise with the *Ferax* group, which he attributed to de Bary. In addition, Cejp (1959a:251) proposed a fourth taxon in *Eusaprolegnia*, the Section *Terrestres*. Three subgenera of *Saprolegnia* --

*Asterophorae* (ornamented oogonia), *Leiothecae* (smooth oogonia), and *Agamae* (lacking oogonia) -- were established by Naumov, in 1954. The subgenus *Leiothecae* was further divided into five sections, *Hypogynae*, *Diclinae*, *Monoicae*, *Ferax*, and *Moniliferae*. We see no reason (other than convenience) for retaining any subgeneric distinction, and are following the precedent set by Seymour (1970).

The taxonomic monograph by Seymour (1970) provided a useful new account of *Saprolegnia* in that it solved some of the most troublesome problems in the genus. His unprecedented treatment of the *S. ferax* complex has been held to be too broadly encompassing (Dick, 1973); a more restrictive concept of *Saprolegnia* is apparent in Dick's (1973) comments on the genus, and also is reflected in his treatment of *Scoliolegnia*. Neish and Green (1976) saw in Dick's circumscription the recognition of twelve "morphospecies" [attributed to Scudder (1974), but first defined by Cain (1953:82) as a group of specimens sufficiently different morphologically from the most closely related forms known as to be given a specific name]. By experimental analyses, Neish and Green found that the species of *Saprolegnia* assayed for DNA base composition data could not be separated on the basis of this parameter. They then suggested that the genus *Saprolegnia* appeared to be a homogeneous taxon, and any isolate whose DNA base composition fell outside the range of 55.5-60.5% GC should be excluded from this taxon. Miller and Ristanović (1975) commented upon the inadequacy and unreliability of the taxonomic markers customarily used in identifying species of *Saprolegnia*. Brief historical accounts of the genus *Saprolegnia* have been published by Dittrich (1956), and Seymour (1970).

#### Key to the Species of *Saprolegnia*

1. Oogonial wall consistently ornamented . . . . . 2
1. Oogonial wall predominantly smooth on outer surface, but if provided with projections these occur on few oogonia and are often inconspicuous . . . . . 5
  2. Ornamentations predominantly truncate . . . . . *S. truncata* (p. 604)
  2. Ornamentations predominantly narrowly or broadly papillate, sometimes cylindrical, and straight or curved, or bifurcate; some oogonia provided with an undulant or wavy wall . . . . . 3
3. Oospores subcentric . . . . . *S. asterophora* (p. 605)
3. Oospores subeccentric . . . . . 4
  4. Antheridial apparatus present; wall ornamentations dense and prominent . . . . . *S. subeccentrica* (p. 607)
  4. Antheridial apparatus lacking; wall ornamentations sometimes sparse . . . . . *S. blelhamensis* (p. 608)
5. Oospores centric, subcentric, or frequently aborting or not maturing . . . . . 6
5. Oospores eccentric . . . . . 21

6. Oospores centric or subcentric, only rarely, if ever, aborting or failing to mature .....	7
6. Oospores subcentric, but frequently aborting or not maturing .....	<i>S. australis</i> (p. 609)
7. Oospores predominantly fewer than three per oogonium .....	19
7. Oospores predominantly more than three per oogonium .....	8
8. Antheridial apparatus hypogynous .....	9
8. Antheridial apparatus androgynous, monoclinous, or diclinous, or absent .....	10
9. Oogonia predominantly obpyriform, spherical, or napiform .....	<i>S. hypogyna</i> (p.610)
9. Oogonia cylindrical, lobed, branched, irregular, or subspherical .....	<i>S. irregularis</i> (p. 612)
10. Oogonial stalks short, their length usually less than the oogonial diameter .....	11
10. Oogonial stalks predominantly as long as the oogonial diameter, in length, or longer .....	12
11. Antheridial branches predominantly androgynous and originating near the oogonial septum; antheridial cells very long, curved, and tubular .....	<i>S. turfosa</i> (p. 613)
11. Antheridial branches predominantly monoclinous; antheridial cells short, clavate, or cylindrical .....	<i>S. uliginosa</i> (p. 615)
12. Oogonial stalks generally 1-7 times coiled, sometimes strongly recurved and oogonium pendulous .....	<i>S. furcata</i> (p. 616)
12. Oogonial stalks not coiled .....	13
13. Oogonial stalks and antheridial branches irregular, contorted and usually provided with short, lateral, cylindrical branches; hyphae developing clusters of short, twig-like branches .....	<i>S. glomerata</i> (p. 617)
13. Oogonial stalks and antheridial branches seldom irregular or contorted and rarely provided with short, lateral, cylindrical branches; hyphae lacking clusters of twig-like branches .....	14
14. Antheridial apparatus absent or very infrequently produced .....	<i>S. ferax</i> (p. 619)
14. Antheridial apparatus present on all or nearly all mature oogonia .....	15
15. Antheridial branches predominantly diclinous, rarely monoclinous or androgynous .....	16
15. Antheridial branches predominantly monoclinous or androgynous, rarely or	

very infrequently diclinous .....	17
16. Oogonia frequently in toruloid chains which may or may not disarticulate with aging; antheridial branches not persisting, and not densely nesting around the oogonia; oospores centric .....	<i>S. torulosa</i> (p. 625)
16. Oogonia not in toruloid chains; antheridial branches persisting, sometimes nesting densely around the oogonium; oospores centric or subcentric .....	<i>S. diclina</i> (p. 627)
17. Oospores centric; oogonia predominantly terminal, and hypha or stalk often expanded at its juncture with the oogonium .....	<i>S. litoralis</i> (p. 633)
17. Oospores subcentric, or subcentric and centric; oogonia predominantly lateral .....	18
18. Antheridial branches associated with all or nearly all oogonia; oospores subcentric, rarely centric; antheridial branches predominantly androgynous .....	<i>S. terrestris</i> (p. 635)
18. Antheridial branches variable in abundance, but often sparse; oospores centric and subcentric; antheridial branches predominantly monoclinal .....	<i>S. ferax</i> (p. 619)
19. Antheridial branches absent .....	<i>S. unispora</i> (p. 637)
19. Antheridial branches present .....	20
20. Antheridial branches predominantly monoclinal or diclinous; oogonial stalks usually short; glomeruli lacking; oospores subcentric, rarely centric .....	<i>S. megasperma</i> (p. 638)
20. Antheridial branches predominantly androgynous; oogonial stalks often branched and oogonia glomerulate; oospores centric and subcentric .....	<i>S. itoana</i> (p. 640)
21. Spores usually of three size ranges (classes) among the sporangia, but rarely within the same sporangium; generally more than three oospores per oogonium .....	<i>S. anisospora</i> (p. 642)
21. Spores of one size class only; generally 1-3 oospores per oogonium .....	22
22. Antheridial branches present .....	23
22. Antheridial branches absent .....	<i>S. eccentrica</i> (p. 644)
23. Predominantly a single oospore per oogonium; oospores generally 35-38 µm in diameter; oogonial wall unpitted .....	<i>S. richteri</i> (p. 645)

23. Predominantly 2-3 oospores per oogonium;  
oospores generally 16-22  $\mu\text{m}$  in diameter;  
pitted, at least at the region of attachment  
of antheridial cells ..... *S. luxurians* (p. 646)

*Saprolegnia truncata* Seymour  
Mycotaxon 92:1-10, figs. 41-51. 2005  
(Figure 91 C-M)

Monoecious. Mycelium limited, dense; hyphae moderately stout (16-) 24-26 (-35)  $\mu\text{m}$  in diameter, sparingly branched. Sporangia rare; naviculate or cylindrical, appearing very early or proliferating from immature oogonia after prolonged culture, then subspherical with a long, cylindrical exit tube; straight or slightly curved; renewal not observed; not persistent; averaging 120 x 28  $\mu\text{m}$ ; discharge papilla with thickened, flaring wall; basal portion often thick-walled. Spores dimorphic; discharge and behavior saprolegnoid; cysts 9-13  $\mu\text{m}$  in diameter. Gemmae, when present, naviculate or spherical; terminal or intercalary; single; smooth. Oogonia abundant; terminal or lateral, rarely intercalary; single; spherical, occasionally ovoid; (18-) 34-38 (-45)  $\mu\text{m}$  in diameter, exclusive of papillae. Oogonial wall unpitted; ornamented with prominent, truncate projections: (9-) 14-16 (-29)  $\mu\text{m}$  long, occasionally intermixed with papillae. Oogonial stalks up to 8 times the diameter of oogonium, in length; straight, slender, unbranched. Oospores subcentric; spherical or ovoid, occasionally ellipsoidal; 1, rarely 2 per oogonium, and plerotic or aplerotic; (36-) 29-33 (-42)  $\mu\text{m}$  in diameter; germination unknown. Antheridial branches rare; androgynous, usually arising immediately below the oogonium to which attached, single; not persistent. Antheridial cells simple; laterally appressed; persisting; fertilization tubes unknown.

Holotype: Fig. 91 (C-M); Accession Nr. MS 242, Randall Library Special Collection, Univ. of North Carolina at Wilmington (USA), isolated from roadside forest soil, highway BR 174 to Boa Vista, 60 km from Manaus, Brazil 5 March 1978.

Among the species of *Saprolegnia* with ornamented oogonia, *S. truncata* is distinctive by reason of its stout, prominent wall protrusions. These generally are truncate (Fig. 91 G, H, L) but on some oogonia (Fig. 91 J) a few rounded papillae also may be produced.

Essentially two types of sporangia are formed by *Saprolegnia truncata*. The terminal, thin-walled sporangia (Fig. 91E) usually associated with species in the genus are rare, and we have not seen how they are renewed. The second type of sporangium -- more commonly developed than the "typical" ones in our specimens -- is in essence a reversal of an oogonial initial to a function as an asexual cell (Fig. 91 C, D). These sporangia therefore are thick-walled and subspherical at the base, but thin-walled distally (except in the vicinity of the exit orifice). Release of spores from these sporangia is characteristically saprolegnoid. So far as we are aware, the sporangia developed from converted oogonium initials are not found in any other species in the genus. The reversion of antheridial branches into vegetative hyphae or oogonia has been documented (Moreau and Moreau, 1935c; T. W. Johnson, 1973a).

Developmentally, *Saprolegnia truncata* is unique among members of the Saprolegniaceae. In most species propagated on hempseed in water culture, immature oogonia appear on colonies after 36 hours, but in *S. truncata*, the oogonia generally are formed and become mature within 8-12 hours following infestation of fresh hempseed. This extremely rapid appearance of oogonia may in some way be associated with suppression of the sporangial phase even during the early stages of mycelial development. This phenomenon commands further study from both a biochemical (regulatory) and developmental standpoint.

The discovery of *Saprolegnia truncata* is the first instance in which we have collected a member of this genus in low-elevation, humid tropical areas. Some representatives of *Saprolegnia* have been recovered from tropical countries in soils at high elevations, but Fajola and his associates (1978) found *S. ferax* and *S. litoralis* in river soils in Nigeria.

SPECIMEN EXAMINED: -- SOUTH AMERICA (1), RLS.

*Saprolegnia asterophora* de Bary  
Jahrb. Wiss. Bot. 2:189, pl. 20, figs. 25-27. 1860  
(Figure 92 A-F)

*Cladolegnia asterophora* (de Bary) Johannes, Feddes Repert. Spec. Nov. Regni Veg., p. 215. 1955.

*Scoliolegnia asterophora* (de Bary) Dick, J. Linn. Soc. Bot. 62:257, pl. 1, figs. G, J, M; fig. 1. 1969.

Monoecious. Mycelium delicate, hyphae often flaccid and flexuous. Sporangia rare or abundant; clavate or fusiform, usually short, renewed internally; 120-821 × 12-43 μm. Spores dimorphic; discharge and behavior saprolegnoid; primary spore cysts 12-14 μm in diameter. Gemmae sparse; clavate or irregular, terminal or intercalary, Oogonia lateral, occasionally terminal, rarely intercalary; spherical, subspherical or oval, infrequently napiform or obpyriform; (25-) 42-56 (-78) μm in diameter, inclusive of wall ornamentations. Oogonial wall unpitted; densely papillate or provided with papillae

and tuberculate projections. Oogonial stalks ( $1/2$ -)  $1-1\frac{1}{2}$  (-3) times the diameter of the oogonium in length; straight, branched, unbranched, or irregular. Oospores subcentric; spherical or subspherical; 1-2 (-6) per oogonium and usually not filling it; (17-) 26-33 (-44)  $\mu\text{m}$  in diameter; germination not observed. Antheridial branches predominantly androgynous, rarely monoclinal, very rarely dichlanous; sometimes arising in a clustered fashion below the oogonium; unbranched or branched, usually irregular in general configuration; persisting. Antheridial cells simple; short-clavate or tuberos; apically or laterally appressed; persisting; fertilization tubes present or absent, not persisting.

The densely papillate oogonia that generally contain only one or two subcentric oospores (Fig. 92 B, C, E) make this species easily identifiable. In gross culture, specimens sometimes can be recognized by reason of the very diffuse, flaccid nature of the mycelium.

Dick (1969a) placed this species in *Scoliolegnia*, a genus that we do not recognize. An unusual "form" of *Saprolegnia asterophora* first described by Dick in 1960(c) later was placed by him (1969a) in *Scoliolegnia* and renamed *Scoliolegnia subeccentrica*. We recognize Dick's species as a valid taxon of *Saprolegnia*.

Of the three taxa that Dick (1969a) considered to be an aggregate species -- *Scoliolegnia* (= *Saprolegnia*) *asterophora*, *S. subeccentrica*, and *S. blelhamensis* -- only *S. asterophora* has subcentric oospores. With respect to the nature and density of its oogonium wall ornamentations, *S. asterophora* (Fig. 92 B) very closely approaches *S. subeccentrica* (Fig. 92 N, O).

CONFIRMED RECORDS: -- BRITISH ISLES: Dick (*loc. cit.*); Forbes (1935b:7, fig. 2a-f). CANADA: Maestres (1977:150, figs. 46, 47). CZECHOSLOVAKIA: Cejp (1959a:253,1 fig. 96) DENMARK: Petersen (1909a: fig. 3h; 1910: fig. 3h). FINLAND: Häyrén (1927:50). GERMANY: de Bary (*loc. cit.*; 1881:269 *et seq.*, pl. 6, figs. 18-29; 1888:614); A. Fischer (1892: 343); Minden (1912:529, fig. 1h); Zopf (1890:297). ICELAND: Howard *et al.* (1970: fig. 26). JAPAN: Kobayasi and Konno (1969:732, fig. 4 I-M); Kobayashi and Ôkubo (1954:567, fig. 9); Shibuya (1959:148, fig. 3). LATVIA: Apinis (1929a:218). MIDDLE EUROPE: Migula (1903:66). NETHERLANDS: Beverwijk (1948:233, fig. 4). POLAND: Staniak (1971:366). REPUBLIC OF CHINA: Chiou and Chang (1976:44, pl. 3, figs. 1-9). SWITZERLAND: Maurizio (1895d:13). UNITED STATES: Beneke (1948b:46); R. L. Butler (1975: figs. 9-12); Coker (1923:64, pl. 19); Humphrey (1893:110, pl. 17, figs. 54, 55); Seymour (1970:23, figs. 12-23). USSR: Morochkovs'kiï *et al.* (1967:126, fig. 110); Naumov (1954:66). [Istvánffi (1895: pl. 35, figs. 19-21; pl. 36, fig. 22) studied this species cytologically, but gave no record of its source.]

RECORDED COLLECTIONS: -- BRITISH ISLES: Cook and Morgan (1934); Dick (1962, 1963, 1964, 1966); Dick and Newby (1961); Perrott (1960); R. E. Roberts (1963); Sparrow (1936). CANADA: Dick (1971c); Maestres and Nolan (1978). DENMARK: A. Lund (1934, 1978). FINLAND: Häyrén (1956). GERMANY: Höhnk (1935a). JAPAN: Shirai *et al.* (1927); Suzuki (1961f). UNITED STATES: Coker (1927); Klich (1980);

Kauffman (1915); V. D. Matthews (1927); C. E. Miller (1965); Monsma (1936). USSR: Érgashev and Kirgizhaeva (1978); Osipyán *et al.* (1974).

SPECIMENS EXAMINED: -- ICELAND (3), NORWAY (1), SWEDEN (9), TWJ. UNITED STATES (3), RLS. Centraalbureau (1); MWD (1).

*Saprolegnia subeccentrica* (Dick) Mil'ko  
Mikol. i Fitopatol. 13:290. 1979  
(Figures 91 A, B; 92 N, O)

*Scoliolegnia subeccentrica* Dick, J. Linn. Soc. Bot. 62:257, pl. 1, figs. B, D, F, H, K, N; fig. 2. 1969.

Monoecious. Mycelium delicate; hyphae flaccid and flexuous. Sporangia abundant in young and old cultures; cylindrical, clavate, or long-fusiform, often curved or slightly irregular; proliferating internally; or renewed sympodially or in a basipetalous fashion; 116-883 x 14-33  $\mu\text{m}$ . Spores dimorphic; discharge and behavior saprolegnoid; primary spore cysts 10-13  $\mu\text{m}$  in diameter. Gemmae absent. Oogonia terminal, occasionally lateral, rarely intercalary; spherical, subspherical or ellipsoidal, dolioform when intercalary; (28-) 39-57 (-76)  $\mu\text{m}$  in diameter, inclusive of wall ornamentations. Oogonial wall unpitted, thin; densely provided with papillae, or with cylindrical, curved, irregular, or bifurcate ornamentations each rounded at the apex. Oogonial stalks variable in length; slender, irregular, unbranched. Oospores subeccentric; spherical or subspherical; 1-2 (-4) per oogonium, and nearly filling it; (16-) 26-36 (-52)  $\mu\text{m}$  in diameter; germination not observed. Antheridial branches generally sparse; when present, androgynous or monoclinal; unbranched or very sparingly branched; persisting. Antheridial cells simple; clavate or tubular; persisting; attached apically or laterally; fertilization tubes present but not persisting.

With respect to the abundance of oogonium wall ornamentations *Saprolegnia subeccentrica* most nearly resembles *S. asterophora*. The wall projections are generally far more numerous in *S. subeccentrica* (Fig. 91 A) than in *S. blelhamensis* (Fig. 92 K). The oospore type in *S. subeccentrica* separates this species from *S. asterophora*, but is identical to that in *S. blelhamensis*.

*Saprolegnia subeccentrica* has antheridial branches, but *S. blelhamensis* lacks such structures. Because the degree of branch development in the former is related to culture conditions, it is possible that *S. subeccentrica* is more closely akin to *S. blelhamensis* than the gross morphology of the oogonial wall ornamentations would suggest. We were unable to isolate our specimens of *S. subeccentrica*, hence could not study variability in this species.

Dick (*loc. cit.*) emphasized in the description of *Scoliolegnia subeccentrica* the narrow, tubular or bulbous (flaring) aspect to the papilla involved in sporangium dehiscence. Such exit papillae occur in our specimens of the species, but similar ones also are found in *S. asterophora* and *S. blelhamensis*. Dick (*loc. cit.*) maintained that the

shape of the sporangial papillae in *S. subeccentrica* and *S. blelhamensis* was not the same, but we have not found this to be the case.

The specimens of *Saprolegnia asterophora* described and illustrated by Dick in 1960 were later (Dick, *loc. cit.*) renamed *Scoliolegnia* (= *Saprolegnia*) *subeccentrica*. Specimens of *S. subeccentrica* obtained from Dick's collections have failed to develop any sexual apparatus in culture.

CONFIRMED RECORDS: -- BRITISH ISLES: Dick (1960:597, figs. 1, 2, 3 M; *loc. cit.*)

SPECIMENS EXAMINED: -- NORWAY (2), TWJ. MWD (2).

*Saprolegnia blelhamensis* (Dick) Mil'ko  
Mikol. i Fitopatol. 13:290. 1979  
(Figure 92 G-M)

*Scoliolegnia blelhamensis* Dick, J. Linn. Soc. Bot. 62:259, pl. 1, figs. A, C, E, I, L, O; fig. 3. 1969.

Monoecious. Mycelium delicate; hyphae flaccid and flexuous. Sporangia formed only in young cultures; clavate or cylindrical; renewed internally; 50-584 x 15-29  $\mu\text{m}$ . Spores dimorphic; discharge and behavior saprolegnoid; primary spore cysts 10-16  $\mu\text{m}$  in diameter. Gemmae absent. Oogonia terminal or lateral, frequently or only occasionally intercalary; spherical, subspherical, or oval, but dolioform when intercalary; (23-) 43-66 (-97)  $\mu\text{m}$  in diameter, inclusive of wall ornamentations. Oogonial wall unpitted; thin; densely or sparsely papillate, and occasionally provided with cylindrical or elongate-papillate projections as well, or nearly smooth. Oogonial stalks  $1/2$ -2 times the oogonial diameter in length; straight, bent, or crooked, often irregular; unbranched or once-branched. Oospores subeccentric; spherical, subspherical, or oval; (1-) 1-3 (-12) per oogonium and nearly filling it; (16-) 26-32 (-41)  $\mu\text{m}$  in diameter, germination not observed. Antheridial apparatus absent.

Dick (*loc. cit.*) recorded in detail the differences among this species, *S. asterophora*, and *S. subeccentrica*. Chiefly, *S. blelhamensis* differs from *S. asterophora* in oospore structure (Fig. 92B-E, G-J), and, of course, in the absence of an antheridial apparatus (in the former). While the wall ornamentations of some oogonia in *S. blelhamensis* (Fig. 92 G, H) approach the configuration of those produced by *S. asterophora* (Fig. 92 C, D), there generally are fewer projections in the former species. A few oogonia of *S. blelhamensis* are intact, devoid of all but one or two papillations (Fig. 92 L). Contrary to the condition in *S. asterophora*, the wall of each of the oogonia in *S. blelhamensis* is very thin (Fig. 92 E, H).

The species name is misspelled (*blelhamenis*) in the original description (Dick, *loc. cit.*), but is used correctly in the accompanying text.

CONFIRMED RECORD: -- BRITISH ISLES: Dick (*loc. cit.*).  
RECORDED COLLECTION: -- BRITISH ISLES: Dick (1966, *pro parte*).  
SPECIMENS EXAMINED: -- NORWAY (1), TWJ. MWD (3).

*Saprolegnia australis* Elliott  
New Zealand J. Bot. 6:103, figs. 2, 4 c-f. 1968  
(Figure 93 A-E)

Monoecious. Mycelium dense, diffuse; hyphae slender or stout. Sporangia cylindrical or clavate; renewed internally or cymosely; primary ones 20-460 x 15-33  $\mu\text{m}$ ; secondary ones usually shorter, but up to 600  $\mu\text{m}$  long. Spores dimorphic; discharge and behavior generally saprolegnoid, occasionally dictyucoid; primary spore cysts 10.5-11.7  $\mu\text{m}$  in diameter. Gemmae sparse or abundant; cylindrical, clavate, spherical, or irregular; terminal or intercalary, usually single. Oogonia generally terminal, occasionally lateral or intercalary, sometimes sessile; obovate, obpyriform, spherical, or napiform, sometimes slightly irregular, fusiform or dolioform when intercalary; (35-) 59-80 (-121)  $\mu\text{m}$  in diameter. Oogonial wall pitted, smooth. Oogonial stalks generally ( $1/3$ -) 1-3 (-4) times the diameter of the oogonium, in length; straight, curved, twisted, or irregular; unbranched. Oospores may or may not mature, or may abort; when mature, subcentric; spherical to subspherical; (1-) 4-12 (-32) per oogonium, but usually not filling it; (10-) 22-27 (-36)  $\mu\text{m}$  in diameter; germination not observed. Antheridial branches, when present, predominantly declinous, occasionally or rarely, monoclinal or androgynous; persisting or deliquescent; sparingly to moderately branched; usually slightly irregular, sometimes conspicuously contorted. Antheridial cells simple or branched, persisting; tubular or attached in a digitate fashion; fertilization tubes present or absent, not persisting.

Until the report by Padgett (1976) of the recovery of specimens from eastern North Carolina, *Saprolegnia australis* was known only from the type locality. *Saprolegnia australis* appears to be most variable with respect to sporangium size and the predominating oospore number and diameter (Padgett, 1976: Table 1; Nolan and Maestres, 1978: Table 1).

The oospores of *Saprolegnia australis* are subcentric with the refractive droplets surrounding the ooplasm (Fig. 93 B) or only partially so (Fig. 93 E); such oospores are referred to by T. W. Johnson (1956b) and Seymour (1970) as types I and III, and both types can occur in the same oogonium. The oospheres of *S. australis* may or may not mature, or the oospores may develop and then abort (Fig. 93 A, C, D). In any event, nearly all oogonia contain at least a few disintegrated cells or imperfectly formed oospheres. Budding of oospheres -- resulting in small, spherical cells -- has been reported (Padgett, 1976).

The preponderance of declinous antheridial branches in *Saprolegnia australis* recalls a like condition in *S. declina*. The oospheres of the latter generally mature, however, yet it must be recognized that some of the "parasitica-like" forms of *S. declina*

(see this species) also produce oogonia with imperfectly developed oospores (Willoughby, 1971a). While the oospores of *S. australis* are subcentric, those of *S. diclina* are predominantly centric. Both species have pitted, generally obpyriform oogonia that, in *S. australis* are primarily terminal, but are predominantly lateral in *S. diclina*. These two species are thus separable on few characters, and those that may be used show degrees of variation that encompass features of both. Further study of additional isolates may show the two to be variants of one species.

Padgett (1978b) demonstrated that *Saprolegnia australis* is capable of actively invading mesohaline estuarine waters (see Chapter 3). The fungus also has been found associated with fish (Pickering and Willoughby, 1977, on *Perca fluviatilis*; Hatai, Egusa, and Nomura, 1977, on fingerlings of rainbow trout); such a habitat further relates Elliott's species to *S. diclina* (which includes *S. parasitica sensu* Kanouse).

The chief experimental work with *Saprolegnia australis* has been that by R. F. Elliott (1968). She propagated the species under a variety of culture conditions noting that oospore number and colony and oogonium sizes could be modified. On the other hand, oospore structure and the origin and degree of branching of the antheridial filaments were not changed by manipulating the environmental parameters during incubation. At 25 °C colonies of *S. australis* produced larger oogonia containing more oospores than did isolates grown at 20 °C. Larger oogonia, and ones with fewer oospores, developed on mycelium propagated in larger culture vessels rather than in smaller ones.

CONFIRMED RECORDS: -- CANADA: Maestres (1977:144, 145, figs. 21-23); Nolan and Maestres (1978:892, figs. 1, 2). JAPAN: Hatai, Egusa, and Nomura (1977:204, figs. 6-9). NEW ZEALAND: R. F. Elliott (*loc. cit.*). UNITED STATES: Padgett (1976:1260, figs. 1, 2); Shipman (1977: fig. 10).

RECORDED COLLECTIONS: -- BRITISH ISLES: Pickering *et al.* (1979); Pickering and Willoughby (1977). CANADA: Maestres and Nolan (1978). UNITED STATES: Klich (1980); Padgett (1978a); Shipman (1979).

SPECIMENS EXAMINED: -- CANADA (1), NEW ZEALAND (1), R. F. Elliott, preserved specimens. NORWAY (1), TWJ. UNITED STATES (1), DEP.

*Saprolegnia hypogyna* (Pringsheim) de Bary  
Bot. Zeitung (Berlin) 41:56. 1883  
(Figure 94 A-D)

*Saprolegnia ferax* var. *hypogyna* Pringsheim, Jahrb. Wiss. Bot. 9:196, pl. 18, figs. 9, 10. 1873-74.

*Saprolegnia hypogyna* var. I Maurizio, Flora 79:126, pl. 4, figs. 5-12. 1894.

*Saprolegnia hypogyna* var. II. Maurizio, *ibid.*, p. 128, pl. 4, figs. 13-16. 1894.

*Saprolegnia hypogyna* var. III. Maurizio, *ibid.*, p. 129, pl. 4, figs. 17-20a. 1894.

*Saprolegnia hypogyna* var. IV. Maurizio, *ibid.*, p. 131, pl. 4, figs. 21-23. 1894.

*Saprolegnia hypogyna* var. V. Maurizio, *ibid.*, p. 132, pl. 4, figs. 24-27. 1894.

*Saprolegnia intermedia* Maurizio, Jahrb. Wiss. Bot. 29:97, pl. 2, figs. 37-51a. 1896.  
*Saprolegnia hypogyna* var. *coregoni* Maurizio, Z. Fischerei und deren Hilfswiss., Mitt.  
Deutsch. Fischerei-Vereins 7:55. 1899.

Monoecious. Mycelium diffuse; hyphae slender, sparingly branched. Sporangia cylindrical, clavate, or fusiform; generally straight or curved, occasionally irregular; renewed internally, rarely by sympodial branching; 76-480 x 13-38  $\mu\text{m}$ . Spores dimorphic; discharge and behavior saprolegnoid; primary spore cysts 10-13  $\mu\text{m}$  in diameter. Gemmae sparse or abundant, obpyriform or clavate, infrequently spherical; terminal or intercalary. Oogonia terminal or lateral, infrequently intercalary; obpyriform or spherical, occasionally napiform, rarely dolioform; (28-) 68-75 (-101)  $\mu\text{m}$  in diameter. Oogonial wall pitted; smooth. Oogonial stalks variable in length; stout or slender, straight or slightly irregular; unbranched. Oospores centric; spherical; (1-) 8-12 (-24) per oogonium; filling the oogonium or clustering in the upper, expanded portion; (18-) 21-26 (-44)  $\mu\text{m}$  in diameter; at germination producing a slender germ hypha. Antheridial branches absent. Antheridial cells hypogynous; fertilization tubes arising apically from the hypogynous cells, branched or unbranched, persisting.

This is one of two species of *Saprolegnia* producing hypogynous antheridial cells. The smooth, generally spherical or obpyriform oogonia (Fig. 94 A, B) of *S. hypogyna* distinguish it immediately from *S. irregularis* (Fig. 94 G-N).

Whether or not *Saprolegnia hypogyna* has an androgynous antheridial apparatus in addition to the hypogynous ones is an open question. Maurizio (1894: fig. 17) illustrated a branched hypogynous cell for his variety III of *S. hypogyna*. He commented on the resemblance of this lateral protrusion to an androgynous antheridium. Hypogynous cells branched at the side were induced in specimens of *S. hypogyna* grown in some of the nutrient solutions used by Kauffman (1908). As these lateral protrusions evidently were not cut off from the hypogynous cell, such an antheridial apparatus now would be termed hemihypogynous.

As to the function of the hypogynous cell in *Saprolegnia hypogyna*, Maurizio (1894:149) contended that the projections from the basal cell into the oogonial cavity (see Fig. 94 A, D) were not fertilization tubes. He regarded these filamentous protrusions as expressions of a tendency toward secondary growth, paralleling, as it were, internal proliferation in sporangia. Kauffman (1908) was of a like mind regarding the fertilization tubes in *S. hypogyna*. He also thought that the hypogynous cells were not true antheridia, but were aborted or latent cells that had lost (or never had attained) a sexual function. Should functional androgynous antheridial branches (or ones of other origins as well) be found in *S. hypogyna*, the species then would approach *S. ferax*.

The relatively extensive synonymy of *Saprolegnia hypogyna* is documented adequately by Seymour (1970).

CONFIRMED RECORDS: -- BRITISH ISLES: R. A. Couch (1951:156, pls. 39, 40) [his illustrations are very doubtfully of this species]. CZECHOSLOVAKIA: Cejp

(1959a:214, fig. 77). DENMARK: A. Lund (1934:17); Petersen (1909a:381; 1910:521). GERMANY: de Bary (*loc. cit.*, 1888:615); A. Fischer (1892:334); Minden (1912:526, 528, 529; fig. 1f); Pringsheim (*loc. cit.*). ICELAND: Seymour (1970:24, figs. 24-31). LAPLAND: Gäumann (1918:158). LATVIA: Apinis (1929a:210). MIDDLE EUROPE: Migula (1903:64, 67). RUMANIA: Moruzi and Toma (1968: pl. 4, figs. 31, 32); Toma (1971:9, pl. 1). SWITZERLAND: Maurizio (*loc. cit.*; 1899:55); Tiesenhausen (1912:268 *et seq.*, figs. 2, 3). UNITED STATES: R. L. Butler (1975: figs. 21-24.); Kauffman (1908: pl. 23); Shipman (1977: fig. 14), USSR: Dudka and Logvinenko (1968:271, fig. 2.3); Naumov (1954:66).

RECORDED COLLECTIONS: -- BRITISH ISLES: O'Sullivan (1965); Perrott (1960); Pickering *et al.* (1979); Willoughby (1974, 1977). DENMARK: Obel (1910a, b). GERMANY: Höhnk (1956a). ICELAND: Howard *et al.* (1970); T. W. Johnson (1968). INDIA: Khulbe (1977, 1980a); Khulbe and Bhargava (1977). NETHERLANDS: Bootsma (1973). ROMANIA: Toma (1969). UNITED STATES: Clausz (1970, 1974); Kauffman (1906); Klich (1980); Monsma (1936); Rooney and McKnight (1972); Shipman (1979). USSR: Érgashev and Kirgizhaeva (1978); Logvinenko (1971); Logvinenko and Meshcheryakova (1971); Osipyán *et al.* (1974). YUGOSLAVIA: Ristanović (1970a, 1973).

SPECIMENS EXAMINED: -- BRITISH ISLES (1), L. G. Willoughby. ICELAND (4), RLS. NORWAY (1), TWJ.

*Saprolegnia irregularis* Johnson and Seymour  
Svensk Bot. Tidskr. 69:90, figs. 1, 2. 1975  
(Figure 94 E-N)

Monoecious. Mycelium dense, compact; hyphae sparingly branched. Sporangia clavate or cylindrical, irregular and secondary ones constricted in passage through exit pore of emptied sporangium, occasionally spherical or subspherical; renewed internally or infrequently in a cymose or sympodial manner; primary ones 60-381 x 17-33  $\mu\text{m}$ . Spores dimorphic; discharge and behavior saprolegnoid; primary or secondary spore cysts 8-12  $\mu\text{m}$  in diameter. Gemmae abundant; cylindrical, lobed, irregular, sparingly papillate, simple or branched; terminal or intercalary, single or catenulate; sometimes converting directly into oogonia. Oogonia terminal or intercalary; subspherical, cylindrical, branched, lobed, or irregular; (51-) 90-157 (-168) x (21-) 66-140 (-231)  $\mu\text{m}$ , including lobes or branches. Oogonial wall conspicuously pitted; smooth, except where wall substance protrudes through pits in a truncate fashion. Oospores centric or subcentric, very infrequently subeccentric; occasionally aborting; spherical, subspherical, or ellipsoidal; 1-40 per oogonium, and occasionally filling it; (18-) 23-27 (-33)  $\mu\text{m}$  in diameter; germination not observed. Antheridial branches absent. Antheridia, when present, hypogynous, and often producing conspicuous unbranched or branched fertilization tubes; evidently proliferating internally, but successive ones may not have a poroid apex and are nonfunctional; fertilization tubes persisting.

*Saprolegnia irregularis* is recognized by its prominently irregular oogonia and often profusely developed fertilization tubes (Fig. 94 H, K, M). No other known species in the genus has this combination of characters.

The hypogynous antheridial cells (not all oogonia are attended by these) of *Saprolegnia irregularis* are of two types. Generally, the apex of the cell is prolonged into a fertilization tube (Fig. 94 M), but occasionally the apex is open (into the oogonial cavity), and secondary antheridial cells proliferate internally (Fig. 94 J, L, N). Precisely how the antheridial apparatus functions in this species is not known, and it is conceivable that the distally poroid cells (Fig. 94 H) simply may represent ones from which the fertilization tube has deliquesced. In any event, the internally proliferated cells recall Maurizio's (1894) belief that the hypogynous cells and fertilization tubes in *S. hypogyna* were merely expressions of renewed growth.

CONFIRMED RECORD: -- ICELAND: Johnson and Seymour (*loc. cit.*). INDIA: J. N. Rai and Misra (1977b:76, fig. 3b).

SPECIMENS EXAMINED: - ICELAND (7), TWJ.

*Saprolegnia turfosa* (Minden) Gäumann  
Bot. Not. 1918:154. 1918  
(Figure 95 A-C)

*Saprolegnia spec.* (2) Reinsch, Jahrb. Wiss. Bot. 11:295, pl. 14, figs. 7-13. 1878.

*Saprolegnia paradoxa* Petersen Bot. Tidskr. 29:379, fig. 1 d, e. 1909 (*also in* Ann. Mycol. 8:520, fig. 1 d, e. 1910); *non S. paradoxa* Maurizio, Z. Fischerei und deren Hilfswiss., Mitt. Deutsch. Fischerei-Vereins 7:46, figs. 10-12. 1899.

*Saprolegnia monoica* var. *turfosa* Minden, Kryptogamenfl. Mark Brandenburg 5:516. 1912.

*Aplanes turfusus* (Minden) Coker, J. Elisha Mitchell Sci. Soc. 42:216. 1927.

*Aplanes ozeensis* Kobayasi, *in* Kobayasi and Ookubo, J. Jap. Bot. 27:181, figs. 9, 10. 1952.

Monoecious. Mycelium stout; hyphae sparingly branched. Sporangia fusiform, clavate, or cylindrical; straight, curved, or moderately irregular; renewed internally; 102-627 x 18-66  $\mu\text{m}$ . Spores dimorphic; discharge and behavior saprolegnoid, infrequently aplanoid; primary spore cysts 9-11  $\mu\text{m}$  in diameter. Gemmae sparse or absent; when present, cylindrical, obpyriform, irregular, or branched; terminal, rarely intercalary; predominantly single. Oogonia lateral, rarely terminal, intercalary, or sessile; spherical, rarely ovoid or subspherical; (18-) 60-85 (-134)  $\mu\text{m}$  in diameter, including wall ornamentations. Oogonial wall conspicuously pitted; smooth or rarely with a few short, broad papillae. Oogonial stalks very short, predominantly  $(1/8\text{-}) 1/4\text{-} 1/2$  (-2) times the diameter of the oogonium, in length; stout, straight or curved; unbranched. Oospores centric; spherical or ellipsoidal; (1-) 6-16 (-42) per oogonium, and usually filling it; (16-) 26-31 (-37)  $\mu\text{m}$  in diameter; germination not observed. Antheridial branches androgynous, infrequently monoclinal and arising near the oogonial stalk; short, curved or bent, unbranched or branched; persisting. Antheridial

cells simple; long, cylindrical or tubular, rarely long-clavate; branched or unbranched; laterally appressed, rarely attached in a digitate fashion; persisting; fertilization tubes not observed.

Aside from the members of *Saprolegnia* with ornamented oogonia, *S. turfosa* is one of the species of the genus that is most easy to recognize. The large, very short-stalked oogonia attended by androgynous antheridial branches each terminated by a long, tubular antheridial cell (Fig. 95 A) mark this species. *Saprolegnia uliginosa* also has short-stalked oogonia (Fig. 95 F) but its antheridial branches are frequently monoclinal (these are infrequent in *S. turfosa*).

In view of the ease with which *Saprolegnia turfosa* can be recognized, its taxonomic history is surprisingly complicated. Seymour (1970:28, 29) reviewed the systematics of this species particularly thoroughly, and only a few additional comments are necessary. Reinsch (*loc. cit.*) was apparently the first to see *S. turfosa*, but chose not to name it. He (*loc. cit.*, p. 311) referred to figure 15 on plate 17 as an illustration of *Saprolegnia* sp. 2, but this was an error; that figure depicts sporangia of a *Gonapodya*. Coker (1923) apparently had difficulty in recognizing *S. turfosa*, a situation which he corrected in his 1927 paper. It appears that A. Lund (1934) misidentified *S. turfosa*, equating it with *Aplanes treleaseanus* (see *Achlya androgyna*). He listed both *S. treleaseana* of Humphrey (1893) and *Achlya treleaseana* (Humphrey) Kauffman as synonyms of what is here recognized as *S. turfosa*. In addition, A. Lund (1934:21) also considered that Petersen's *S. paradoxa* was synonymous with *Aplanes treleaseanus*; Petersen's species, on the contrary, is conspecific with *S. turfosa*. It is very likely that the *Aplanes turfusus* reported from the Soviet Union by Morochkovs'kiĭ *et al.* (1967) was *Achlya androgyna*. In their account of the Russian material, papillate oogonia are described for the specimen they encountered.

*Saprolegnia turfosa* is evidently not common (although it is widely distributed). In our experience, individuals appear most frequently in water or debris from *Sphagnum* spp. bogs. We have recovered *S. turfosa* repeatedly from acid waters (not bogs) in Norway and Sweden. A specimen collected on hempseed baited in a bog water sample from Norway was infected with *Olpidiopsis saprolegniae* var. *saprolegniae*.

CONFIRMED RECORDS: -- CZECHOSLOVAKIA: Cejp (1959a:271, figs. 104, 105). DENMARK: A. Lund (1934:20, fig. 7); Petersen (*loc. cit.*). GERMANY: Minden (*loc. cit.*); Reinsch (*loc. cit.*); Richter (1937:259, fig. 17). ICELAND: Howard *et al.* (1970: fig. 36). JAPAN: Kobayasi and Ookubo (*loc. cit.*). LAPLAND: Gäumann (*loc. cit.*). LATVIA: Apinis (1929a:227). UNITED STATES: Beneke (1948b:38, pl. 3); R. L. Butler (1975: figs. 29-32); Coker (1923:79, pl. 20; *loc. cit.*); Kobayasi *et al.* (1967:10, pl. 14, fig. M; text fig. 3); Milanez (1966:110, pl. 12, fig. d; pl. 13); Milanez and Beneke (1968:19, pl. 2, fig. 10); Overman (1970:36); Seymour (1970:27, figs. 40-48); A. W. Ziegler (1948b:16, pl. 1, figs. 1-9; 1952:13, pl. 5, fig. 4). USSR: Logvinenko and Meshcheryakova (1971: fig. 7).

RECORDED COLLECTIONS: -- BRITISH ISLES: Dick (1962, 1963, 1966); Dick and Newby (1961). CANADA: Dick (1971c). CZECHOSLOVAKIA: Cejp (1931).

DENMARK: A. Lund (1978). ICELAND: T. W. Johnson (1968). JAPAN: Kobayashi and Ôkubo (1954); Ookubo (1954); Suzuki (1961f). UNITED STATES: Coker (1927); Klich (1980); V. D. Matthews (1927).

SPECIMENS EXAMINED: -- BRITISH ISLES (1), W. R. I. Cook (Centraalbureau, Baarn). ICELAND (12), NORWAY (6), SWEDEN (11), TWJ. UNITED STATES (22), RLS.

*Saprolegnia uliginosa* Johannes  
Archiv Mikrobiol. 14:595, fig. 1. 1950  
(Figure 95 D-F)

Monoecious. Mycelium moderately dense, extensive; hyphae slender, flaccid. Sporangia clavate, cylindrical, or fusiform, sometimes irregular, renewed internally, rarely in basipetalous succession; 108-266 x 12-42  $\mu\text{m}$ . Spores dimorphic; discharge and behavior saprolegnoid; primary and secondary spore cysts 9-12  $\mu\text{m}$  in diameter. Gemmae sparse; spherical, obpyriform, cylindrical, fusiform, or irregular; terminal or intercalary, single or catenulate. Oogonia sparse or abundant; lateral, rarely terminal, occasionally intercalary; spherical, infrequently napiform or obpyriform; (32-) 60-68 (-91)  $\mu\text{m}$  in diameter. Oogonial wall pitted under the region of attachment of antheridial cells; smooth. Oogonial stalks ( $1/12$ -)  $1/8$ -1 (-2) times the diameter of the oogonium, in length; stout, straight, curved or recurved, infrequently bent; unbranched. Oospores centric, rarely subcentric; spherical; (2-) 5-7 (-25) per oogonium, and nearly filling it; (21-) 25-33(-36)  $\mu\text{m}$  in diameter; germination not observed. Antheridial branches predominantly monoclinal, and arising very near the oogonial stalk; infrequently androgynous; rarely declinal; slender, slightly irregular, occasionally producing one or two short, lateral branches; persisting. Antheridial cells simple; generally tubular, straight or curved, occasionally faintly cylindro-clavate; laterally appressed, persisting; fertilization tubes present, not persisting.

Like *Saprolegnia turfosa*, *S. uliginosa* usually has spherical oogonia borne laterally on short stalks (Fig. 95 E, F) and containing predominantly centric oospores. The similarity between these two species does not go beyond these features since the antheridial branches of *S. uliginosa* generally are monoclinal (Fig. 95 A) whereas androgynous ones clearly predominate in *S. turfosa*.

*Saprolegnia uliginosa* seems allied to *S. glomerata* -- with respect to antheridial branch origin, for example -- but can be distinguished from that species because it lacks the short, lateral twig-like evaginations (Fig. 96 I) arising from the hyphae and antheridial filaments. Moreover, in *S. glomerata* the oogonia are most often obpyriform; spherical ones are usually encountered in *S. uliginosa*. While the oogonia of *S. uliginosa* are pitted under the region of antheridial cell contact, those of *S. glomerata* usually are pitted elsewhere as well. In view of the characteristics of the Iceland specimens reported by Howard *et al.* (1970), *S. uliginosa* and *S. glomerata* cannot be separated with confidence on predominating oospore diameter.

It would appear on the surface that *Saprolegnia uliginosa* is a relatively rare species. One of the Norwegian isolates in our collections is latent in the development of its sporangia and the sexual apparatus, and grows very slowly in water culture. This suggests that the species may be overgrown quickly by more rapidly developing species, and thus not appear at all in gross cultures.

The description and illustrations of a *Saprolegnia* sp. recovered by Shibuya (1959) suggest that he may have collected Johannes' species, but we cannot be certain; we include the Japanese record as an unconfirmed one.

CONFIRMED RECORDS: -- GERMANY: Johannes (*loc. cit.*). ICELAND: Howard *et al.* (1970:77, fig.37). INDIA: J. N. Rai and Misra (1977b:76, fig. 3c). UNITED STATES: Seymour (1970:47, figs. 78-84).

RECORDED COLLECTION: -- JAPAN: Shibuya (1959:149, fig. 4)(?).

SPECIMENS EXAMINED: -- ICELAND (1), NORWAY (2), TWJ. UNITED STATES (5), RLS.

*Saprolegnia furcata* Maurizio

Z. Fischerei und deren Hilfswiss. Mitt. Deutsch. Fischerei-Vereins 7:48 *et seq.*, figs. 13-15. 1899

(Figure 97 E-I)

*Saprolegnia retorta* Horn, Ann. Mycol. 2:233, fig. 21. 1904.

Monoecious. Mycelium moderately delicate, sparingly branched. Sporangia clavate, cylindrical, or fusiform, straight, curved, or irregular; renewed internally or by cymose branching; 60-420 x 16-40  $\mu\text{m}$ . Spores dimorphic; discharge and behavior saprolegnoid; primary spore cysts 10-13  $\mu\text{m}$  in diameter. Gemmae sparse; clavate, spherical, subspherical, pyriform, or irregular; terminal, single. Oogonia lateral, occasionally terminal, very rarely intercalary; obpyriform or napiform, infrequently spherical, very rarely dolioform; (33-) 43-48 (-81)  $\mu\text{m}$  in diameter. Oogonial wall unpitted or sparsely pitted; smooth. Oogonial stalks ( $1/2$  -) 1-6 (-8) times the diameter of the oogonium, in length; slender, branched or unbranched; usually coiled, strongly bent, or irregular and twisted. Oospores centric, rarely subcentric; spherical; (1-) 4-10 (-28) per oogonium, and usually nearly filling it; (16-) 20-24 (-45)  $\mu\text{m}$  in diameter; germination not observed. Antheridial branches predominantly androgynous, rarely monoclinal or diclinous; slender, occasionally branched, usually twisted or irregular; infrequently bearing oogonia; persisting. Antheridial cells simple; tubular, clavate, or irregular, rarely once-branched; persisting; laterally or apically appressed; fertilization tubes present, not persisting.

The strongly bent (Fig. 97 F) or conspicuously coiled (Fig. 97 E), relatively long oogonial stalks constitute the chief feature by which this species can be recognized. Maurizio (*loc. cit.*) emphasized that the antheridial branches in *Saprolegnia furcata* could

revert to oogonium production. However, as Seymour (1970) pointed out, this feature is too variable among isolates to be of much taxonomic value.

*Saprolegnia furcata* has been reported under several names. Cornu (1872) possibly described this species as *S. spiralis*, but the fungus as he reported it was infected, and the taxon is not valid. Horn's (*loc. cit.*) *Saprolegnia retorta* appears to have been identical to Cornu's *S. spiralis*, yet apparently was not infected. Quite likely *S. monoica* var. *tortipes* Shkorbatov (1923) was *S. furcata* as well, but as there are no illustrations of the variety, this supposition cannot be confirmed. Apinis (1929a) gives as a synonym of *S. furcata* Tiesenhausen's *S. monoica* var. *glomerata*. That variety is synonymous with *S. glomerata*, however, as A. Lund (1934) pointed out. We are including Cejp's (1959a) account of *S. spiralis* in *S. furcata*, but only with reservation. The illustrations he provided (Cejp, 1959a; fig. 95) do not show a fungus infected by *Rozella* (as Cornu had illustrated *S. spiralis*), hence it is difficult to see how Cejp could have identified his Czechoslovakian specimens with Cornu's species. The one good illustration by A. Braun (1856: pl. 5, fig. 22) of an uninfected filament of *S. ferax* shows oogonia on strongly recurved stalks; he may well have observed what was later to be described by Maurizio as *S. furcata*.

*Saprolegnia furcata* has been used extensively in research on ultrastructure. The accounts by Beakes and Gay (1977: 1978a, b), Heath and Greenwood (1968), Heath *et al.* (1971), and Howard and Moore (1970) are notable in this respect (*see* Chapters 13-15).

CONFIRMED RECORDS: -- CZECHOSLOVAKIA: Cejp (1959a:236, 251, fig. 95)(?). GERMANY: A. Braun (1856: pl. 5, fig. 22); Horn (*loc. cit.*); Minden (1912:517); Richter (1937:238, fig. 2). ICELAND: T.W. Johnson (1974b: figs. 160-162). LATVIA: Apinis (1929a:213, fig. 1). MIDDLE EUROPE: Migula (1903:67). SWITZERLAND: Maurizio (*loc. cit.*).

RECORDED COLLECTIONS: -- BRITISH ISLES: Dick and Newby (1961), O'Sullivan (1965). GERMANY: Höhnk (1935a). USSR: Logvinenko and Meshcheryakova (1971).

SPECIMENS EXAMINED: -- BRITISH ISLES (2), A. E. Apinis, M. W. Dick. ICELAND (2), UNITED STATES (13), RLS.

*Saprolegnia glomerata* (Tiesenhausen) Lund  
Kongel. Danske Vidensk. Selsk. Naturvidensk. Math. Afh. 9 6:14 fig. 4. 1934  
(Figure 96 G-J)

*Saprolegnia monoica* var. *glomerata* Tiesenhausen, Arch. Hydrobiol. Planktonk. 7:277, figs. 6-8. 1912.

Monoecious. Mycelium delicate; some principal hyphae stout and provided with numerous short, scattered or clustered lateral, often twig-like branches. Sporangia abundant or sparse; cylindrical, fusiform, clavate, or irregular; rarely pyriform; straight, curved, or bent, occasionally twisted, and sometimes enlarged at base; renewed

internally; 40-220 × 18-28 μm. Spores dimorphic; discharge and behavior saprolegnoid, rarely aplanoid; primary spore cysts 10-14 μm in diameter. Gemmae very sparse; clavate or obpyriform; terminal, single. Oogonia spherical, obpyriform, napiform, or subspherical, rarely dolioform; lateral, occasionally terminal, rarely intercalary; (32-) 46-60 (-107) μm in diameter. Oogonial wall pitted or unpitted; smooth. Oogonial stalks ( $\frac{1}{4}$  -) 1-2 (- $3\frac{1}{2}$ ) times the diameter of the oogonium, in length; stout; straight, curved, or bent; unbranched or with one or more short, lateral branches. Oospores centric; spherical, often nearly filling the oogonium; (1-) 6-16 (-28) per oogonium; (18-) 23-26 (-30) μm in diameter; at germination producing a germ hypha which may or may not bear a terminal sporangium. Antheridial branches androgynous or monoclinal, rarely dichlanous; slender, usually contorted, twisted, or irregular and sparingly branched; persisting. Antheridial cells simple, generally tubular, occasionally clavate or slightly irregular; persisting; laterally appressed, very rarely attached apically; fertilization tubes present, not persisting.

*Saprolegnia glomerata* is readily recognizable by the short, branched or unbranched, contorted, lateral (and often clustered) hyphal extensions (Fig. 96 G, I). Secondary characters of recognition are the contorted, branched antheridial filaments (Fig. 96 G, H, J) and the short, lateral evaginations on many of the oogonial stalks (Fig. 96 H). In *S. litoralis*, the hypha immediately below a terminal oogonium, may bear short, lateral branches (Fig. 96 B) as does *S. glomerata*, but in the former, the hypha is usually swollen at its juncture with the oogonial septum (Fig. 96 A, B). In any case, the oospores in *S. litoralis* are occasionally subcentric, a condition not known to occur in *S. glomerata*.

Although A. Lund recognized as early as 1934 that Tiesenhausen's (*loc. cit.*) variety *glomerata* deserved specific rank, not all investigators followed (or were aware of) this disposition. For example, T. Ito (1944) retained the variety of *glomerata* and reduced *Saprolegnia furcata* and *S. glomerata* (Tiesenhausen) Lund to synonymy with it. Cejp (1959a) listed both Lund's species and *S. monoica* as synonyms of Tiesenhausen's variety. In addition, *S. glomerata* has been misidentified by some mycologists. Apinis (1929a, b) believed that Maurizio's (1899) *S. furcata* was the same as Tiesenhausen's variety *glomerata*. The specimens recorded by T. W. Johnson (1950b:399) as the variety *glomerata* were misidentified; he had collected forms of *S. ferax*. The *S. monoica* reported by Humphrey (1893) was not, as Coker (1923) maintained, identifiable as *S. monoica* var. *glomerata*; Humphrey's material was very likely representative of *S. ferax*.

CONFIRMED RECORDS: -- BRITISH ISLES: R.A. Couch (1951:161, p1s. 41-45); Forbes (1935a:226). CZECHOSLOVAKIA: Cejp (1959a:231, fig. 85 a-f). DENMARK: Lund (*loc. cit.*). GERMANY: Richter (1937:237). ICELAND: Howard *et al.* (1970: figs. 27, 28). INDIA: Thakur Ji (1970:182, figs. 15-18). JAPAN: T. Ito (1942:124, fig. 1 e-g; 1944:52). LATVIA: Apinis (1929a: 213, text fig. 1). NETHERLANDS: Beverwijk (1948:232, fig. 3). POLAND: Szwanke (1938:8, pl. 2, figs. 10, 11; pl. 3, figs. 1-5). SWITZERLAND: Tiesenhausen (*loc. cit.*). UNITED STATES: Beneke (1948b:36); T. W. Johnson (1956a:186);

Rose (1932:25, pl. 1, figs. 6-9); Sorenson (1962: pl. 7, figs. A, B); A. W. Ziegler (1952:7, pl. 2, figs. 7,8).

RECORDED COLLECTIONS: -- BRITISH ISLES: Apinis (1960, 1964); Cook and Forbes (1933); Cook and Morgan (1934). GERMANY: Höhnk (1935a). JAPAN: Suzuki (1961f). POLAND: Zaborowska (1965). RUMANIA: Toma (1969). UNITED STATES: Cotner (1930b); G. C. Hughes (1959, 1962); Poitras (1955); Sparrow (1952b); A. W. Ziegler (1958b). YUGOSLAVIA: Ristanović (1973).

SPECIMENS EXAMINED: -- ICELAND (66), NORWAY (4), TWJ. UNITED STATES (26), RLS.

*Saprolegnia ferax* (Gruith.) Thuret  
Ann. Sci. Nat. Bot. (3<sup>e</sup> sér.) 14:229 *et seq.*, pl. 22. 1850  
(Figure 98)

*Conferva ferax* Gruithuisen, Nova Acta Phys.-Med. Acad. Caes. Leop-Carol. Nat. Cur. 10:445, pl. 38, figs. 14-16. 1821.

*Saprolegnia molluscorum* Nees von Esenbeck, Nova Acta Phys.-Med. Acad. Caes. Leop.-Carol. Nat. Cur. 11:514. 1823.

*Leptomitus ferax* Agardh, Systema Algarum, p. 49. 1824.

*Achlya prolifera* Pringsheim, Nova Acta Phys.-Med. Acad. Caes. Leop-Carol. Nat. Cur. 23:399 *et seq.* pls. 46-50. 1851.

*Saprolegnia monoica* Pringsheim, Jahrb. Wiss. Bot. 1:292, pls. 19, 20. 1858.

*Achlya intermedia* Bail, Amtl. Ber. Versamml. Deutsch. Naturf. Aerzte, Königsberg 35:257. 1860.

*Diplanes saprolegnioides* Leitgeb, Jahrb. Wiss. Bot. 7:385, pl. 24. 1869-70.

*Achlya ferax* (Kützing) Duncan, Proc. Roy. Soc. London 25:253, pl. 7, figs. 36-38, 40-42. 1876.

*Saprolegnia thureti* de Bary, Abh. Senckenberg Naturf. Ges. 12:326, pl. 5, figs. 1-10. 1881. (Also in de Bary and Woronin, Beitr. Morphol. Physiol. Pilze, 4: 102, pl. 5, figs. 1-10. 1881.)

*Saprolegnia mixta* de Bary, Bot. Zeitung (Berlin) 41:56. 1883.

*Saprolegnia monoica* var. *montana* de Bary, *ibid.*, 46:617. 1888.

*Saprolegnia esocina* Maurizio, Jahrb. Wiss. Bot. 29:82, pl. 1, figs. 4-17. 1896.

*Saprolegnia heterandra* Maurizio, *ibid.*, p. 87, pl. 1, figs. 18-27. 1896.

*Saprolegnia bodanica* Maurizio, *ibid.*, p. 107, pl. 2, figs. 52-59a. 1896.

*Saprolegnia paradoxa* Maurizio, Z. Fischerei und deren Hilfswiss. Deutsch. Fischerei-Vereins 7:46 *et seq.*, figs. 10-12. 1899; *non S. paradoxa* Petersen, Bot. Tidsskr. 29:379. 1909. (Also in Petersen, Ann. Mycol. 8:520. 1910.)

*Saprolegnia floccosa* Maurizio, *ibid.*, p. 50 *et seq.*, figs. 16, 17. 1899.

*Saprolegnia semidioica* Petersen, Bot. Tidsskr. 29:378, fig. 1f. 1909. (Also in Petersen, Ann. Mycol. 8:519, fig. 1f. 1910.)

*Saprolegnia monoica* var. *vexans* Pieters, Bot. Gaz. (Crawfordsville) 60:489. 1915.

*Saprolegnia mixta* var. *asplundii* Gäumann, Bot. Not. 1918:155. 1918.

*Saprolegnia lapponica* Gäumann, *ibid.*, p. 156. 1918.  
*Saprolegnia tokugawana* Emoto, Bot. Mag. (Tokyo) 37:15, pl. 1. 1923.  
*Saprolegnia monoica* var. *floccosa* (Maurizio) Cejp, Oomycetes I, Flora ČSR, Ser. B, Part 2, p. 234, figs. 85 g-j, 86. 1959.  
*Saprolegnia ferax* var. *lapponica* (Gäumann) Cejp, *ibid.*, p. 245. 1959.  
*Saprolegnia ferax* var. *esocina* (Maurizio) Cejp, *ibid.*, p. 246. 1959.  
*Saprolegnia monoica* var. *acidamica* Suzuki, J. Jap. Bot., 36:234. 1961.

Monoecious. Mycelium stout, hyphae moderately to sparingly branched. Sporangia clavate, fusiform, cylindrical, or slightly irregular, sometimes nearly spherical; straight or bent; renewed internally with secondary ones nesting inside discharged primary ones, or partially emerged through orifices of empty sporangia and forming bead-like chains or cylindrical segments, or emerging fully through orifices of previously emptied sporangia; rarely renewed in a basipetalous or cymose manner; 31-624 x 18-67  $\mu\text{m}$ . Spores dimorphic; discharge and behavior saprolegnoid, rarely aplanoid or dictyucoid, very rarely achlyoid or leptolegnoid; primary spore cysts 9-12  $\mu\text{m}$  in diameter. Gemmae, when present, variable in shape and position. Oogonia lateral, terminal, or intercalary and then single or catenulate, infrequently occurring in emptied sporangia or sessile; spherical, obpyriform, napiform, sometimes obovate or clavate, cylindrical when in discharged sporangia, often dolioform when intercalary; (28-) 60-80 (-194)  $\mu\text{m}$  in diameter. Oogonial wall generally conspicuously and abundantly pitted, rarely unpitted; smooth or rarely with one or two short, papilliform evaginations, or apiculate. Oogonial stalks ( $1/3$  -) 1-2 ( $3^{1/2}$ ) times the diameter of the oogonium, in length; stout, straight, bent, or curved; very rarely once-branched. Oospores centric or subcentric, spherical or ellipsoidal; (1-) 10-18 (-54) per oogonium and nearly filling it, (12-) 22-28 (-44)  $\mu\text{m}$  in diameter; germinating by a slender germ hypha that may or may not bear a small, apical, clavate sporangium. Antheridial branches variable in abundance and density, and sometimes absent; when present, monoclinal or androgynous, rarely dichlanous; slender, slightly to prominently irregular, unbranched or very sparingly branched; persisting. Antheridial cells simple; generally tubular or clavate, occasionally irregular, infrequently once-branched; usually persisting; laterally appressed, very rarely attached apically; fertilization tubes present, not persisting.

Based on a survey of existing literature and the characterization of a generous collection of living material, Seymour (1970) demonstrated that *Saprolegnia ferax* was a complex of morphological variants. Many of the various forms that had from time to time been described, he concluded, were recognizable as individuals, but at the same time occupied some point in a long series of morphological gradients. Accordingly, he proposed a very extensive synonymy (Seymour, 1970:29, 30) for *S. ferax*; this is adopted here with minor corrections. Discussion of the synonymous species beyond that provided by Seymour is unnecessary. Florinskaya (1968) has also studied extensively the degree of morphological variability in *S. ferax*, particularly that to be found in

oogonial shape and position. She did not propose any taxonomic changes, however, as a result of the analyses she performed.

*Saprolegnia ferax* is a ubiquitous and very common species. Generally it is most easily recognized by reliance on a combination of predominating characters: large, conspicuously or sparsely pitted oogonia, centric and subcentric oospores (sometimes in the same oogonium), occasional development of oogonia in discharged sporangia, and a preponderance of androgynous or monoclinal antheridial branches (when these filaments are present at all). Identification of the species often is complicated by the fact that the abundance of antheridial branches is especially variable among cultures. Antheridial filaments are usually sparse, but specimens nearly devoid of an antheridial apparatus, or ones generally provided with such branches are common as well. In any event, even when a large percentage of the oogonia in any colony are attended by antheridial branches the filaments are seldom branched, and are usually not long and extensively developed. In the general configuration of its oogonia, *S. diclina* approaches *S. ferax*. Cultures of *S. diclina* consistently have a generous production of predominantly diclinous antheridia (such a branch origin is rare in *S. ferax*).

The discovery of oogonia in *Saprolegnia ferax* is attributable to Thuret (1850:229 *et sqq.*, pl. 22) although he believed these cells were only lateral sporangia. The status of the species was early called into question, and several names appeared in the literature. Kützing (1843, 1849), for example, who thought the fungus was an alga, listed eleven synonyms for *S. ferax*. The species was put into *Leptomitus* by Agardh (1824), and into *Achlya* by Duncan in 1876(b). Without a doubt some of the earliest reports of the collection of *S. ferax* were based on misidentifications, and curious conclusions about the species were fashioned. In some remarks on this species published in 1871, M. C. Cooke concluded that *Sporendonema muscae* Fries or *Empusa musca* Cohn were imperfectly formed "terrestrial conditions" of *S. ferax*. De Bary (1881:254 *et sqq.*) understood *S. ferax* to be a collective name only.

*Saprolegnia ferax* has been implicated as an active agent in saprolegniosis (R. C. Srivastava, 1976; Nolard-Tintigner, 1970, among others). Some investigators, however, deduced that representatives of the species simply acted as secondary invaders of already diseased or injured fish (Drew, 1909). *Saprolegnia ferax* also is associated with ulcerative dermal necrosis (Chapter 29).

Because of its ready availability and rapid growth in culture, *Saprolegnia ferax* has proven to be a useful experimental subject in a variety of studies, examples of which follow. Nolan's (1976) physiological study of *S. ferax* demonstrated for the first time the use and release by a fungus of cadaverine (Chapter 22). *Saprolegnia ferax* also has been employed extensively in ultrastructural work (Chapters 13-15), notably by such investigators as Manton *et al.* (1951, 1952), Heath (1975a, b), Heath and Greenwood (1968; 1970a, c), and Holloway and Heath (1977b). Under the binomial *S. monoica*, *S. ferax* was made use of in an investigation of hyphal elongation and branching by Larpent (1963a-c, 1964), and in experimental analyses by Borkowski (1967; 1968a, b; 1969; 1970) of the axial ordination of primary spores during release.

Using *Saprolegnia ferax* among other fungi, Ho (1978) performed a quantitative analysis of hyphal branching at the periphery of colonies grown on an agar medium. He selected ten parameters for the analysis: apical segment ratio, diameter ratio, and hyphal density, among others. The mycelium of *S. ferax* typically produced very long apical segments (distance from apex of hypha to first “internode” or branch hypha), and a very low total branch ratio (total number of branches on a primary hypha in relation to the total number of primary or “leading” hyphae in the mycelium). The ratio between the sum of the length of all filaments and the total number of hyphal apices indicated that this species displayed a very large hyphal growth unit (one of the ten parameters measured). Ho suggested that the nature of the hyphal branching system might be characteristic enough of some species to have taxonomic value.

Among the numerous records of the collection of *Saprolegnia ferax* (in its broadest sense) there are four that must remain suspect, even though the specimens so identified were described or illustrated, or both. The following reports are in this very doubtful category: Almeida *et al.* (1943: pl. 21 fig. 6), Richter (1937:241, fig. 3; *see S. latvica*), Stirling (1878: 1 unnumbered fig.), and Walz (1870a:556, pl. 9, figs. 20, 21; also *in* Val'ts, 1870: figs. 20, 21; conidia are described and illustrated).

CONFIRMED RECORDS: -- ASIA: Sorokine (1889-90:142). AUSTRALIA: Crooks (1937:211, fig. 1A-G). AUSTRIA: Keissler (1917: fig. 2). BELGIUM: Nolard-Tintigner (1970:765, fig. 1; 1973:25, figs. 9, 10). BRITISH ISLES: E. M. Brown (1938:163, 166, figs. 1, 2.4-2.6); M. C. Cooke (1871: figs. 308, 309); R. A. Couch (1951:139, 144, 172, 175, pls. 32-38, 46-48); Duncan (*loc. cit.*); Forbes (1935a:223-225; 1935b: 10 figs. 1a, b); Masee (1891:132, 137, figs. 38; pl. 5, figs. 91-93); Manton *et al.* (1951: pls. 1-8; 1952: pls. 1-3); Newby (1948b:266, figs. 1-6); O'Sullivan (1965: fig. 1-1- 3); W. G. Smith (1878a: figs. 104-106; 1878b: 3 unnumbered figs.); Walpole and Huxley (1882: figs. 1-5). CANADA: Maestres (1977:146, 147, fig. 45); C. L. Moore (1908-09:222, figs. 1, 2). CZECHOSLOVAKIA: Cejp (1934:187, pl. 1, figs. 5, 6; *loc. cit.*; 1957: fig. 118.3 and 119.2; 1959a:229, 231, 235, 236, 241, 245, 247, figs. 76, 84, 85a-f, 88-94). DENMARK: A. Lund (1934:12); Petersen (*loc. cit.*; 1909a:380, figs. 1a, b; 1910:519, 521, figs. 1a, b). EAST GERMANY: Borkowski (1967: figs. 1-3; 1968a: figs. 1, 5, 9; 1968b: figs. 1-3; 1969: figs. 1, 2; 1970: figs. 1-4). FRANCE: Lechmere (1910:308, pls. 1, 2; 1911a: 178-188, 201, figs. 1-14 (p. 180), figs. 1-15 (p. 184), figs. 1-17 (p. 186); 1911b:376, figs. 2-43; Moreau and Moreau (1938:227, 228, pl. 1, figs. 1-28; pl. 6, figs. 1-5; pl. 20; 1948:225, 226); Thuret (*loc. cit.*). GERMANY: Bail (*loc. cit.*); de Bary (*loc. cit.*; 1852: pl. 7, figs. 24, 25; 1881:254 *et sqq.*, pl. 5, figs. 11-19; pl. 6, figs. 1, 2; 1883:56; 1888:615, 616, 617); Bock (1956:32); Claussen (1908: pls. 6, 7); A. Fischer (1892:337, 339, figs. 51a, b, e, d; 52); Gotze (1918: figs. 7-9); Hagedorn and Weinert (1971: figs. 1-36); Höhnk (1935b: figs. 1-7; 1953a: 56, pl. 1; 1969:136); Klebs (1899: fig. 1); Kützing (1843:157, pl. 1); Leitgeb (*loc. cit.*); Mäckel (1928: figs. 1, 2, 3c-i, 4-21, 25, 26); Maurizio (*loc. cit.*); Minden (1912:514, 515, 519, 521, figs. 1b-d, i); Pieters (1915b:307 *et sqq.*, pl. 170); Pringsheim (*loc. cit.*); Reinke (1869: pl. 12); Schröter (1889:252); Wemmer (1954: fig. 1); Zopf (1890:297, fig. 68). INDIA: Chaudhuri *et al.*

(1947:27, 29, fig. 8); Dayal and Thakur Ji (1968c:34, figs. 14-20; Khulbe (1977:22, 23, pl. 2, figs. 1-6; pl. 7, figs. 7-11; pl. 10, fig. 4; 1980c:79, 80, figs. 7, 8); S. B. Saksena and Rajagopalan (1958:11, figs. 8-12); Shah *et al.* (1977:143); G. C. Srivastava (1967a:283, pl. 1, figs. 4-8); R. C. Srivastava (1976: pl. 5, fig. A); Sydow *et al.* (1907:511); Talukdar and Baruah (1952:125); Thakur Ji (1970:182, figs. 10-14). IRAQ: Ismail *et al.* (1975:85, figs. 1-3); Muhsin [1977:30, figs. A-C (on two plates)]. JAPAN: Emoto (*loc. cit.*); S. Ito (1936:77, 78, 79); T. Ito (1942:121, 1221 fig. 1a-d; 1944:52); Kobayasi and Konno (1969:732, fig. 5); Kobayasi and Ookubo (1952b:184, fig. 12); Nagai (1931: 6, pl. 2, figs. 2-15); Okane (1976:2, fig. 4; 1977: figs. U, V); Suzuki (*loc. cit.*). LAPLAND: Gäumann (*loc. cit.*; 1918:152). LATVIA: Apinis (1929a:213, 215). MIDDLE EUROPE: Migula (1903:65, 66, 67); Reinke (1869: pl. 12). NEPAL: Bhatt and Manandhar (1971:56, figs. 4-7); Joshi (1967:45). NETHERLANDS: Boedjin (1921:118, pl. 3, figs. 1-6; 1923:85). PEOPLE'S REPUBLIC OF CHINA: Er (1973:37); Ou (1940:434); Shen and Siang (1948:191, 192). POLAND: Stpiczyńska (1962:101, 102, 104, figs. 4, 6); Stpiczyńska-Tober (1965:69, fig. 4); Zaborowska (1965:41, fig. 4). REPUBLIC OF CHINA: Chiou *et al.* (1975:167, pl. 2, figs. 20, 21); Chung (1973: figs. 5, 6). RUMANIA: Moruzi and Toma (1968:172, pl. 1, figs. 5-10; pl. 4., figs. 28, 29); Toma (1968:113, pl. 3., figs. 24-27; pl. 7, figs. 56-61; 1969:215). SOUTH AMERICA: Beneke and Rogers (1970:58); Milanez (1968:103, fig. 6); A. L. Rogers *et al.* (1970: 103). SWITZERLAND: Maurizio (*loc. cit.*; 1895d:11, figs. 1-3); Tiesenhausen (1912:277, 280, 283, fig. 9). UNITED STATES: Beers and Sherwood (1966: figs. 8-14); Beneke (1948b:27, 32, 34, 35, pl. 2); Bretsnyder (1943:10, 11); R. L. Butler (1975: figs. 33-36); Coker [1923:40, 46, 51, pls. 4 (upper fig.), 11-13]; Fox and Wolf (1977a:102, fig. 5); Graff (1928:171); J. V. Harvey (1942:20, 21, pl. 1, figs. 1-5); Holland (1958:21, 22); Humphrey (1893:104, 105, 106, pl. 16, figs. 37-45); Hutchison (1940:8, 9, figs. 5, 8); T. W. Johnson (1950b:397, 399; 1956a:186); Kauffman (1908:368, 369); Milanez (1966:103); Neish (1975a:1424, figs. 1-16); O'Bier (1960:23, 28, pl. 1, figs. a-d; pl. 3, figs. a-m); Overman (1970:35); Pieters (*loc. cit.*; 1915b:307 *et sqq.*, pl. 170); Rajagopalan (1963:117, fig. 2A-H); Rose (1932:24, 26, 28, 29, pl. 1, fig. 5; pl. 2, figs. 10-14, 17-19); Shipman (1977: fig. 13); Sorenson (1962: pl. 5, figs. D, G-I; pl. 6, figs. C, D; pl. 7, fig. C; pl. 8, figs. B, C); W. N. Tiffney (1936:19); Wolf (1937a: figs. 1-6; 1944:21, 23, pl. 1, figs. 3, 4). USSR: Domashova (1971:190, figs. 3, 4); Dudka and Florinskaya (1971:432, figs. 1, 2); Dudka and Logvinenko (1968: fig. 1.1); Florinskaya (1968:151 *et sqq.*, figs. 1-6; 1969:108-111, figs. 3-6; 1971: figs. 2,4); Milovtsova (1935a:32, 34, pl. 2-a, figs. F<sub>1</sub>, F<sub>2</sub>, G<sub>1</sub>, G<sub>2</sub>); Morochkovs'kiĭ *et al.* (1967:127, 128, figs. 111-113); Naumov (1954:67, fig. 34); Naumova (1955:136, fig. 5); Shkorbatov (1927:74, 75, 77).

RECORDED COLLECTIONS: -- AFRICA: Fajola *et al.* (1978). AUSTRALIA: Johnston (1917). BELGIUM: Bommer and Rousseau (1884); Nolard-Tintigner (1971). BRITISH ISLES: Apinis (1960, 1964); Berkeley (1944); Dick (1962, 1963, 1964, 1966); Beakes (1980a); M. J. Berkeley (1864); Cook and Forbes (1933); Cook and Morgan (1934); Dick and Newby (1961); Drew (1909); Greenhalgh (1974); Hallett and Dick (1976); Hartog (1895); Hunter (1975); Massee and Crossland (1905); Murray (1885); J. H. Patterson (1903); Perrott (1960); Pickering *et al.* (1979); R. E. Roberts (1963); Rushton (1926); W. G. Smith (1878b); Stirling (1880a,b); Stuart and Fuller (1968a); Swan (1889);

Trow (1895); Willoughby (1965, 1971a, 1974, 1977); Willoughby and Collins (1966); Willoughby and Pickering (1977). BULGARIA: Valkanov (1931a). CANADA: Dick (1971c); Maestres and Nolan (1978); Nolan (1976). CZECHOSLOVAKIA: Cejp (1931; 1959b). DENMARK: A. Lund (1934, 1978); Obel (1910a, b). FAEROES: Höhnk (1960). FINLAND: Häyrén (1902-03; 1943-44, 1956). FRANCE: Dop (1905a); Radais (1898); Schnetzler (1887; 1888a, b). GERMANY: Bock (1956); Dubitzky (1934); Höhnk (1935a; 1952c, d; 1956a, b; 1957a; 1958); Krause (1960); Lindstedt (1872); F. Müller (1911); Pieters (1915a); Remy (1950); Schröter (1893); Stoll (1936); Walentowicz (1885). GREENLAND: Höhnk (1956b). HUNGARY: Moesz (1937-38). ICELAND: Larsen (1932); Howard *et al.* (1970). INDIA: Bhargava *et al.* (1971); Bhattacharya and Baruah (1953); E. J. Butler and Bisby (1931); Dayal and Tandon (1962, 1963); Dayal and Thakur Ji (1965, 1966); Khulbe (1980a); Khulbe and Bhargava (1977); Mekrani (1980); Mer *et al.* (1980); G. C. Srivastava (1967b); G. C. Srivastava and R. C. Srivastava (1976b; 1977a, e); R. C. Srivastava and G. C. Srivastava (1978a); Thakur Ji (1967). IRAQ: Al-Saadi *et al.* (1979). JAPAN: Hoshina *et al.* (1958, 1960); S. Ito and Nagai (1931); Kobayashi and Okubo (1954); Okane (1978); Ookubo (1954); Ookubo and Kobayasi (1955); Shirai *et al.* (1927); Suzuki (1960a-d, f-h; 1961b, d, e, g-j; 1962 a-c, e; 1964); Suzuki and Hatakeyama (1960); Suzuki and Nimura (1960; 1961 b, d; 1962); Suzuki and Nishita (1963); Suzuki and Tatsuno (1964; 1965a, b). NETHERLANDS: Beverwijk (1948). NEW ZEALAND: Karling (1966f). OCEANIA: Karling (1968b). POLAND: Dominik (1936); Walentowicz (1885); Żebrowska (1976a). RUMANIA: Toma (1971). SOUTH AMERICA: Beneke and Rogers (1962); Herter (1930:33); Karling (1946); Milanez (1970); Upadhyay (1967). SWITZERLAND: Blanc (1887). TASMANIA: Rodway (1897). UNITED STATES: Agersborg (1933); Atkinson (1897); Beneke and Schmitt (1961); Clausz (1970, 1974); Coker (1927); Coker and Braxton (1926); W. B. Cooke and Bartsch (1959, 1960); W. B. Cooke and Matsuura (1969); Crane and Vermillion (1966); J. J. Davis (1914); Farr and Paterson (1974); Galloway (1891); Gaertner and Sparrow (1966); Gerard (1879); Harkness and Moore (1980); J. V. Harvey (1925a, b; 1927b, c; 1930; 1952); Höhnk (1935a); G. C. Hughes (1959; 1962); T. W. Johnson (1950b); Kauffman (1906; 1915); Klich (1980); Kuehn (1960); Lounsbury (1927); R. Martin (1968a); V. D. Matthews (1927); Monsma (1936); C. E. Miller (1965); Pieters (1915a); Poitras (1955); Ricker (1902); Ristanović *et al.* (1973); Rooney and McKnight (1972); Schmitt and Beneke (1962); Scott (1960b); Scott and O'Bier (1962); Scott *et al.* (1963); Shipman (1979); Slifkin (1964); Sparrow (1952b); W. N. Tiffney (1939); Trelease (1882); Webber (1889); Whiffen (1945); Wolf (1937b); Wolf and Wolf (1941); Ziegler (1948b, 1958b). USSR: Domashova (1974b); Dudka (1965, 1966); Érgashev and Kirgizbaeva (1978); Kirgizbaeva (1976); Kirgizbaeva *et al.* (1975); Logvinenko (1970, 1971); Logvinenko and Meshcheryakova (1971); Meshcheryakova (1970, 1974, 1977); Mikheeva (1969); Mil'ko and Belyakova (1968); Mil'ko and Dudka (1968); Mil'ko and Zakharova (1976); V. Miller (1906); Osipyán *et al.* (1974); Shcherbak' (1910); Walz (1870b); Yachevskim' (1895). WEST INDIES: Sparrow (1952a). YUGOSLAVIA: Ristanović (1970a, b; 1973).

SEPCIMENS EXAMINED: -- ENGLAND (1), CMI (A. Apinis). ICELAND (37), NORWAY (61), SWEDEN (57), TWJ. UNITED STATES (154), TWJ, RLS. Centraalbureau (1).

*Saprolegnia torulosa* de Bary  
Abh. Senckenberg Naturf. Ges. 12:326, pl. 6, figs., 3-17. 1881  
(Figure 97A-D)

*Saprolegnia* sp. Lindstedt, Synopsis der Saprolegniaceen . . ., p. 48, pl. 4. 1872.

*Saprolegnia monilifera* de Bary, Bot. Zeitung (Berlin) 41:56. 1883.

*Saprolegnia rhaetica* Maurizio, Flora 79:112, pl. 3, figs. 1-16; pl. 4, figs. 1-4. 1894.

*Saprolegnia variabilis* Minden, Kryptogamenfl. Mark Brandenburg 5:524. 1912.

*Isoachlya toruloides* Kauffman and Coker, in Kauffman, Amer. J. Bot. 8:231, pls. 13, 14. 1921.

*Isoachlya monilifera* (deBary) Kauffman, *ibid.*, p. 231. 1921.

*Isoachlya torulosa* var. *paucispora* Moreau and Moreau, Bull. Soc. Mycol. France 64:228, fig. 2. 1948.

*Isoachlya rhaetica* (Maurizio) Cejp, Oomycetes I, Flora ČSR, Ser. B, Part 2, p. 201, fig. 71. 1959.

*Isoachlya torulosa* (de Bary) Cejp, *ibid.*, p. 205. 1959.

Monoecious. Mycelium dense or sparse; hyphae usually sparingly to moderately branched. Sporangia sparse or abundant, cylindrical, clavate, fusiform, or irregular; straight, curved, or bent; terminal or intercalary and moniliform; renewed internally, or in a basipetalous or cymose succession; 80-457 x 44-39  $\mu\text{m}$ . Spores from primary sporangia dimorphic, but monomorphic or dimorphic from secondary ones; discharge and behavior saprolegnoid, occasionally achlyoid; primary spore cysts 10-12  $\mu\text{m}$  in diameter. Gemmae, when present, sparse or abundant; spherical, pyriform, obpyriform, cylindrical, clavate, or irregular; terminal or intercalary, single or catenulate. Oogonia lateral, terminal or intercalary and single or catenulate; sometimes found in empty sporangia; catenulate ones variable in frequency and degree of disarticulation; spherical, subspherical, ovoid, obpyriform, napiform, or cylindrical, rarely irregular; (40-) 50-65 (-108)  $\mu\text{m}$  in diameter. Oogonial wall unpitted, or with a few inconspicuous pits; smooth, but wall substance sometimes protruding through the pits giving a pseudopapillate aspect. Oogonial stalks ( $1/2$  -) 1-2 ( $-3^{1/2}$ ) times the diameter of the oogonium, in length; stout, straight, curved, or irregular; unbranched. Oospores centric; spherical or nearly ellipsoidal; (1-) 2-8 (-14) per oogonium and usually nearly filling it; (12-) 23-28 (-35)  $\mu\text{m}$  in diameter; at germination forming a branched or unbranched hyphal system, some branches bearing small, terminal sporangia. Antheridial branches declinous, infrequently androgynous; slender, sparingly branched or unbranched; persistent or evanescent. Antheridial cells simple; clavate or cylindrical, occasionally slightly irregular, rarely once-branched; persisting; laterally appressed; fertilization tubes uncommon, not persisting.

*Saprolegnia torulosa* is an exceptionally variable species, but all the isolates we have examined express two characteristics, namely catenulate oogonia (which may or may not disarticulate; Fig. 97 A), and predominantly declinuous antheridial branches (Fig. 97 A, B) of varying densities. In a few instances watermolds identified as *S. torulosa* have been described as having oogonia positioned in terminal, discharged, primary sporangia (Fig. 97 D). This feature, however, is also quite characteristic of *S. ferax*. In his description of *S. monilifera* (= *torulosa*) from Japan, Nagai (1931:8) wrote that an antheridium-like “body” formed from the basal septum of the oogonium but was not involved in fertilization. Prominent protrusions or extensions of the septum into the oogonial cavity are commonly encountered in species of *Saprolegnia*, but are of no consequence taxonomically.

The lengthy synonymy suggests that *Saprolegnia torulosa* has had a less than tranquil taxonomic history. For the most part, contradictory reports on the morphology of the species seem to have centered on the abundance of antheridial hyphae in isolates, and whether or not the catenulate oogonia disarticulated. Seymour (1970) first directed attention to the uncertain status principally of three species -- *S. torulosa*, *Isoachlya* (= *Saprolegnia*) *toruloides*, and *S. monilifera* de Bary. He was unable to resolve the taxonomy of these species, and considered them imperfectly known. From a comparative study of a number of specimens from Iceland, Howard and his collaborators (1970) succeeded in defining *S. torulosa* in a broad sense, and justifying a lengthy synonymy. Reed (1973:43) did not follow the nomenclature proposed by Howard and his associates. In a thesis manuscript Reed made a new combination (*I. toruloides* was the basionym): *Saprolegnia toruloides* (Kauffman and Coker). As this name has not been published it is excluded.

Howard *et al.* (1970) established experimentally that antheridial branch abundance and the tendency of oogonia to disarticulate could be modified in *Saprolegnia torulosa*. It is reasonable to suppose that the reported absence of antheridial branches in some specimens (earlier identified as *I. toruloides*, for example) was attributable to the evanescent nature of these filaments. The analysis of *Saprolegnia torulosa* by Howard *et al.* (1970) leaves no doubt that there are no sharp distinctions among the elements of the *torulosa* complex. Seymour's (1970:64) views support the disposition of taxa proposed by Howard and his associates.

In connection with a watermold isolated from Madeira Island Höhnk (1962) used the name *Cladolegnia toruloides* (Kauffman et Coker) Johannes. This is an error since Johannes (1955a:212) included *Isoachlya toruloides* with *Saprolegnia torulosa*, and not as a new combination in his genus *Cladolegnia*.

CONFIRMED RECORDS: -- BRITISH ISLES: E. M. Brown (1938:166); R. A. Couch (1951:115, pls. 22-24); O'Sullivan (1965:323, 343, figs. II-50-60, II-62-74). CANADA: Maestres (1977:147, figs. 14-20). CZECHOSLOVAKIA: Cejp (1934:88; 1957: fig. 119, 1; 1959a:203, 207, figs. 72-75). DENMARK: A. Lund (1934:17, 18, figs. 6a-e). FRANCE: Lechmere (1911a:169-174, 175, figs. 1-19 (p. 170), 1-16 (p. 172); 1911b: fig. 1); Moreau and

Moreau (*loc. cit.*). GERMANY: de Bary (*loc. cit.*; 1883:56; 1888:618, 629, pl. 9, fig. 6); Bock (1956:33); A. Fischer (1892:340, 342); Götze (1918: fig. 10); Richter (1937:241). ICELAND: Howard *et al.* (1970:73, figs. 29-33). INDIA: Chaudhuri and Banerjee (1942:224, pl. 3); Chaudhuri and Kochhar (1935:140, pl. 6, figs. 1-9); Chaudhuri *et al.* (1947:27, 29, figs. 8, 9); Dayal (1958:50, pl. 3); Khulbe (1977:18, 19, pl. 6, figs. 8-11); 1980c:78, 79). JAPAN: Kobayashi and Ôkubo (1954:567, fig. 8); Nagai (1931:8, pl. 2, figs. 16-26). LATVIA: Apinis (1929a:223). MIDDLE EUROPE: Migula (1903:66). PEOPLE'S REPUBLIC OF CHINA: Shen and Siang (1948:194). POLAND: Staniak (1971:363); Stpiczyńska (1962:112, fig. 12). RUMANIA: Toma (1971:11, pls. 2, 9). SWITZERLAND: Maurizio (*loc. cit.*); Tiesenhausen (1912:283). UNITED STATES: Beneke (1948b:51); R. L. Butler (1975: figs. 29-32); Coker (1923:82, 88, pls. 21, 25; pl. 50, figs. 6-12); Graff (1928:172); Humphrey (1893:107, pl. 16, figs. 46-49); T. W. Johnson (1956a:189); Kauffman and Coker (*in* Kauffman, *loc. cit.*); Milanez (1966:109, pl. 12, figs. a-c); Milanez and Beneke (1968:19, pl. 2, figs. 8, 9); Reed (1973:43: fig. 17); Rose (1932:31, pl. 2, figs. 15, 16); Wolf (1944:23, 25, pl. 1, fig. 8). USSR: Domashova (1971:192) (?); Milovtsova (1935a:32, pl. 2, fig. E<sub>1</sub>); Morochkovs'kiï *et al.* (1967:133, figs. 118, 119); Naumov (1954:68); Shkorbatov (1927:75, 76).

RECORDED COLLECTIONS: -- BRITISH ISLES: Cook and Morgan (1934); Dick (1962, 1963, 1966); Dick and Newby (1961); Hartog (1895); Hodkinson and Dalton (1973); Hunter (1975); Perrott (1960); R. E. Roberts (1963). CANADA: Dick (1971c); Maestres and Nolan (1978). CZECHOSLOVAKIA: Cejp (1931). DENMARK: Obel (1910a, b). FINLAND: Häyrén (1902-03, 1956). FRANCE: Volkonsky (1934). GERMANY: Höhnk (1933, 1935a, 1956a); Stoll (1936). INDIA: Dayal (1959); Dayal and Tandon (1962, 1963); Dayal and Thakur Ji (1965, 1966); Khulbe (1980a); Khulbe and Bhargava (1977); Thakur Ji (1967). JAPAN: S. Ito and Nagai (1931); Suzuki (1961f). LAPLAND: Gäumann (1918). MADEIRA: Höhnk (1962). NETHERLANDS: Beverwijk (1948). POLAND: Dominik (1936); Stpiczyńska-Tober (1965); Żebrowska (1976a). SOUTH AMERICA: Upadhyay (1967). UNITED STATES: Coker and Braxton (1926); V. D. Matthews (1927); K. B. Raper (1928); Scott (1960b); Slifkin (1964); Sparrow (1952b); A. W. Ziegler (1958b). USSR: Kirgizbaeva *et al.* (1975); Logvinenko (1970, 1971); Logvinenko and Meshcheryakova (1971); Mil'ko and Belyakova (1968).

SPECIMENS EXAMINED: -- ICELAND (16), TWJ, RLS.

*Saprolegnia diclina* Humphrey

Trans. Amer. Phil. Soc. (N.S.) 17:109, pl. 17, figs. 50-53. 1893

(Figure 99)

*Saprolegnia dioica* de Bary, Bot. Zeitung (Berlin) 41:56. 1883.

*Saprolegnia crustosa* var. I. Maurizio, Z. Fischerei und deren Hilfswiss., Mitt. Deutsch. Fischerei-Vereins 7:52.1899.

*Saprolegnia crustosa* var. II. Maurizio *ibid.*, p. 53. 1899.

*Saprolegnia crustosa* var. III Maurizio, *ibid.*, p. 54. 1899.

*Saprolegnia stagnalis* Tiesenhausen, Arch. Hydrobiol. Planktonk. 7:276. 1912.

- Saprolegnia delica* Coker, Saprolegniaceae, p. 30, pls. 4 (lower photo), 5, 6, 14 (lower photo). 1923.
- Saprolegnia parasitica sensu* Coker, *ibid.*, p. 57, pl. 18. 1923.
- Isoachlya parasitica* (Coker) Nagai, J. Fac. Agric. Hokkaido Imp. Univ. 32:12, pl. 2, figs. 27-34. 1931.
- Saprolegnia parasitica* Coker *emend.* Kanouse, Mycologia 24:447, pls. 12, 13. 1932.
- Saprolegnia pseudocrustosa* Lund, Kongel. Danske Vidensk. Selsk. Naturvidensk. Math. Afh. 9 6:9, fig. 2. 1934.
- Isoachlya anisospora* var. *indica* Saksena and Bhargava, Curr. Sci. 13:79, figs. 1, 2. 1944.
- Cladolegnia stagnalis* (Tiesenhausen) Johannes, Feddes Repert. Spec. Nov. Regni Veg., p. 212. 1955.
- Saprolegnia diclina* var. *numerosa* Cejp, Oomycetes I, Flora ČSR, Ser. B, Part 2, p. 219. 1959.
- Saprolegnia diclina* var. *minima* Cejp, *ibid.*, p. 219, fig. 78h. 1959.
- Saprolegnia crustosa* var. *similis* Cejp, *ibid.*, p. 224. 1959.
- Saprolegnia crustosa* var. *punctulata* Cejp, *ibid.*, p. 225. 1959.
- Saprolegnia shikotsuensis* Hatai, Egusa, and Awakura, Fish Pathol. 12:105, figs. 1-9. 1977.

Monoecious. Mycelium sparingly to moderately branched. Sporangia cylindrical, clavate, fusiform, or irregular; straight or slightly curved, sometimes faintly sigmoid; renewed internally, or in cymose or basipetalous succession; 75-1050 × 20-80 μm. Spores dimorphic; discharge and behavior saprolegnoid, or very rarely aplanoid; encysted spores 9-12 μm in diameter. Gemmae, when present, pyriform, obpyriform, cylindrical, clavate, or irregular; terminal or intercalary, single or catenulate. Oogonia sparse to moderately abundant, and often appearing in culture only after prolonged incubation; terminal, lateral, or intercalary, single or catenulate; spherical, subspherical, obpyriform, napiform, or slightly irregular, dolioform or subspherical when intercalary; spherical ones (30-) 50-70 (-130) μm in diameter, subspherical or obpyriform ones 54-146 × 18-72 μm. Oogonial wall unpitted, pitted, or with pits only under the region of attachment of antheridial cells; pits sometimes inconspicuous; smooth. Oogonial stalks ( $\frac{1}{3}$  -) 1-1 $\frac{1}{2}$  (-3) times the diameter of the oogonium, in length; stout, straight or curved; unbranched or once-branched. Oospores centric or subcentric, both types occurring in some oogonia; spherical, (1-) 8-16 (>100) per oogonium, and may or may not fill it; (12-) 18-26 (-44) μm in diameter; at germination forming a slender, irregular germ tube terminating in a small, cylindrical or clavate sporangium. Antheridial branches diclinous, rarely monoclinal or androgynous; slender, irregular, sparingly branched or unbranched; frequently, occasionally, or infrequently wrapping about or closely applied to the oogonium; persisting or deliquescing. Antheridial cells simple, very rarely compound; tubular or clavate, often irregular, sometimes branched or lobed; persisting or deliquescing; laterally appressed, very rarely apically attached to the oogonial wall; fertilization tubes, when present, persisting or deliquescing.

The predominance of diclinous antheridial branches (Fig. 99 A-C) -- these are often very abundant and may indeed enwrap oogonia partially or fully (Fig. 99 G) -- sets *Saprolegnia diclina* apart readily from all species in the genus except *S. australis* (see discussion, this species). In the general configuration of its oogonia, *S. diclina* certainly resembles *S. ferax*, but in the latter, the antheridial branches (when present) are predominantly monoclinal or androgynous, and are not as prominently displayed. Like *S. ferax*, *S. diclina* produces both centric and subcentric oospores, and the two types may occur in the same oogonia. Milanez (1968:100) observed subcentric oospores in some oogonia of his specimens of Humphrey's species.

A characteristic of *Saprolegnia diclina* not amply emphasized in previous treatments of the species is its proclivity toward latent development of the oogonia. Gross cultures hastily examined -- and as hastily discarded as nonsexual specimens -- may indeed account for the apparent absence of this very common and widely distributed species in accounts of surveys and floristic studies. Nonsexual cultures of *Saprolegnia* should be kept for at least 4-5 weeks, and preferably incubated at 10-18 °C (Coker, 1923; Kanouse, 1932; O'Bier, 1960; Willoughby, 1971a).

It was Humphrey (1893) who first recognized that de Bary's *Saprolegnia dioica* was a distinct species but one with a preempted name. Pringsheim (1858) had used the epithet *dioica* for a watermold parasitized by a chytridiaceous fungus. The name *dioica* also appears as a new name in a publication by Schröter and Schneider (1870) but without description or illustrations (*nomen nudum*). Humphrey renamed de Bary's species *diclina* in reference to the preponderance of diclinous antheridial branches.

A thorough analysis and circumscription of *Saprolegnia diclina* appears in Seymour's (1970:45-46) monograph and the justification for the taxonomic changes he proposed is adequate and need not be repeated here. Additionally, Seymour (1970:47) commented on the similarities between *S. diclina* and *S. parasitica* (as Kanouse had defined this taxon). He emphasized that these two species shared four rather prominent characteristics, and suggested that the relationship between *S. diclina* and *S. parasitica* was not fully understood. Evidence accumulated since Seymour's monograph -- notably in accounts by Neish (1976, 1977) and Willoughby (1971a, 1978) and our own study of specimens -- convinces us that *S. parasitica* (*sensu* Kanouse, not Coker) no longer can be retained as a species separate from *S. diclina*.

Neish (1976, 1977) divided 20 isolates of *Saprolegnia* (from fish) into four categories based on sporangium and oogonium production at 10°, 14°, and 21° C. Isolates in one category produced oogonia consistently, and were assignable, he concluded, to the *S. diclina*-*S. parasitica* complex. Included in a second group (his category D) were those isolates that were sporadic in their production of the sexual apparatus, but oogonia could be induced by incubating the cultures at 10° C for four months. Neish emphasized that these isolates in category D closely resembled saprolegnians recovered from English salmonids by Willoughby (1968b, 1969, 1971a). Further, Neish commented that the majority of his isolates could not be identified precisely. He found that values for the DNA base composition (buoyant density

determinations) of isolates was not useful in separating the species that had been recognized classically on morphological grounds.

In evaluating his observations and experimental data, Neish (1976) defined the *Saprolegnia diclina*-*S. parasitica* complex as one consisting of specimens with predominantly diclinous antheridial branches, and thin-walled, unpitted or inconspicuously pitted oogonia. He proposed (Neish, 1976:118) that the name *parasitica* be discarded as a *nomen ambiguum*, and a much-broadened interpretation of *S. diclina* be adopted.

Detailed morphological analyses by Willoughby (1968b, 1969 1970, 1971a), Willoughby and Pickering (1977), and Pickering and Willoughby (1977) of water molds associated with fish led to a decision that isolates could be grouped into types. Willoughby (1978) recognized three types of *Saprolegnia diclina* (parasitic forms from salmonids and perch, and strictly saprophytic ones) based upon the ratio of oogonium length to diameter. He concluded that it was impossible to maintain a two-species concept consisting of *S. diclina* and *S. parasitica*, and conserved the former name. We agree with his decision and are herewith formally reducing *S. parasitica* to synonymy.

In his study on salmonid fish saprolegnians, Willoughby (1978) called attention to the fact that some isolates of the *diclina-parasitica* complex produced very extensive antheridial branches that closely invested the oogonia to which they were attached. Much earlier, Tiesenhausen (1912) had referred to profuse antheridial branch development, and illustrated clearly what Willoughby (1978: fig. 2e-h) was to refer to as a "bird nest" condition. We find the heavily enwrapped oogonia to be produced (Fig. 99 F, G) in some specimens of *S. diclina* recovered from water and mud samples. Willoughby also discovered that the oospheres did not mature consistently. This condition recalls immediately the infrequency of mature oospores in *S. australis*, and strengthens the view that R. F. Elliott's (1968) species might prove to be only a variant of *S. diclina*.

In sum, it may be stated that a broadened, flexible interpretation of *Saprolegnia diclina* emerges from an analysis of all the data at hand. Specimens isolated from fish may show profuse antheridial development, but sparse development is characteristic of other specimens. The same may be said for "saprophytic" (saprotrophic) forms of the species, as is shown by Willoughby's (1978: fig. 4) *S. diclina* Type 3, and our own isolates from water (Fig. 99 G). With respect to oospore size -- Willoughby (1978) analyzed this character thoroughly in his specimens -- there is noticeable overlap and intergrading among isolates. It may be recalled, however, that the oospores of *S. parasitica sensu* Kanouse (1932) were smaller than those of *S. diclina (sensu* Seymour, 1970). This distinction fades when additional isolates are examined (*see* Willoughby, 1978, fig. 5).

There remains the troublesome matter of a name to be applied to the nonsexual specimens of *Saprolegnia* associated with fish. To these, of course, Coker (1923) had applied the name *parasitica*, and this subsequently was widely adopted even after Kanouse (*loc. cit.*) had discovered the sexual stage of individuals she chose to identify with Coker's species. There is no way to be certain that the water molds studied by Kanouse were indeed identical to Coker's specimens. In the final analysis, it appears to

us best to identify any nonoogonial isolates of *Saprolegnia* from fish simply as *Saprolegnia* sp., and all accounts of nonsexual *S. parasitica* referred to in the literature subsequent to Kanouse's redefinition of the taxon should be so treated.

The affinities of Pieters' (1915c) ill-defined *Saprolegnia kauffmaniana* to other taxa in the genus were analyzed amply by Seymour (1970); he retained Pieters' species in the category of imperfectly known species. We now see no justification for continuing to recognize *S. kauffmaniana* since its critical characters still remain unknown. Although Seymour (1970:39) included *S. parasitica* var. *kochhari* Chaudhuri (Chaudhuri and Kochhar, 1935:139, pl. 5, figs. 1-6) as a synonym of *S. parasitica*, the variety has no status (since it is known from the asexual stage only), and the name may be excluded from the genus. The material described by Chaudhuri properly could only be identified as *Saprolegnia* sp.

*Saprolegnia shikotsuensis* (Hatai, Egusa, and Awakura, *loc. cit.*), the most recent addition to the genus, is but one of many forms of *S. diclina*. With respect to the usual characteristics that are taxonomically critical (oogonial wall pitting, antheridial branch origin, oospore structure, and sizes of the oogonia and oospores), *S. shikotsuensis* does not differ from either *S. diclina* or *S. australis*. Like *S. diclina* (and the "*S. parasitica* forms" of this species), the Japanese species exhibits latent production of oogonia. Hatai and his associates report their species to have predominantly 1-8 oospores per oogonium - in *S. diclina* the usual number is larger - but if the illustrations accompanying the description of *S. shikotsuensis* are of the "typical" morphology, the oogonia are in fact generally provided with more than this modest number of oospores. Some of the photographs of the sexual apparatus of *S. shikotsuensis* are indistinguishable from illustrations of Willoughby's (1978) *S. diclina* type 3. A subculture of the type (deposited at Sankyo, Ltd., Tokyo) has failed to produce oogonia and antheridia even with prolonged incubation. With the merging of *S. shikotsuensis* into *S. diclina*, the host range of the latter may be extended to include kokanee salmon, *Oncorhynchus nerka* var. *adonis* (see Chapter 29).

CONFIRMED RECORDS: -- BELGIUM: Nolard-Tintigner (1973:25, 29, 30, figs. 11-13; 1974:767, fig. 2). BRITISH ISLES: E. M. Brown (1938:164, 166, figs. 2.1-2.3); R. A. Couch (1951:123, pls. 25-31); Forbes (1935a:226); J. L. Harrison and Jones (1971: fig. 5); F. E. V. Smith (1923:64); Willoughby (1968b:872, figs. 1-5; 1977: 133 *et seq.*, figs. 1, 2; 1978: figs. 1-4). CANADA: Chong (1973: 19); Lester (1974:196); McKay (1967: pls. 2, 3); Maestres (1977:145, 146, 148, figs. 27, 58); C. L. Moore (1908-09:222, fig. 3); Neish (1976: pls. 3, 5, 7; pl. 8, figs. 4-6; 1977: pl. 2) CZECHOSLOVAKIA: Cejp (1931:97; 1934:186, pl. 1, figs. 1-4; *loc. cit.*; 1957: fig. 118, 4; 1959a:217, 219, 220, 223-225, figs. 78 a-g, 79-83). DENMARK: A. Lund (*loc. cit.*; 1934:10, 11, 21, figs. 3a, 3b, 8); Petersen (1909a: fig. 1c; 1910: fig. 1c). FINLAND: Häyrén (1942: figs. 1, 2; 1954: figs. 1-27). FRANCE: Aleem *et al.* (1953:45-47, figs. 1-16); Moreau and Moreau (1938:231, pl. 2, pl. 6, figs. 8, 9; 1948:227). GERMANY: de Bary (*loc. cit.*; 1888:619, pl. 10, figs. 12, 13); Bock (1956:31); A. Fischer (1892:335); Minden (1912:512, fig. 1e); Richter (1937:235, 236, 239); Zopf (1890:298). ICELAND: Howard *et al.* (1970: fig. 35). INDIA: Chaudhuri and Kochhar (1935:139);

Chaudhuri *et al.* (1947:25, 26, 30, figs. 6, 7); Dayal (1958:49, pl. 1; 1959); Khulbe (1977:17, 19-21, 24, pl. 1, figs. 3-7; pl. 6, figs. 4-7; pl. 7, figs. 1-6, 12-15; pl. 9, figs. 4, 5; pl. 10, figs. 1-3; 1980c: 78, 79, 80, figs. 3, 4); Prabhujii (1979:76, pl. 8, figs. 14-18); Saksena and Bhargava (*loc. cit.*); Shah *et al.* (1977:143); G. C. Srivastava (1967a:282, pl. 1, figs. 1-3); R. C. Srivastava (1976: pl. 2, fig. A; pl. 5, fig. A; pl. 6, fig. A; pl. 7, fig. B); Thakur Ji (1970:180, figs. 1-9). IRAQ: Ismail *et al.* (1979:87, 90, figs. 8, 9, 12-15); Muhsin (1977:35, 40, figs. A-C, A-D). JAPAN: Hatai and Egusa (1977:188, figs. 1-4); Hatai, Egusa, and Awagura (*loc. cit.*); Hoshina *et al.* (1960:61, 70, figs. 2, 6); S. Ito (1936:74, 75, figs. 32.2, 32.3b, 32.4, 32.7-32.11); Kobayasi and Ôkubo (1954:569, fig. 10); Nagai (*loc. cit.*; 1931:4, pl. 1, figs. 12-21); Nagai and Takahashi (1962: figs. 1-19); Okane (1977:5, figs. R-T); Ookubo (1954:53, 54, figs. 42, 43); Shibuya (1959:146, fig. 1). LATVIA: Apinis (1929a:210, 221). MIDDLE EUROPE: Migula (1903:65). NEPAL: S. C. Singh (1968a:13). PEOPLE'S REPUBLIC OF CHINA: Er (1973:37); Ou (1940: 434, fig. 6); Shen and Siang (1948:192). POLAND: Stpiczyńska (1962:99, 100, 101, figs. 2, 3); Stpiczyńska-Tober (1965:68); Szwanke (1938:4, 5, 9, pl. 1, figs. 1-6; pl. 3, figs. 6, 7); Zaborowska (1965:39, fig. 1). PORTUGAL: Vasconcellos and d'Oliveira (1947: 2 unnumbered figs.). REPUBLIC OF CHINA: Chiou and Chang (1976:49, pl. 6, figs. 1-5); Chiou *et al.* (1975:168, pl. 2, fig. 23). RUMANIA: Moruzi and Toma (1968: pl. 1, figs. 1-4; pl. 4, fig. 30); Toma (1969:215, pl. 1). SOUTH AMERICA: Beneke and Rogers (1970:59); Milanez (1968:102, figs. 7, 8; 1970: 32); A. L. Rogers *et al.* (1970:103). SWITZERLAND: Maurizio (*loc. cit.*); Tiesenhausen (*loc. cit.*; 1912:273 *et seq.*, figs. 4, 5). UNITED STATES Beneke (1948b:25, 26, 41); Bretsnyder (1943:9, 10); Coker (*loc. cit.*; 1923:26, 57, pls. 3, 4, 14, 18); Graff (1928:170); J. V. Harvey (1942:19); Hubschman and Schmitt (1969: fig. 1); Humphrey (*loc. cit.*); Hutchison (1940:6, fig. 6); T. W. Johnson (1950b:398, 399; 1956a: 185, 186); Kanouse (*loc. cit.*); Milanez (1966:100, 107); Milanez and Beneke (1966:175, pls. 1, 2); O'Bier (1960:21, 26, pl. 1, figs. f-i; pl. 2; pl. 4, figs a-g); Rose (1932:21, 22, pl. 1, figs. 1-4); Rossy-Valderrama (1955:39, pl. 7, figs. 1-7); Rucker (1944: figs. 1-5, 7, 8, 10-13, 15, 17-19, 21); Seymour (1970:43, figs. 71-77); Shipman (1977: fig. 12); Slifkin (1967a: figs. 1-26, 28, 29, 31-70); Sorenson (1962: pl. 6, figs. A, B; pl. 8, figs. A, D); Szanislo (1965: fig. 1); W. N. Tiffney (1936:19); Wolf (1944:25, pl. 1, figs. 5, 6); A. W. Ziegler (1948b: pl. 2, figs. 4-6; 1952:7, pl. 2, figs. 1,2). USSR: Domashova (1971:191, 192, fig. 5); Dudka and Florinskaya (1971:433, fig. 3); Dudka and Logvinenko (1968: figs. 1.1, 1.2); Florinskaya (1969:107, 112, 113, figs. 1, 2, 7, 8; 1971: fig. 3); Milovtsova (1935:33, pl. 2-a, fig. M); Morochkovs'kiï *et al.* (1967:129-131, figs. 114-116); Shkorbatov (1927:75). WEST INDIES: Volz and Beneke (1972:2).

RECORDED COLLECTIONS (this section contains records of *S. parasitica sensu* Coker and are therefore unconfirmed and questionable): -- AFRICA: El-Hissy (1974). BRITISH ISLES: M. E. Brown (1968); M. E. Brown and Collins (1966); Cook and Forbes (1933); Cook and Morgan (1934); Dick (1963, 1964, 1966); Dick and Newby (1961); Forbes (1935b); B. R. Green and Dick (1972); Hallett and Dick (1976); Hunter (1975); H. Meier and Webster (1954); Newton (1971); O'Sullivan (1965); Perrott (1960); Pickering *et al.* (1979); Pickering and Willoughby (1977); R. H. Richards and Pickering (1978); R. E. Roberts (1963); Stuart and Fuller (1968a); Trow (1895); Willoughby (1969, 1970, 1971a, 1972); Willoughby and Collins (1966); Willoughby and Pickering (1977).

CANADA: Chong (1973); Dick (1970, 1971c); Maestres and Nolan (1978); Neish and Green (1976). CZECHOSLOVAKIA: Cejp (1931). DENMARK: A. Lund. (1978); Obel (1910a, b). FINLAND: Häyrén (1902-03, 1956) FRANCE: Aleem *et al.* (1953); Rioux and Achard (1956); Volkonsky (1934.). GERMANY: Höhnk (1935a, 1953a, 1956a); Schlösser (1929); Stoll (1936). ICELAND: T. W. Johnson (1974b). INDIA: Bhargava *et al.* (1971); Chaudhuri *et al.* (1947); Dayal (1959); Dayal and Thakur Ji (1965, 1966); Gopalakrishnan (1964, 1965); Jhingran (1966); Khulbe (1980a); Khulbe and Bhargava (1977); Mer *et al.* (1980); Mekrani (1980); Prabhuji and Srivastava (1977); G. C. Srivastava (1967b); G. C. Srivastava and Srivastava (1976b; 1977e, f); R. C. Srivastava and G. C. Srivastava (1978a); Thakur Ji (1967). IRAQ: Al-Saadi *et al.* (1979). JAPAN: Arasaki *et al.* (1958a); Egusa (1963, 1965); Egusa and Nishikawa (1965); Hoshina and Ookubo (1956); S. Ito and Nagai (1931); Miyazaki *et al.* (1977); Nagai and Takahashi (1962); Okane (1967, 1978); Suzuki (1960c, d, h, g; 1961a, b, d, f, h-j; 1962a, b, d); Suzuki and Hatakeyama (1960, 1961); Suzuki and Nimura (1960, 1961a, 1962); Suzuki and Tatsuno (1964; 1965,a, b). LAPLAND: Gäumann (1918). NETHERLANDS: Boedijn (1923). PHILIPPINES: Dogma (1975). POLAND: Staniak (1971). PORTUGAL: Camara *et al.* (1936). RUMANIA: Toma (1971). SOUTH AMERICA: Beneke and Rogers (1962). UNITED STATES: Allison (1950); Atkinson (1897); Bangham (1933); Bangham and Hunter (1939); Beneke and Schmitt (1961); Clausz (1970, 1974); W. B. Cooke and Bartsch (1959, 1960); Coker and Braxton (1926); Crane and Vermillion (1966); Fox and Wolf (1977a); Graff (1928); J. V. Harvey (1952); Hoffman (1949); G. C. Hughes (1959, 1962); Kauffman (1915); Klich (1980); Kuehn (1960); Lennon (1955); McLain (1951); Martin (1968a); V. D. Matthews (1935); Mohr (1901); Monsma (1936); Paterson (1967); Pieters (1915b); Poitras (1955); Powell *et al.* (1972); Ristanović *et al.* (1973); Rooney and McKnight (1972); Rossy-Valderrama (1956); Salvin (1941); Schmitt and Beneke (1962); Scott (1960b); Scott and O'Bier (1962); Scott *et al.* (1963); Shipman (1979); Slifkin (1964, 1967a); Sorenson (1964); Sparrow (1952b); S. G. Taylor and Bailey (1979); TeStrake (1958, 1959); W. N. Tiffney 1939); W. N. Tiffney and Wolf (1937); Vishniac and Nigrelli (1957); M. W. Ward (1939); Wolf and Wolf (1941); Wu (1979); A. W. Ziegler (1948b, 1958b). USSR: Domashova (1974b); Dudka (1964a, b; 1965; 1966); Érgashev and Kirgizbaeva (1978); Florinskaya (1971); Kirgizbaeva (1976); Kirgizbaeva *et al.* (1975); Logvinenko (1970, 1971); Logvinenko and Meshcheryakova (1971); Mikheeva (1969); Mil'ko (1965); Mil'ko and Belyakova (1968); Mil'ko and Dudka (1968); Mil'ko and Zakharova (1976); Naumova (1955: 136, fig. 4)(?); Osipyan *et al.* (1974); Suchevyanu (1966). YUGOSLAVIA: Ristanović (1970b, 1973).

SPECIMENS EXAMINED: -- ICELAND (11), NORWAY (7), SWEDEN (38), TWJ. UNITED STATES (231), TWJ, RLS. Centraalbureau (3).

*Saprolegnia litoralis* Coker  
Saprolegniaceae, p. 54, pls. 15, 16. 1923  
(Figure 95 G, H; 96 A, B)

Monoecious. Hyphae stout, sparingly branched; in some specimens, hypha subtending terminal oogonia may be conspicuously irregular and provided with short,

cylindrical or papilliform lateral evaginations. Sporangia sparse; cylindrical, fusiform, or irregular, straight, bent or curved; sometimes branched or lobed, rarely subspherical or hemispherical; renewed internally; cylindrical or fusiform ones 80-270 x 16-35  $\mu\text{m}$ . Spores dimorphic; discharge and behavior saprolegnoid; primary spore cysts 10-12  $\mu\text{m}$  in diameter. Gemmae abundant; spherical, obpyriform, or cylindrical; terminal or intercalary; single or catenulate. Oogonia terminal, occasionally lateral, rarely intercalary; spherical, obpyriform, or napiform, dolioform when intercalary, terminal ones sometimes apiculate; (42-) 51-57 (-80)  $\mu\text{m}$  in diameter. Oogonial wall sparsely but conspicuously pitted; smooth. Oogonial stalks ( $1/4$ -) 1-1 $1/2$  (-3) times the diameter of the oogonium, in length; stout; straight, curved, or irregular; unbranched or sparingly branched; occasionally with 4 to a few cylindrical or papilliform lateral protrusions. Oospores centric; spherical or ellipsoidal; (1-) 2-6 (-24) per oogonium, and usually filling it, or nearly so; (18-) 30-36 (-58)  $\mu\text{m}$  in diameter; at germination producing a slender hypha which may or may not bear a terminal sporangium. Antheridial branches androgynous or monoclinal, very rarely dichlinal; stout, slightly irregular, unbranched or sparingly branched; some specimens producing gnarled, twisted branches provided with one or more short, papilliform lateral protrusions; persisting. Antheridial cells simple, tubular or tubular and slightly irregular, unbranched; persisting; laterally appressed; fertilization tubes rarely observed, and evidently not persisting.

The predominance of androgynous antheridial branches arising from just below the oogonium (Fig. 95 G, H) and the occasional flaring of the hypha subtending terminal oogonia (Fig. 96 A, B) constitute the chief features by which *Saprolegnia litoralis* is recognized. Some specimens have a branched cluster of antheridial filaments below the oogonium (Coker, *ibid.*, pl. 16, figs. 3, 7); others form conspicuously gnarled and irregular hyphae immediately below the oogonium (Fig. 96 B).

Neither Coker (*loc. cit.*) nor Seymour (1970) gave a size range for the sporangia of *S. litoralis*. The measurements in the foregoing description are taken from a single isolate from Norwegian bog soil. Coker (*loc. cit.*) described some of the terminal oogonia as apiculate cells; we have not seen such structures in any of our collections of the species.

The lateral, short-stalked oogonia of *Saprolegnia litoralis* resemble in their general aspect those of *S. uliginosa* (compare Fig. 95 F, G). In the latter species, however, the antheridial branches are predominantly monoclinal (Fig. 95 D, F) and the oogonial wall is pitted only under the region of attachment of antheridial cells. Although some oogonia of *S. ferax* are equipped with androgynous antheridial branches these are not as abundant as in *S. litoralis*, and are seldom as extensively branched. Other characteristics of *S. ferax* also distinguish it readily from Coker's species.

Cejp (1959a:238) considered (through apparently without firm assurance) that *Saprolegnia spiralis* Cornu *sensu* Minden, and *S. spiralis* var. *charkoviensis* Shkorbatov were synonymous with *S. litoralis*. *Saprolegnia spiralis* is properly excluded from the valid taxa of the genus.

CONFIRMED RECORDS: -- AFRICA: El-Hissy (1974: pl. 2, figs. b, c). BRITISH ISLES: Dick (1969b: pl. 1, fig. 1: pl. 2, fig. 2) (collection site not recorded). CZECHOSLOVAKIA: Cejp (1959a:238, fig. 87). DENMARK: A. Lund (1934:13, fig. 3c-e). FRANCE: Moreau and Moreau (1938:229, pl. 1, figs. 29-34; pl. 6, figs. 6, 7). GERMANY: Richter (1937:237, fig. 1). GREENLAND: Kobayasi *et al.* (1971:22, fig. 11). ICELAND: Howard *et al.* (1970: fig. 38). INDIA: Dayal and Thakur Ji (1965:317, pls. 1, 2). JAPAN: Hoshina *et al.* (1958:36, figs. 1, 2). LATVIA: Apinis (1929a:216, text fig. 2). POLAND: Stpiczyńska (1962:103, fig. 5); Zaborowska (1965: fig. 3). UNITED STATES: Beneke (1948b:44); R. L. Butler (1975: figs. 45-48); Coker (*loc. cit.*); Hutchison (1940:7, fig. 7); A. W. Ziegler (1948b: pl. 2, fig. 3; 1952: 7, pl. 2, figs. 5, 6). USSR: Dudka and Logvinenko (1968: fig. 2.2).

RECORDED COLLECTIONS: -- AFRICA: Fajola *et al.* (1978). BRITISH ISLES: Dick (1962, 1963, 1966); Dick and Newby (1961); Perrott (1960); R. E. Roberts (1963). CANADA: Dick (1971c). HUNGARY: Bérczi (1940a: 87, fig. 45; 1940b)(?). INDIA: Dayal and Thakur Ji (1966); Thakur Ji (1967). JAPAN: Suzuki and Hatakeyama (1961). NEW ZEALAND: Karling (1966f). POLAND: Stpiczyńska-Tober (1965). SOUTH AMERICA: Upadhyay (1967). UNITED STATES: Coker (1927); Coker and Braxton (1926); Fox and Wolf (1977a); G. C. Hughes (1959, 1962); T. W. Johnson (1956a); V. D. Matthews (1927, 1935); C. E. Miller (1965); Poitras (1955); Sparrow (1952b); M. W. Ward (1939); A. W. Ziegler (1958b). USSR: Logvinenko and Meshcheryakova (1971); Mil'ko and Zakharova (1976).

SPECIMENS EXAMINED: -- ICELAND (1), NORWAY (1), SWEDEN (2), TWJ. UNITED STATES (19), TWJ, RLS. Centraalbureau (1), CMI (1).

*Saprolegnia terrestris* Cookson ex Seymour  
Nova Hedwigia (Beiheft) 19:37, figs. 56-64. 1970  
(Figure 96 C-F)

*Saprolegnia terrestris* Cookson, Proc. Royal Soc. Victoria (N.S.) 49:235, pl. 11; figs. 1,2. 1937.

Monoecious. Hyphae slender, sparingly branched. Sporangia fusiform, pyriform, obpyriform, or clavate, frequently spherical or nearly so, often irregular and contorted; renewed internally, by cymose branching, or in basipetalous succession; 60-400 x 16-48  $\mu\text{m}$ . Spores dimorphic; discharge and behavior saprolegnoid; primary spore cysts 6-11  $\mu\text{m}$  in diameter. Gemmae, when present, fusiform or obpyriform, infrequently conspicuously irregular or branched; terminal or intercalary. Oogonia lateral or terminal, infrequently intercalary; spherical or obpyriform, sometimes oval or apiculate, infrequently dolioform; (35-) 60-65 (9l)  $\mu\text{m}$  in diameter, inclusive of papillae, if any. Oogonial wall pitted or unpitted; smooth or occasionally very sparsely papillate. Oogonial stalks ( $1/2$  -) 1-2 (-11) times the diameter of the oogonium in length; stout, straight or curved, and slightly irregular; unbranched. Oospores subcentric, rarely

centric; spherical or ellipsoidal; (1-) 2-11(-18) per oogonium, and nearly filling it; (20-) 24-32 (-41)  $\mu\text{m}$  in diameter; germination not observed. Antheridial branches androgynous and sometimes arising close to the oogonial septum, or infrequently monoclinal; stout or delicate, irregular, infrequently branched; persisting. Antheridial cells simple; generally clavate; not persisting; apically or laterally appressed; fertilization tubes sometimes present, not persisting.

Like *Saprolegnia litoralis*, *S. terrestris* commonly has androgynous antheridial branches (compare Fig. 95 H, 96 E), and the general configuration of the laterally produced sexual apparatus in both is very similar. The oospores of *S. litoralis* are generally slightly larger than those of *S. terrestris*, but the latter usually has subcentric ones while those of the former are consistently centric. In Cookson's species (*loc. cit.*) lateral oogonia prevail, but terminal ones are most frequently encountered in Coker's *S. litoralis*.

That *Saprolegnia terrestris* may be somewhat variable is borne out by the specimens recovered from Iceland soil by Howard *et al.* (1970). The oogonia in those isolates commonly were attended by three or more androgynous antheridial branches, recalling to a degree the condition in *S. glomerata*. Furthermore, the oospores were more numerous in the Iceland material (6-11 predominantly; 2-6, Cookson, *loc. cit.*), and their average diameter smaller (24  $\mu\text{m}$  as opposed to 29  $\mu\text{m}$ ) than in Cookson's specimens.

In a paper published in 1968 Elliott reported that the culture conditions in which *Saprolegnia terrestris* was grown influenced the expression of colony and oogonium size, and number of oospores. Colony age also was a determining factor in the morphological expression of Cookson's species. For example, the oogonia of *S. terrestris* were larger and had more oospores if the mycelium was grown at 25° C than at 20° C. When a large culture vessel was used colonies produced large oogonia with few oospores. Oospore structure, antheridial branch origin, and degree of branching by these filaments were not modified by culture condition manipulation (Elliott, 1968). The concentration of calcium chloride in the growth medium has an effect on certain aspects of the sexual apparatus in *S. terrestris*, according to J. Fletcher (1979c); see Chapter 20.

Bryant and Howard [1969: figs. 2-24, 26 (diagrammatic)] using the Iceland specimens recovered by Howard *et al.* (1970) concluded that meiosis in *Saprolegnia terrestris* took place in the formation of gametes and not in germination of the zygote. The same specimens also were employed by Howard and Moore [1970: figs. 1-57; 58, 59, (diagrammatic)] in an analysis of the subcellular structure of oospores. In their 1974 paper Holloway and Heath described asynchronous retraction of flagella in the primary planonts of *S. terrestris*. However, in a later paper (1977b) Holloway and Heath concluded that their specimens were probably representative of *S. ferax* rather than *S. terrestris*.

In her treatment of *Saprolegnia terrestris*, Cookson (1937:236, 237) made special mention of the presence of oospores in which a lunate series of refractive droplets was present. She concluded that these oospores were quite different from subcentric ones,

and proposed that they be called eccentric. The latter term, however, traditionally had been applied to a very different oospore type, but Cookson made no mention of this fact. The eccentric oospore described for *S. terrestris* by its author was merely one of the two possible types of subcentric refractive droplet disposition.

Although the reports of *Saprolegnia terrestris* by Bhatt and Manandhar (1971) and Shipman (1977) are accompanied by illustrations, the figures are not entirely convincing evidence that they had in fact collected Cookson's species. Thus we cannot confirm the identity of their specimens.

CONFIRMED RECORDS: -- AUSTRALIA: Cookson [*loc. cit.*; also in Seymour (*loc. cit.*)]. BRITISH ISLES: Willoughby (1974: fig. 13d). CANADA: Maestres (1977:148, 149). ICELAND: Howard *et al.* (1970:71, fig. 34). IRAQ: Ismail *et al.* (1979:87, figs. 10, 11); Muhsin (1977:39, figs. A-C). NEW ZEALAND: R. F. Elliott (1968:102, figs. 1, 4 A, B). REPUBLIC OF CHINA: Chiou *et al.* (1975:167, pl. 2, fig. 22).

RECORDED COLLECTIONS: -- BRITISH ISLES: Dick (1964, 1966). CANADA: Dick (1971c); Maestres and Nolan (1978). JAPAN: Suzuki (1961 f, h; 1962a). NEPAL: Bhatt and Manandhar (1971: 56, figs. 1-3)(?). UNITED STATES: Klich (1980); Shipman (1977: fig. 15; 1979)(?). YUGOSLAVIA: Ristanović (1973).

SPECIMENS EXAMINED: -- CANADA (1), RLS. ICELAND (3), NORWAY (1), TWJ. Centraalbureau (1); subculture of type.

*Saprolegnia unispora* (Coker and Couch) Seymour  
Nova Hedwigia (Beiheft) 19:57, figs. 130-136. 1970  
(Figure 100 I-K)

*Isoachlya unispora* Coker and Couch, in Coker, Saprolegniaceae, p. 85, pls. 22, 23. 1923.  
*Cladolegnia unispora* (Coker and Couch) Johannes, Feddes Repert. Spec. Nov. Regni Veg., p. 217. 1955.

Monoecious. Mycelium extensive; hyphae stout, sparingly branched. Sporangia clavate, fusiform, pyriform, cylindrical, or subspherical basally and attenuated apically; often slightly irregular or curved; renewed internally or in a cymose fashion, rarely sympodially; 88-317 × 21-127 μm. Spores dimorphic, or rarely monomorphic; discharge and behavior saprolegnoid, rarely dictyuoid; primary spore cysts 10-12 μm in diameter. Gemmae abundant, fusiform, pyriform, obpyriform, cylindrical, spherical, subspherical, or irregular; terminal or intercalary; single or catenulate. Oogonia lateral, occasionally terminal or sessile, rarely intercalary; frequently clustered on the hyphae or arranged in a sympodially branched glomerulus; spherical or obpyriform, occasionally subspherical, oval, or broadly clavate, very rarely angular, sometimes cylindrical (in old sporangia); (18-) 45-55 (-91) μm in diameter, inclusive of wall ornamentations. Oogonial wall pitted or unpitted; smooth or very rarely with one to a few short, inconspicuous broad papillae, or a single apiculus. Oogonial stalks ( $\frac{1}{8}$ -)  $\frac{1}{2}$  -1 $\frac{1}{4}$  (-3) times the diameter of the oogonium, in length; stout, straight or curved, sometimes slightly

irregular; unbranched, branched, or forming a glomerulus. Oospores centric or subcentric; spherical or compressed at one side, or ellipsoidal; 1-2 (-4) per oogonium, and generally not filling it; (16-) 32-38 (-43)  $\mu\text{m}$  in diameter; germination not observed. Antheridial apparatus absent.

*Saprolegnia unispora* is recognized chiefly by its short-stalked, large, generally spherical oogonia (often in glomeruli or on once-branched stalks) usually containing a single, large, centric or subcentric oospore, but having no attendant antheridial filaments. Thus, in all essential features but one -- the lack of an antheridial apparatus -- *S. unispora* is hardly distinguishable from *S. megasperma* (compare Figs. 93 H, 100 K). Nolan (1975a), in fact, theorized that *S. unispora* might represent part of an evolutionary trend from *S. megasperma* through a form of the latter possessing what were alleged to be parasitic antheridial branches.

Although *Saprolegnia unispora* shares with *S. itoana* the characteristic of a single oospore (predominantly) in each oogonium (Fig. 100 C-H), these species are unlike in two other features of taxonomic value. The oogonial stalks of *S. itoana* (formerly recognized as *S. subterranea* by Seymour, 1970) are consistently longer than those of *S. unispora*. Moreover, *S. itoana* usually forms antheridia whereas *S. unispora* is not known to do so.

Coker and Couch (Coker, *loc. cit.*, pl. 23, fig. 12) describe the oospores of *Isoachlya* (= *Saprolegnia*) *unispora* as centric, but the illustration of the "...ripe..." eggs depicts them unmistakably as subcentric. This error is repeated in Coker and Matthews (1937). In all probability the *S. unisperma* referred to by Dick (1973:138) was *S. unispora*.

CONFIRMED RECORDS: -- AUSTRALIA: Cookson (1937:241). BRITISH ISLES: R. A. Couch (1951:107, p1s. 19-21). CANADA: Maestres (1977:149, fig. 64). CZECHOSLOVAKIA: Cejp (1959a:199, fig. 70g-l). INDIA: Dayal (1958:50, pl. 2). JAPAN: Okane (1977:6, figs. W, X). REPUBLIC OF CHINA: Volz *et al.* (1974:231, fig. 8). UNITED STATES: R. L. Butler (1975: figs. 49-52); Coker and Couch (*loc. cit.*); Seymour (*loc. cit.*); A. W. Ziegler (1948b:19, pl. 2, figs. 7-11; pl. 3, fig. 1; 1952: 8, pl. 2, fig. 10). USSR: Morochkovs'kii *et al.* (1967: 134, fig. 120).

RECORDED COLLECTIONS: -- BRITISH ISLES: Apinis (1964); Cook and Morgan (1934). CANADA: Dick (1971c); Maestres and Nolan (1978). GERMANY: Höhnk (1935a; 1956a). INDIA: Dayal (1959). JAPAN: Okane (1978); Suzuki (1961f, i). NEW ZEALAND: Karling (1966f). REPUBLIC OF CHINA: Liu and Volz (1977). SOUTH AMERICA: Upadhyay (1967). UNITED STATES: G. C. Hughes (1959, 1962); T. W. Johnson (1956a); T. W. Johnson and Surratt (1955); V. D. Matthews (1935); Scott (1960b); Slifkin (1964); A. W. Ziegler (1958b). USSR: Dudka (1965, 1966); Logvinenko and Meshcheryakova (1971).

SPECIMENS EXAMINED: -- UNITED STATES (11), TWJ, RLS. Centraalbureau (2).

*Saprolegnia megasperma* Coker

Saprolegniaceae, p. 56, pl. 17. 1923  
(Figure 93 F-H)

Monoecious. Hyphae sparingly branched. Sporangia filiform, cylindrical, pyriform, or irregularly clavate; straight, curved, or irregular; renewed internally, or by cymose or sympodial branching, or in basipetalous succession; 40-432 x 10-63  $\mu\text{m}$ . Spores dimorphic, or rarely monomorphic; discharge and behavior saprolegnoid, rarely dictyocoid or aplanoid; primary spore cysts 10-13  $\mu\text{m}$  in diameter. Gemmae abundant; spherical, oval, or irregular; terminal, rarely intercalary; catenulate or single. Oogonia lateral, occasionally terminal, very rarely intercalary; occasionally glomerulate; spherical, napiform, or obpyriform, rarely (?) apiculate; (36-) 42-56 (-106)  $\mu\text{m}$  in diameter. Oogonial wall pitted or unpitted; smooth. Oogonial stalks stout; ( $1/4$ -) 1 (-4) times the diameter of the oogonium, in length; straight, curved, or irregular; unbranched or branched. Oospores subcentric, rarely centric; 1-2 (-12) per oogonium, and usually not filling it; (14-) 32-38 (-52)  $\mu\text{m}$  in diameter; germination not observed. Antheridial branches, when present, monoclinal or declinal, occasionally androgynous; slender, curved or slightly irregular, unbranched or branched; persisting. Antheridial cells simple; persisting; apically or laterally appressed; fertilization tubes usually present, not persisting.

Generally, each oogonium of *Saprolegnia megasperma* has only one large and prominent oospore. As Coker (*loc. cit.*) mentioned, the oogonia of this species occasionally are arranged racemously in clusters near the ends of hyphae. Furthermore, Seymour (1970) found the oogonia to be glomerulate at times. Both of these authors reported the monoclinal antheridial filaments to be unbranched, but in the specimen we have from Sweden, they are occasionally once-branched.

Insofar as we can determine, the only difference between *Saprolegnia megasperma* and *S. unispora* is that the former has antheridia but the latter does not. The arrangement of oogonia in *S. unispora* in a scorpioid cyme (Coker, 1923: pl. 23, figs. 2, 3) is a characteristic found also occasionally in *S. megasperma*.

An isolate identified as *S. megasperma* deposited at the Centraalbureau, Baarn, lacks antheridial filaments. That specimen must therefore be identified as *S. unispora*.

CONFIRMED RECORDS: --AUSTRALIA: Cookson (1937:241). CANADA: Nolan (1975a: fig. 1; 1975b: figs. 5-7). JAPAN: Shibuya (1959:147, fig. 2). LATVIA: Apinis (1929a:218). SOUTH AMERICA: Beneke and Rogers (1970:59). UNITED STATES: Beneke (1948b:45); R. L. Butler (1975: figs. 53-56); Coker (*loc. cit.*); A. W. Ziegler (1948b:18, pl. 2, figs. 1, 2; 1952: pl. 2, fig. 3). USSR: Logvinenko and Meshcheryakova (1971: fig. 4).

RECORDED COLLECTIONS: -- BRITISH ISLES: Dick (1962, 1963, 1966); Dick and Newby (1961); Willoughby and Collins (1966). JAPAN: Suzuki (1961f); Suzuki and Hatakeyama (1960). SOUTH AMERICA: Upadhyay (1967). UNITED STATES: Farr and Paterson (1974); G. C. Hughes (1959, 1962); Poitras (1955); A. W. Ziegler (1958b).

SPECIMENS EXAMINED: -- SWEDEN (1), TWJ. UNITED STATES (12), RLS. Centraalbureau (1).

*Saprolegnia itoana* (Nagai) Seymour  
Mycotaxon 92:11-32, figs. 57-64. 2005, and present fig. 100 A-H

- Isoachlya subterranea* Dissmann, Beih. Bot. Centralbl. 48:110, figs. 1-7. 1931.  
*Isoachlya itoana* Nagai, J. Fac. Agric. Hokkaido Imp. Univ. 32:11, pl. 2, figs. 35-37; pl. 3, figs. 1-8. 1931. Basionym  
*Isoachlya glomerata* Richter, Flora 131:241, fig. 4. 1937.  
*Cladolegnia itoana* (Nagai) Johannes, Feddes Repert. Spec. Nov. Regni Veg., p. 213. 1955.  
*Cladolegnia subterranea* (Dissmann) Johannes, *ibid.*, p. 213. 1955.  
*Cladolegnia glomerata* (Richter) Johannes, *ibid.*, p. 214. 1955.  
*Saprolegnia subterranea* (Dissmann) Seymour, Nova Hedwigia (Beiheft) 19:59, figs. 146-153. 1970.

Monoecious. Mycelium dense, extensive; hyphae stout, moderately branched. Sporangia fusiform or cylindrical, frequently curved, bent, or irregular, infrequently branched; sometimes having short, lateral protrusions basally; apex usually narrow and tapering; renewed internally or by sympodial branching, internally renewed ones usually formed outside the discharged sporangium; 161-560 x 21-52  $\mu\text{m}$ . Spores dimorphic, or rarely monomorphic; discharge and behavior saprolegnoid rarely dictyucoid. Gemmae variable in abundance; fusiform, spherical, obpyriform, or irregular; terminal or intercalary, single or catenulate. Oogonia lateral, occasionally terminal, rarely intercalary and single; frequently in clusters on the hyphae; spherical or obpyriform, rarely cylindrical; (19-) 40-50 (-60)  $\mu\text{m}$  in diameter, including any wall projections. Oogonial wall pitted, unpitted, or pitted only under the region of attachment of antheridial cells; smooth; occasionally with one to a few papillate ornamentations. Oogonial stalks ( $1/4$ -) 1-3 (-5) times the diameter of the oogonium, in length; straight, curved, bent, or irregular; unbranched or branched and bearing oogonia in a glomerulate fashion. Oospores centric or subcentric; spherical, but ellipsoidal or flattened at one side when crowded in the oogonium; 1 (-2-4) per oogonium and usually nearly filling it; (18-) 30-40 (-46)  $\mu\text{m}$  in diameter; germinating to form a long, slender, unbranched germ hypha bearing a small, terminal sporangium. Antheridial branches, when present, predominantly androgynous, occasionally monoclinal, infrequently or rarely dichlinal; when androgynous, arising from any point on the oogonial stalk, and occasionally very short and attached near the oogonial septum; slender, curved or slightly irregular, unbranched or sparingly branched; persisting. Antheridial cells simple; tubular or slightly clavate, sometimes irregular; persisting; laterally appressed, very rarely attached apically or in a digitate fashion; fertilization tubes present in some oogonia, and persisting.

Basionym: *Isoachlya itoana* Nagai.

The choice of Nagai's (*loc. cit.*) *Isoachlya itoana* as the basionym rather than Dissmann's *I. subterranea* is arbitrary. There evidently is no record of when, in 1931, the individual numbers of volume 48 (Abteilung 2) of the Beihefte zum Botanischen Centralblatt were issued, hence the publication date of Dissmann's paper is unknown. Circumstantial evidence (Merxmüller, communication) suggests that Dissmann's account appeared in the latter part of 1931, but perhaps as early as July 31 of that year. Part 1 of volume 32 of the Journal of the Faculty of Agriculture, Hokkaido Imperial University, carries the issue date August 1931, but Nagai's article is dated July 1931. Since there is at least a date on Nagai's paper but not Dissmann's, we have chosen the former as having priority.

A combination of two characteristics sets *Saprolegnia itoana* apart from other taxa in the genus, namely, the production of only one oospore in the majority of oogonia (Fig. 100 C, D), and the predominance of androgynous antheridial branches (Fig. 100 D-G). The species most nearly resembles *S. unispora* (Fig. 100 K) in general configuration of the oogonia (including the formation of glomeruli), and the presence of centric and subcentric oospores. *Saprolegnia itoana* however, has an antheridial apparatus which *S. unispora* does not. Other species -- as, for example, *S. eccentrica* -- may have a small number of oospores per oogonium, but these are eccentric.

The close proximity of some androgynous antheridial branches in *Saprolegnia itoana* to the oogonium to which they are attached (Fig. 100 F) is a feature recalling some species of *Pythiopsis* (Fig. 85 J, K, P). The same may be said for the strongly tapering configuration of the sporangia (Fig. 100 A, B). The spores of *Pythiopsis* species, however, are monomorphic (monoplanetic according to Coker, 1923, and others) as opposed to the dimorphic condition in *S. itoana*. Both Nagai (*loc. cit.*) in describing *Isoachlya itoana*, and Dissmann (*loc. cit.*) in his account of *I. subterranea* referred to the diplanetic condition or emergence of two spore types. Accordingly, their species are not assignable to *Pythiopsis* in spite of some obvious similarities with members of that genus.

Although Kelman (1947), who isolated *Isoachlya* (= *Saprolegnia*) *itoana* from North Carolina soils, recognized the similarities between it and Dissmann's (*loc. cit.*) *I. subterranea*, he did not choose to modify the taxonomic status of the two. Somewhat later, T. W. Johnson and Surratt (1955) redefined certain species of *Isoachlya*, and reduced Nagai's species to a synonym of Dissmann's taxon. There is no doubt that some specimens identified as Nagai's or Dissmann's species were misidentified, and in reality were representative of *Pythiopsis humphreyana*. This was true, for example, of isolate 569 illustrated by T. W. Johnson and Surratt (1955) as figures 14, 16, and 24.

*Pythiopsis intermedia* Coker and Harvey (J. V. Harvey, 1925b) was believed by Seymour (1970:59) to be synonymous with Dissmann's *Isoachlya subterranea*, a conclusion certainly supported by Coker and Matthews (1937) who placed *P. intermedia* into *Isoachlya*. We have analyzed the characteristics of a large number of isolates of *Pythiopsis* in comparison with existing descriptive and illustrative matter. We are satisfied that *Isoachlya intermedia* and *Pythiopsis intermedia* were merely new names applied to *Pythiopsis humphreyana*, a valid and recognizable species as Coker (1914)

originally thought it to be. Accordingly, the names *Pythiopsis intermedia* and *Isoachlya intermedia* are not considered to be synonymous (Seymour, *loc. cit.*) with *Saprolegnia itoana*.

The *Saprolegnia* sp. No. 28 described by Kobayasi and Konno (1971a) appears to have some affinities with *S. itoana* in general configuration of the oogonia. As their species had catenulate oogonia and seldom formed antheridial branches, it cannot be equated confidently with *S. itoana*. Kobayasi and Konno, moreover, did not describe the oospore type of their isolate. We are listing their fungus among the unidentified members of the genus.

In their study of DNA base compositions, B. R. Green and Dick (1973) stated that the GC values obtained by them supported Seymour's (*loc. cit.*) removal of *Isoachlya subterranea* to *Saprolegnia*.

CONFIRMED RECORDS: -- BRITISH ISLES: O'Sullivan (1965:233, 272, figs. I-4-6, I-13, I-14, II-1-19, II-21-34). GERMANY: Dissmann (*loc. cit.*); Richter (*loc. cit.*). JAPAN: S. Ito (1936:73, fig. 31); Nagai (*loc. cit.*). REPUBLIC OF CHINA: Chiou *et al.* (1975:165, pl. 2, fig. 19). UNITED STATES: R. L. Butler (1975: figs. 13-16); Fox and Wolf (1977:102, fig. 6); T.W. Johnson and Surratt (1955:124, figs. 1-13, 15, 17-21, 23, 25-34); Kelman (1947:210, pl. 27); Seymour (*loc. cit.*); A. W. Ziegler (1948b:20).

RECORDED COLLECTIONS: -- BRITISH ISLES: Dick (1964, 1966); Pickering and Willoughby (1977). JAPAN: S. Ito and Nagai (1931); Suzuki (1961f). UNITED STATES: T. W. Johnson (1956a).

SPECIMENS EXAMINED: -- UNITED STATES (14) RLS. Centraalbureau (1); MWD (2).

*Saprolegnia anisospora* deBary  
Bot. Zeitung (Berlin) 46:619, pl. 9, fig. 4. 1888  
(Figure 101 D-G)

*Isoachlya anisospora* (de Bary) Coker and Matthews, North Amer. Fl. 2(1):26. 1937.

Monoecious. Sporangia cylindrical, clavate, or fusiform, but usually curved or irregular in general configuration; renewed internally or by cymose branching or basipetalous succession; 60-227 x 16-37  $\mu\text{m}$ . Spores dimorphic or rarely monomorphic; discharge and behavior saprolegnoid, rarely dictyucoid; primary spores commonly of three size groups: 25-33 x 10-12  $\mu\text{m}$ , 20-24 x 10-13  $\mu\text{m}$ , or 11-14 x 8-11  $\mu\text{m}$ , such groups are usually in separate sporangia rather than being intermixed in the sporangium. Oogonia lateral, terminal, or intercalary; spherical, obpyriform, or dolioform, occasionally napiform; (36-) 40-60 (-93)  $\mu\text{m}$  in diameter. Oogonial wall pitted under region of attachment of antheridial cells, very infrequently elsewhere; smooth. Oogonial stalks ( $1/4$ -)  $1/2$  (-3) times the diameter of the oogonium, in length; stout, straight or curved, unbranched or once-branched. Oospores eccentric, but sometimes aborting; spherical, usually nearly filling the oogonium; wall thin or thickened; (1-) 4-6 (-18) per

oogonium, and filling it or not; (14-) 18-26 (-42)  $\mu\text{m}$  in diameter; germination not observed. Antheridial branches predominantly dichinous, rarely or infrequently monochinous or androgynous; sparingly branched or unbranched; generally somewhat irregular in contour; persisting. Antheridial cells simple; irregularly tubular or clavate; occasionally once-branched; persisting; laterally appressed; fertilization tubes usually present, but not persisting.

This is one of four species of *Saprolegnia* which produce eccentric oospores (see *S. richteri*, *S. eccentrica*, *S. luxurians*); all were, until the study by Seymour (1970), placed in *Isoachlya* or *Cladolegnia*, genera now not recognized as valid ones. *Saprolegnia anisospora* is distinguishable from these species (as well as all others in the genus) by reason of the three sizes of primary planonts produced.

Although the oospores of *Saprolegnia anisospora* are generally eccentric, both Newby (1948a) and Seymour (1970) called attention to a variant type. In some isolates (Fig. 101 D) some oospores had two or more refractive droplets arranged in an eccentric fashion in the ooplasm. Newby remarked that such oospores were likely to be immature, and Seymour agreed. Coker (1923: pl. 9, fig. 4) illustrated an oogonium of *S. anisospora* with one oospore of a type that has since been termed subeccentric. Two other oospores which Coker figured in the same oogonium are shown as centric. Indeed, Coker (1923:34, 35) thought de Bary (*loc. cit.*) had erred in describing and figuring the oospores of *S. anisospora* as eccentric.

Planont size is taxonomically important in *Saprolegnia anisospora*. Coker (1923) recognized two size "classes" and subdivided one of these (the small-size group) into two "subclasses". Newby (1948a) concluded that although there were three sizes of motile primary spores, only two sizes were recognizable in the encysted primary planonts. The most extensive and critical study of spore dimensions in *S. anisospora* was that by Hallett and Dick (1976). They determined that spores of all isolates at hand of this species had either a bimodal or trimodal distribution as to size. Moreover, the relative frequencies of the three size classes responded to the level of incubation temperature (Chapter 8). Hallett and Dick calculated that the overall ratio among the three classes (mean spore diameters of 12.9, 16.6, and 21.1  $\mu\text{m}$ , respectively, and mean spore volumes of 1120, 2400, and 4920  $\mu\text{m}^3$ ) was 1:2:4. In his specimens of *S. anisospora* Newby (1948a) found some "double" planonts with four flagella.

*Isoachlya anisospora* var. *indica* (R. K. Saksena and Bhargava, 1944) is not a variety of *Isoachlya* (= *Saprolegnia*) *anisospora*, but is a variant of *S. diclina* (Seymour, 1970). A water mold identified by Goldsmith (1948:137, pl. 15, figs. 1-3) as *S. delica* differed from *S. anisospora* only by reason of the absence of various sized spores. Seymour (1970) attributed this discrepancy to a strain difference (Monsma, 1936), and considered Goldsmith's fungus to be a representative of *S. anisospora*. Although no new evidence has come to light to support this view, we are following Seymour's decision.

*Saprolegnia anisospora* has been isolated from fish eggs (Chapter 29) and dead fish (Monsma, 1936; Newby, 1961), and has been reported (S. Ito and Nagai, 1931) as one of several saprotrophic fungi that can infect rice seeds and seedlings (*Oryza sativa* L.).

CONFIRMED RECORDS: --AFRICA: Goldsmith (1948:137, pl. 15, figs. 1-3). AUSTRALIA: Cookson (1937:241). BRITISH ISLES: Hallett and Dick (1976:179 *et seq.*); Newby (1948a:264, figs. 1-23). CANADA: Maestres (1977:144). CZECHOSLOVAKIA: Cejp (1934:188, pl. 1, fig. 7; 1959a:193, figs. 67, 68). GERMANY: de Bary (*loc. cit.*); A. Fischer (1892:337); Richter (1937:235). INDIA: G. C. Srivastava (1967a:283, pl. 2, figs. 1-4). IRAQ: Ismail *et al.* (1979:87, figs. 4-7); Muhsin 1977:34, figs. A-D). JAPAN: S. Ito (1936:76, fig. 32.1-32.3a, 32.5, 32.6); Nagai (1931:5, pl. 1, figs. 22-30; pl. 2, fig. 1). LATVIA: Apinis (1929a:221, text fig. 3). MIDDLE EUROPE: Migula (1903:65). NETHERLANDS: Beverwijk (1948: 235). RUMANIA: Toma (1969:217, pl. 2). UNITED STATES: Coker (1923:33, pls. 7-10); Coker and Matthews (1937:26); Fox and Wolf (1977:102); Overman (1970:34); Setzer (1941: pls. 1, 2); Seymour (1970:51, figs. 102-110). USSR: Naumov (1954:67).

RECORDED COLLECTIONS: -- BRITISH ISLES: Apinis (1964); Dick (1963, 1966); Dick and Newby (1961); R. E. Roberts (1963). CANADA: Maestres and Nolan (1978). CZECHOSLOVAKIA: Cejp (1931). DENMARK: Obel (1910a, b). GERMANY: Höhnk (1935a). INDIA: G. C. Srivastava (1967b). IRAQ: Al-Saadi *et al.* (1979). JAPAN: S. Ito and Nagai (1931); Suzuki (1961f). REPUBLIC OF CHINA: Liu and Volz (1977). RUMANIA: Toma (1971). UNITED STATES: R. L. Butler (1975(?); Monsma (1936); Slifkin (1964). USSR: Logvinenko (1971); Logvinenko and Meshcheryakova (1971).

SPECIMENS EXAMINED: -- NORWAY (1), TWJ. UNITED STATES (6), W. W. Scott, RLS. Centraalbureau (1).

*Saprolegnia eccentrica* (Coker) Seymour  
Nova Hedwigia (Beiheft) 19:53, figs. 111-121. 1970  
(Figure 101 A-C)

*Isoachlya eccentrica* Coker, Saprolegniaceae, p. 87, pl. 24. 1923.

*Cladolegnia eccentrica* (Coker) Johannes, Feddes Repert. Spec. Nov. Regni Veg., p. 217. 1955.

Monoecious. Mycelium delicate; hyphae sparingly branched. Sporangia cylindrical or clavate, infrequently obpyriform, pyriform, or fusiform; renewed sympodially, occasionally in basipetalous succession, rarely internally; 130-380 x 25-36  $\mu\text{m}$ . Spores dimorphic or rarely monomorphic; discharge and behavior saprolegnoid, rarely dictyucoid; primary spore cysts 10-12  $\mu\text{m}$  in diameter. Gemmae abundant; clavate, pyriform, or obpyriform, frequently irregular; terminal or intercalary, single or catenulate. Oogonia lateral, infrequently terminal; spherical, obpyriform, or napiform, infrequently irregular; (15-) 30-36 (-47)  $\mu\text{m}$  in diameter. Oogonial wall pitted or unpitted; smooth. Oogonial stalks ( $1/2$ -) 1-2 (-3) times the diameter of the oogonium, in length; stout, straight or curved, infrequently irregular, rarely once-branched. Oospores eccentric; spherical or ellipsoidal; 1 (-4) per oogonium; usually not filling it; (12-) 24-30 (-32)  $\mu\text{m}$  in diameter; germination not observed. Antheridial apparatus lacking.

Among the species of *Saprolegnia* with eccentric oospores, *S. eccentrica* is easily recognized because it lacks antheridial branches (Figs. 101 A-C). Its chief characteristics are shared with *S. richteri*, save for the presence of antheridia in the latter. We have not seen specimens of *S. richteri*, but should the presence or absence of antheridial branches prove to be variable, *S. richteri* properly would be merged with *S. eccentrica*. Like *S. eccentrica*, *S. luxurians* has predominantly one oospore in the oogonium; the latter has larger oospores (and oogonia) than the former, and possesses a well-developed antheridial apparatus.

Dick (1960c: fig. 3 H-K) figures subeccentric oospores for *Isoachlya* (= *Saprolegnia*) *eccentrica*. None of the oospores in the specimens of *S. eccentrica* that we have examined possessed such a refractive body disposition pattern, and certainly Coker (*loc. cit.*) had described and illustrated the oospores of *I. eccentrica* as eccentric. It is possible that Dick had at hand another species. Although V. D. Matthews (1935) reported seeing internally proliferated sporangia (saprolegnoid renewal), in specimens of *I. eccentrica*, Coker (*loc. cit.*) had earlier stated that his species never displayed such a pattern.

CONFIRMED RECORDS: -- BRITISH ISLES: O'Sullivan (1965:301, fig. II-36-48). CANADA: Maestres (1977:146). CZECHOSLOVAKIA: Cejp (1959a:198, fig. 70). POLAND: Staniak (1971:362). UNITED STATES: Coker (*loc. cit.*); V. D. Matthews (1935:307); Seymour (*loc. cit.*). USSR: Morochkovs'kiĭ *et al.* (1967:132, fig. 117).

RECORDED COLLECTIONS: -- BRITISH ISLES: Cook and Morgan (1934); Dick (1962, 1963); Dick and Newby (1961); Hunter (1975). CANADA: Maestres and Nolan (1978). GERMANY: Höhnk (1935a). INDIA: J. N. Rai and Misra (1977b:76, fig. 3a). JAPAN: Suzuki (1960c). UNITED STATES: R. L. Butler (1975: figs. 17-20); Coker (1927); J. V. Harvey (1925a, b; 1927b, c; 1930); G. C. Hughes (1959, 1962); Klich (1980); V. D. Matthews (1927); A. W. Ziegler (1958b).

SPECIMENS EXAMINED: -- SWEDEN (1), TWJ. UNITED STATES (14), RLS. Centraalbureau (1).

*Saprolegnia richteri* Richter ex Seymour  
Nova Hedwigia (Beiheft) 19:53. 1970

*Isoachlya terrestris* Richter, Flora 131:242, figs. 5, 6. 1937.

*Cladolegnia terrestris* (Richter) Johannes, Feddes Repert. Spec. Nov. Regni Veg., p. 216. 1955.

Monoecious. Hyphae delicate, sparingly branched. Sporangia cylindrical or slightly irregular, or fusiform and tapering toward the apex; producing lateral, cylindrical or fusiform branches; renewed internally or by sympodial branching; 293-543 x 25-44  $\mu$ m. Spores apparently dimorphic; discharge and behavior saprolegnoid; primary(?) spore cysts 8-10  $\mu$ m in diameter. Gemmae unknown. Oogonia lateral; globose, seldom somewhat irregular; 32-44  $\mu$ m in diameter. Oogonial wall unpitted;

smooth or with a few irregular evaginations 10-12 µm long. Oogonial stalks  $1/2$  - 3 times the diameter of the oogonium, in length; straight, seldom curved; unbranched or branched and bearing oogonia in a glomerulate fashion. Oospores eccentric; globose or ovoid; (1-) 2-3 (-5) per oogonium and filling it; 16-27 µm in diameter. Antheridial branches present on about half of the oogonia; monoclinal or diclinal; slender, irregular, branched or unbranched; often arising at a distance from the oogonium to which attached. Antheridial cells laterally appressed; fertilization tubes not observed. (Adapted from Richter, *loc. cit.*)

*Saprolegnia richteri* resembles *S. eccentrica*, but may be separated from that species by two features primarily. Antheridial branches are produced by *S. richteri* (although not all oogonia are so attended), but none is formed in *S. eccentrica*. *Saprolegnia richteri* generally has 2-3 oospores per oogonium, while in Coker's species, a single oospore predominates. There also are noticeable similarities between *S. richteri* and *S. luxurians*; see discussion of the latter species.

The species was not validly published (Richter, *loc. cit.*) when placed in *Isoachlya*. Johannes (1955a) transferred Richter's species to *Cladolegnia*, but he also failed to validate the species with a Latin diagnosis. Seymour (*loc. cit.*) chose to accept Richter's species, but not recognizing either *Isoachlya* or *Cladolegnia*, assigned it to *Saprolegnia*. A new name was chosen (Seymour, 1970:54) since the epithet *terrestris* had been used by Cookson (1937) for another *Saprolegnia*.

Richter (*loc. cit.*) described his species as having pitted sporangia. These were not pits in the sense of the thin areas common in the oogonial walls of water molds, but were orifices through which spores escaped during discharge.

*Saprolegnia richteri* is known from only two collections, that by Richter, and a later one by Willoughby (1971a). The latter investigator did not provide a description or any illustrations of his specimens, but such would have been helpful in assessing the status of the species.

Hoshina and his associates (1960:71, fig. 8) reported the isolation of an *Isoachlya* sp. from eel culture ponds in Japan. They thought their water mold was similar to *I. terrestris* (= *richteri*) but differed from Richter's species in having much smaller oospores (10-15 µm in diameter) that lacked an oil reserve globule. There is no way to be certain of the identification of *Isoachlya* sp., but from what is provided in their report it assuredly was not Richter's species.

CONFIRMED RECORD: -- GERMANY: Richter (*loc. cit.*).

RECORDED COLLECTION: -- BRITISH ISLES: Willoughby (1971a).

*Saprolegnia luxurians* (Bhargava and Srivastava) Seymour  
Nova Hedwigia (Beiheft) 19:55: figs. 122-129. 1970  
(Figure 102 A-C)

*Isoachlya luxurians* Bhargava and Srivastava. Trans. Brit. Mycol. Soc. 49:269, pl. 8; text fig. 1. 1966.

Monoecious. Mycelium diffuse, luxuriant; hyphae slender, delicate, sparingly branched. Sporangia fusiform, cylindrical, or clavate; straight, curved, or irregular; renewed internally, by cymose branching or occasionally in basipetalous succession, rarely by sympodial branching; 110-926 × 14-60 μm. Spores dimorphic; discharge and behavior saprolegnoid; primary spore cysts 10-14 μm in diameter. Gemmae rare; when present, generally very irregular, lobed, or branched; terminal or lateral. Oogonia lateral, rarely terminal or intercalary; spherical, subspherical, or obpyriform, rarely cylindrical or dolioform; (16-) 45-58 (-74) μm in diameter. Oogonial wall moderately and inconspicuously pitted, or pitted only under the region of attachment of the antheridial cells, rarely unpitted; smooth on outer surface, rarely very sparingly papillate; infrequently irregular on inner surface. Oogonial stalks ( $1/4$ -) 1-3 ( $-4^{1/2}$ ) times the diameter of the oogonium, in length; stout; straight or curved; unbranched or very sparingly branched. Oospores eccentric; spherical or rarely ellipsoidal; 1 (-6) per oogonium, and sometimes filling it; (14-) 35-38 (-62) μm in diameter; germination not observed. Antheridial branches monoclinal, androgynous, or declinal; slender, curved or slightly irregular; unbranched, infrequently very sparingly branched; persisting. Antheridial cells simple or compound; tubular, clavate, or irregular; persisting; laterally appressed, sometimes apically attached; fertilization tubes observed, not persisting.

One of four species of *Saprolegnia* with eccentric oospores, *S. luxurians* is by reason of its antheridial filaments separable from *S. eccentrica*. *Saprolegnia luxurians* can be distinguished from *S. anisospora* (also having antheridial branches) on the basis of the predominance of a single oospore in the oogonia of the former. Additionally, *S. anisospora* produces three sizes of planonts; *S. luxurians* does not. We have not seen specimens of *S. richteri* (Seymour, 1970:54), but it would appear to differ from *S. luxurians* chiefly in oogonium and oospore size: *S. luxurians* has proportionately larger cells than *S. richteri*. It should be emphasized that one of Richter's (1937: fig. 6a) illustrations of his *Isoachlya terrestris* (= *S. richteri*; Seymour, 1970) shows a luxuriantly branched portion of the mycelium. If *S. richteri* should prove to have such a growth pattern consistently, and to be somewhat variable in antheridial branch origin, it might properly be merged with *S. luxurians*.

Seymour (1970:56) examined a subculture of type material of *Isoachlya luxurians*. He found that some characteristics of the isolate were more variable than Bhargava and Srivastava (*loc. cit.*) had observed. This variation was particularly noticeable in sizes of the oogonia, and diameter and number of oospores.

CONFIRMED RECORD: -- INDIA: Bhargava and Srivastava (*loc. cit.*).

RECORDED COLLECTIONS: -- INDIA: Prabhuji (1979); G. C. Srivastava (1967b).

SPECIMENS EXAMINED: -- INDIA (1), K. S. Bhargava (subculture of type). UNITED STATES (2), RLS.

*Saprolegnia* sp. 12241  
Mycotaxon 2:190, figs. 1-15. 1975

Monoecious. Sporangia oval, ovoid, pyriform, or broadly fusiform, occasionally subspherical; apex a broad, nearly truncate papilla; renewed internally and confined within an old sporangium or forming outside the orifice, or infrequently by sympodial branching; 44-81 x 20-51  $\mu\text{m}$ . Spores dimorphic; escaping slowly through a broad, apical orifice as laterally biflagellate cells; swimming sluggishly and by slight amoeboid motion becoming subapically (anteriorly) biflagellate; encysting before germinating to produce a new hyphal system. Gemmae very sparse; pyriform; confined to discharged sporangia. Oogonia sparse, terminal on hyphae proliferating through discharged sporangia; spherical or obpyriform; (38-) 41-77 (-121)  $\mu\text{m}$  in diameter, including wall ornamentations. Oogonial wall pitted, at first smooth, then becoming papillate or undulate as maturation proceeds; papillae usually formed by the protrusion of wall substance through the pits. Oospores centric; spherical; (3-) 12-24 (-64) per oogonium and generally filling it; (14-) 16 (-19)  $\mu\text{m}$  in diameter; germination not observed. Antheridial branches declinous; slender, unbranched or sparingly branched; originating as hyphae proliferating through discharged sporangia or as sympodial branches; persisting. Antheridial cells simple; clavate or tubular; persisting; apically or laterally appressed; fertilization tubes not observed.

This unusual watermold, tentatively assigned to *Saprolegnia*, is known only from four sites (in Norway). The fungus was collected on chironomid exuviae, and on bits of snakeskin baited in samples of water and sediment. One group of specimens (TWJ 12255) was parasitized by a species of *Phlyctochytrium*, but the chytrid disappeared as the watermold was subcultured (in unifungal culture).

As the description shows, the planont behavior pattern in this as yet unnamed watermold is unlike that of any other member of the family. The planonts are laterally biflagellate on emergence, and only become anteriorly biflagellate as they move about with amoeboid (and weak flagellar) motion upon release from the sporangium. In all other members of the family where the primary spores are not suppressed, these cells emerge as apically biflagellate swimmers.

A further unusual feature of the Norwegian fungus is that of the configuration of the sexual apparatus. The oogonia are formed (always?) terminally on hyphal branches proliferating through old sporangia, and the declinous antheridial filaments may have a like origin. The majority of the oogonia in all collections were papillate. However, the papillate condition was in most instances the result of wall substance(?) protruding partially from pits. Such a condition has been detected in other species of *Saprolegnia*, but it is by no means of common occurrence.

The sporangium discharge mechanism (not planont behavior), renewal by internal proliferation, and oogonia with multiple centric oospores are characteristics that ally this unidentified fungus to *Saprolegnia*, and exclude it from *Pythiopsis* (its sporangia resemble those of members of this latter genus) and *Protoachlya*, two other genera whose representatives have motile spores at discharge.

Until the fungus is propagated in axenic culture and its growth pattern on other substrates determined, it must remain unidentified. However, we may speculate that the affinities of sp. 12241 would seem to be with *Saprolegnia ferax* or *S. diclina*. These two species may be found (although infrequently) on snakeskin bait in gross cultures, and while they have a much-reduced mycelium (as does this *Saprolegnia* from Norway) on this substratum, the behavior of their sporangia and spores is not modified. It will be necessary to confirm the spore behavior pattern in the unidentified *Saprolegnia* before it can be assigned to any genus with finality. The fungus should be sought in *Sphagnum* bogs.

CONFIRMED RECORD: -- NORWAY: T. W. Johnson (*loc. cit.*).  
SPECIMENS EXAMINED: -- NORWAY (4), TWJ.

*Saprolegnia* sp.

The citations to follow record with or without descriptions or illustrations unidentified (in some instances unidentifiable) specimens of *Saprolegnia*. Most such records are simply of asexually reproducing individuals, a number of which were found on living fish, in fish eggs, or associated with other aquatic animals. These latter records are designated by an asterisk. (\*); reference to the specific publication will provide the name of the invaded animal. The citations also include the unidentified specimens assigned to *Isoachlya*.

AFRICA: Eicker (1976); El-Hissy (1974); Karling (1976); Nolard-Tintigner (1974: figs. 8, 9\*). AUSTRALIA: M. I. Collins (1920: figs. 1-11); Hardy (1910\*); Johnston (1917\*); Johnston and Bancroft (1921\*); McKenzie and Hall (1976\*; reported merely as "Saprolegniaceae"). BELGIUM: Nolard-Tintigner (1971\*; 1973: figs. 14 -16\*). BRITISH ISLES: Ajmal and Hobbs (1967\*); Apinis (1964); C. J. A. Berkeley (1944: fig. 1); J. C. Collins and Willoughby (1962); Dick (1963, 1966); Dick and Newby (1961); Edington (1889: 372 *et seq.*); H. J. Fletcher (1979); Hodkinson and Dalton (1973); Hodkinson and Hunter (1970a\*, 1970b\*); Lechmere (1910: pls. 1, 2; in 1911a paper reported as *S. thureti*, but as he saw no oogonia, this identification is doubtful); Newton (1971); O'Sullivan (1965); Park (1972a); Pickering *et al.* (1979); R. H. Richards and Pickering (1978\*); R. J. Roberts *et al.* (1969\*, 1973\*); R. J. Roberts, Leckie, and Slack (1970\*); R. J. Roberts and Shepherd (1974); Rushton (1933\*, 1935\*, 1936\*); Stenton (1953); Willoughby (1962, 1971a\*); Willoughby and Collins (1966). CANADA: Chong (1973\*); Dick (1970, 1971c); Duff (1929\*); Golini and Sherry (1979); Graham (1956\*); F. C. Harrison (1918\*); Huntsman (1918\*); Lester (1974\*); D. L. McKay (1967\*); Maestres (1977: figs. 59-63, in

part); N. V. Martin (1956\*); Neish (1977\*); Neish and Green (1976\*); Pippy and Hare (1969\*). CZECHOSLOVAKIA: Cejp (1959a: 33, 191). DENMARK: A. Lund (1978); Petersen (1903, 1909a\*, 1910\*). "EAST" GERMANY: Johannes (1939: fig. 18). FAEROES: Höhnk (1960). FINLAND: Häyrén (1930; 1955\*). FRANCE: Chaze (1925\*); Chiappelli (1933\*; as "*saprolegnacea*"); P.-A. Dangeard (1916); Griffon and Maublanc (1911\*); Guilliermond [1923; reported from decaying fungus (agaric?) among other unusual substrates]. GERMANY: Höhnk (1935a; 1939: 351, fig. 7; 19-56b; 1958); Lenz (1924); Lindstedt (1872); Maurizio (1896b:80, 81, pl. 1, figs. 1-3); Minden (1916); Reinsch (1878); Rothert (1890: pl. 10\*); Schlösser (1929:538); Unger (1843: pl. 4\*; 1844: pl. 1\*; as *Achlya prolifera*); Vlk (1939: fig. 1a); Wunder (1938). GREENLAND: Höhnk (1960); Kobayasi *et al.* (1971: 25, fig. 12). HONG KONG: Yung and Stenton (1964); INDIA: Bhargava (1943; possibly same as *Isoachlya anisospora* var. *indica* of R. K. Saksena and Bhargava, 1944); Chaudhuri and Kochhar (1935:140, pl. 5, figs. 20-29; reported erroneously as *Aplanes* sp.); Chaudhuri *et al.* (1947:19, fig. 3; reported erroneously as *Aplanes* sp.); Chidambaram (1942\*); Khulbe (1977, 1980a); Khulbe and Bhargava (1977); Mer *et al.* (1980); A. K. Srivastava (1978b\*); G. C. Srivastava (1976\*); R. C. Srivastava and G. C. Srivastava (1978a\*); Thakur Ji and Dayal (1966). IRAQ: Ismail *et al.* (1979); Muhsin [1977:48, figs. A-D (two plates)]. JAPAN: Hoshina *et al.* (1960:71, fig. 8\*; possibly *S. ferax*); Kobayasi and Konno (1971a:13, 14, fig. 5A-G); Kobayasi and Watari (1934:722, figs. 67, 68); Nakamura (1962\*); Okane (1978); Shibuya (1959:149, 151, fig. 4; possibly *S. ferax*); Suzuki (1960a, b, d, f; 1961b, d, h, i, k, 1; 1962c, e); Suzuki and Hatakeyama (1960, 1961); Suzuki and Nimura (1960; 1961a, d, e; 1962); Suzuki and Nishita (1963); Suzuki and Tatsuno (1964, 1965a); Suzuki *et al.* (1960, 1961); Tanaka (1935\*). MADEIRA: Höhnk (1962). NETHERLANDS: Beverwijk (1948); Bootsma (1973: figs. 1-6\*). NEW ZEALAND: Jolly (1967\*); NORWAY: Kobayasi *et al.* (1968:36, fig. 2). PAKISTAN: Ali (1968\*). PEOPLE'S REPUBLIC OF CHINA: Jettmar (1947\*). POLAND: Sakowicz and Gottwald (1958\*). REPUBLIC OF CHINA: Chung (1973\*); Sawada (1912:72, pl. 10, figs. 1-10; 1919:44, 66; 1961). SOUTH AMERICA: Conroy and Vasquez (1976); Milanez (1968:103, figs. 1-5); Möller (1901); Viegas and Teixeira (1943). SWEDEN: Areschoug (1844\*). SWITZERLAND: Maurizio (1895a: fig. 3\*; 1896b: 111, pl. 2, figs. 60-65; 1897b\*). TASMANIA: Johnston (1917\*). UNITED STATES: Armstrong (1955, 1956); G. C. Atkins (1897: pl. 18, lower fig.\*); Bandoni *et al.* 1975); G. C. Becker and Shaw (1955); Beneke and Schmitt (1961); Benoit and Matlin (1966\*); E. H. Brown (1960\*, as "fungus"; 1968\*); M. C. Carlson (1920: pls. 1-3); Clausz (1970, 1974); Clinton (1893\*); Coker (1927); Collins and Dechtiar (1974\*); W. B. Cooke (1976a); W. B. Cooke and Bartsch (1959, 1960); W. B. Cooke and Matsuura (1969); Cummins (1954\*); Farr and Paterson (1974); Fox and Wolf (1977); Fuller and Poyton (1964); Gaertner and Sparrow (1966); Haenseler *et al.* (1923); J.V. Harvey (1927b; 1942:24, 25, pl. 1, figs. 6-9; pl. 2; 1952); Hine (1878: pl. 4\*; pl. 5 also alleged to be of a *Saprolegnia* sp., but the figures leave no doubt that a mixture of representatives of other genera was illustrated); Ho (1975a); Humphrey (1893: pl. 14, figs. 1, 3, 8, 14, 15); T. W. Johnson (1950b); Kanouse (1925); Karling (1977); Kauffman (1908); Klich (1980); D. L. Koch (1973\*; 1976\*); Kuehn (1960); S. Lockwood (1890\*; mixed culture specimens); Lounsbury (1927:545, pls. 1-3); Marnell and Hunsaker (1970\*);

Milanez (1966:112); C. E. Miller (1965); O'Bier (1960\*); Oseid (1977\*); Overman (1970; 37); Padgett (1978a); Paterson (1967); Povah (1935); Raney (1942\*); Salvin (1941); Schmitt and Beneke (1962); Scott (1960b; Scott and O'Bier (1962); Scott and Warren (1964: fig. 1\*); Shipman (1979); Slifkin (1964); Sorenson (1962: pl. 5, figs. E, F); Sparrow (1965); Stanley and Colby (1971\*); Stevens and Keil (1931\*); TeStrake (1958); D. A. Webster (1945\*, as "fungus"); White (1975); Wolf (1944); A. W. Ziegler (1952). USSR: Astakhova and Martino (1968\*); De-La-Rue (1873: figs. 1-9); Florinskaya (1969); Ivankov (1971\*); Mikheeva (1969: fig. 1); Mil'ko and Belyakova (1968); Mil'ko and Zakharova (1976); Shereshevskaya (1932: figs. 1-5\*). YUGOSLAVIA: Chorine and Baranoff (1929\*); Ristanović (1970a); Wunder (1954\*).

## IMPERFECTLY KNOWN SPECIES OF *SAPROLEGNIA*

*Saprolegnia curvata* Minden  
Kryptogamenfl. Mark Brandenburg 5:609. 1915

*Isoachlya curvata* (Minden) Cejp, Oomycetes I, Flora ČSR, Ser. B, Part 2, p. 197, figs. 69c, d. 1959.

Monoecious. Hyphae 40-60  $\mu\text{m}$  in diameter, 1 -1.5 mm long. Sporangia cylindrical, seldom weakly fusiform, straight, clavate, or [some] other shape; predominantly curved, hook-like, bent, or spiral; renewed internally; 200-400 x 40-60  $\mu\text{m}$ . Spores dimorphic; discharge and behavior saprolegnoid; encysted spores 25  $\mu\text{m}$  in diameter. Gemmae not observed. Oogonia intercalary, lateral, terminal or sessile; single or catenulate; irregular, asymmetrical, elongate, seldom globose. Oogonial wall unpitted; smooth but having irregular contour, or some papilla-like processes. Oogonial stalks short. Oospores spherical, seldom more or less elongate or ellipsoidal; (1-) 3-5 (-10) per oogonium; germination not observed. Antheridial branches abundant, long, sinuous, wrapping about the oogonium. Antheridial cells irregularly clavate or tubular; apically or laterally appressed. (Adapted from Minden *loc. cit.*; 1916.)

This species, known only from the original collection by Minden (*loc. cit.*; see also 1916:218, figs. 23a, b; pl. 5, figs. 38-44), has two distinctive features. The sporangia are bent or curved processes ("hirtenstabartig"), a characteristic shared with no other species in the genus, and the oogonia are conspicuously irregular and asymmetrical. Some characteristics necessary for a critical evaluation of Minden's species are not known; chiefly these are the type of oospore structure and the origin of the antheridial branches. One oospore depicted by Minden (1916: pl. 5, fig. 41) might be interpreted as a centric one, but not with any degree of certainty. The species must again be recovered (originally collected on the eggs of *Bunynia* sp.) and examined at least in unifungal culture before it can be identified properly.

Cejp's (*loc. cit.*) transfer of *Saprolegnia curvata* to *Isoachlya* was done without benefit of a study of specimens.

CONFIRMED RECORD: -- GERMANY: Minden (*loc. cit.*).

#### EXCLUDED TAXA

*Saprolegnia androgyna* Archer  
Quart. J. Microscop. Sci. (N. S.) 7:123, pl. 6, fig. 1. 1867

Humphrey (1893) assigned this species to *Aplanes*, but it is doubtless an *Achlya*, and is so treated here.

*Saprolegnia bernardensis* Harvey  
J. Elisha Mitchell Sci. Soc. 58:22, pl. 3. 1942

This is an illegitimate name, having been published without an accompanying Latin diagnosis. The specimens as described by Harvey were probably only forms of *Saprolegnia ferax*. Upadhyay (1967) reported finding this species in Brazil.

*Saprolegnia candida* Kützing  
Species Algarum, p. 159. 1849

The filaments (hyphae) were described as having obtuse apices. Kützing (*loc. cit.*) placed Agardh's (1824) *Leptomitus candidus* into synonymy with *Saprolegnia candida*, but from Agardh's description, it would appear likely that he was indeed describing a *Leptomitus*. This being the case, and assuming that Kützing was correct in his decision, *S. candida* was probably a *Leptomitus*.

*Saprolegnia capitulifera* Braun  
Betrachtungen über die Erscheinung der Verjüngung in der Natur..., p. 201. 1851

The fungus described by A. Braun (*loc. cit.*; 1853) was doubtless an *Achlya*, but in writing of the "fruit clubs" (sporangia), he stated that they were imperfect because new ones did not grow through the emptied ones as in *Saprolegnia ferax*. Clearly, Braun saw spore formation and discharge, and oogonium and oospore development, but was unaware of the significance of the latter. There is insufficient information in his account to identify this *Achlya* with certainty. Schröter's (1889) contention that Braun's species was *Achlya prolifera* is not supported by direct evidence.

*Saprolegnia corcagiensis* Hartog  
Quart. J. Microscop. Sci. (N. S.) 27:429 f. 1886-87

It is likely that Hartog was dealing with a mixed culture, since the sporangia of this species as he described them were of a leptomitaceous fungus, and the oogonia of

some unidentifiable saprolegnian. Ramsbottom (1915b) believed Hartog's species to be *Apodya lactea* (= *Leptomitus lacteus*). Coker and Matthews (1937:61) list *S. corcagiensis* as a synonymy of *L. lacteus* (Roth) Agardh.

*Saprolegnia debari* Walz  
Bot. Zeitung (Berlin) 28:545, pl. 9, figs. 1-12. 1870

Reported to occur in *Spirogyra densa* Kützing, Walz's species is a *Pythium*. It is described also in the Russian edition of this paper: Valt's, 1870:27, figs. 1-12.

*Saprolegnia dichotoma* Suhr  
In, Brentel, Flora Germanicae Exsiccati No. 206

A specimen of *Leptomitus lacteus* (Lechmere, 1911b; Cejp, 1959a) described as a species of *Saprolegnia*.

*Saprolegnia dioica* Pringsheim  
Jahrb. Wiss. Bot. 2:206 et sqq., pl. 22, figs. 1-6. 1860

The *Saprolegnia dioica* described by Pringsheim (*loc. cit.*) is not the species of the same name circumscribed by Schröter (Schröter and Schneider, 1870) or de Bary (1883). Pringsheim's *S. dioica* was based on parasitized specimens and therefore has no validity.

In reference to a fungus he identified as *Saprolegnia dioica* Pringsheim, M. J. Berkeley (1864:150) followed Pringsheim's conclusion and conjectured that the minute, uniflagellate bodies "produced" by the organism passed through the "... apertures of the Oögonia, and thus vivify the resting spores." Pringsheim contended that fertilization was accomplished by motile male gametes. In reality, of course, the "sperms" were the planonts of a parasitic chytrid.

Walz (1870a:556, pl. 9, figs. 20, 21) collected in Russia a watermold which he referred to Pringsheim's species (also in the Russian edition of this paper, as Valt's, 1870, figs. 20, 21). It is quite unlikely that Walz even saw specimens similar to the parasitized "*Saprolegnia dioica*"; one illustration (fig. 21) is suspiciously like a representation of the columella of a mucoraceous fungus.

*Saprolegnia dioica* Schröter  
In, Schröter and Schneider Jahresber. Schles. Ges. Vaterl. Cult. 47:143. 1810

As there are no illustrations or description accompanying this name, the species is a *nomen nudum*. Accordingly, it cannot be disposed of as a synonym of a known (and valid) species, although Seymour (1970:30) so treats it under *Saprolegnia ferax*. His listing of *S. dioica* Schröter among the synonyms of *S. diiclina* also is corrected by excluding this species from the genus. Cejp (1959a:248) lists *S. dioica* Schröter with *S. mixta* (= *ferax*), although he also clearly held this synonymy in question.

*Saprolegnia dioica* form *pseudodioica* Schlösser  
Planta 8:537. 1929

There is no formal description of this form, and the name appears merely to represent Schlösser's attempt to single out a collection that could not with certainty be identified with *Saprolegnia dioica* de Bary (itself synonymous with *S. diclina*).

*Saprolegnia dioica-racemosa* De-La-Rue  
Bjull. Moskovsk. Obshch. Isp. Prir., Otd. Biol. 42:469. 1869

This name -- it was not written as the variety *racemosa* of *Saprolegnia dioica* as has been thought (Seymour, 1970:30) -- was applied to a specimen described only as being much branched. There are no illustrations, and the description is far too brief to allow any judgment as to the correct identification. Furthermore, it cannot be listed as a synonymous species (A. Fischer, 1892; Seymour, 1970) for the same reason.

*Saprolegnia divisa* Pringsheim  
Phycomyceteae, Berlese and De Toni, in P. A. Saccardo, Sylloge  
fungorum omnium hucusque cognitorum. Vol. 7, p. 269. 1888

This name is an orthographic error committed by Berlese and De Toni (*loc. cit.*), presumably in transcribing *Saprolegnia dioica* Pringsheim.

*Saprolegnia elongata* Masee  
British Fungi, p. 271. 1891

As Coker (1923:76) pointed out, Masee's species was based in part on a *Pythium* and in part on a *Saprolegnia*. Goldie-Smith (1952:287n) thought the *Pythium* component might have been *P. undulatum* Petersen. The other component is not identifiable.

*Saprolegnia exigua* Murgoci  
Bull. Acad. Roumâna, Bucharest Sect. Stînifica 30:158 *et sqq.*, figs. 5-11. 1947

Without a doubt, Murgoci observed a fungus in the notocord and cartilaginous portions of the vertebra (and in adjacent musculature and connective tissue) of sterlet from Rumania, but its identity is obscure. She reported that secondary sporangia were formed in empty ones, and illustrated the spores as biflagellate cells. However, she gave the dimensions of the oospores as 3.5-4.8  $\mu\text{m}$  in diameter. The description is inadequate, and, moreover, unaccompanied by a Latin diagnosis. These are sufficient grounds on which to exclude the species.

*Saprolegnia invaderis* Davis and Lazar  
Trans. Amer. Fish. Soc. 70:264 *et sqq.*, figs. 11-6. 1940

There is no precise, formal description of this species in the paper by H. S. Davis and Lazar, and nowhere in the account does a Latin diagnosis appear. The morphology of the disease condition caused by this species (Davis and Lazar, *loc. cit.*; Chapter 29) identifies the fungus as a form of *Saprolegnia ferax*.

*Saprolegnia Kauffmaniana* Pieters  
Bot. Gaz. (Crawfordsville) 60:488, pl. 21, figs. 5-7. 1915

As the critical features required for identification of Pieters' species are absent from the description, it is excluded. Seymour (1970) retained the taxon, but in the category of doubtful ones. See discussion of *Saprolegnia diclina*.

A fungus identified as *Saprolegnia kauffmaniana* was collected by T. W. Johnson (1956a), but he thought it might be only a strain of *S. ferax*. Fungi under the name of Pieters' species have also been reported (but without description or illustrations) by Slifkin (1961) and Ristanović *et al.* (1973). These records cannot now be confirmed. Khulbe's (1980c:79, figs. 5, 6) report of this species probably is incorrect; *S. diclina* seems the correct identification.

*Saprolegnia lactea* (Roth) Braun  
Betrachtungen über die Erscheinung der Verjüngung in der Natur..., p. 287. 1851

Humphrey (1893), Coker and Matthews (1937), Cejp (1959a), and Sparrow (1960) list this species as a synonym of *Leptomitus lacteus*.

*Saprolegnia lactea* Pringsheim  
Jahrb. Wiss. Bot. 2:228, pl. 23, figs. 6-10; pl. 25, figs. 1-6. 1860

Although Pringsheim preserved the name *lactea* within *Saprolegnia*, his account leaves the impression that he equated *S. lactea* with Agardh's *Leptomitus lacteus*.

*Saprolegnia latvica* Apinis  
Acta Horti Bot. Univ. Latv. 4:211, pl. 1. 1929

As is evident from Apinis' later (1933a, b) account of *Archilegnia*, a new genus erected to accommodate this species, the watermold was infected, and therefore must be excluded as a species. See remarks, *Archilegnia*. Aage Lund (1978) has reported isolating this species from Danish soils.

*Saprolegnia libertiae* Kützing  
Species Algarum, p. 160. 1849

Kützing described *Saprolegnia libertia* as an organism consisting of tubular, nonseptate, simple, hyaline filaments aggregated in tufts, and evidently took the characterization directly from Agardh (1824:49). The latter described *Leptomitus libertiae*, a species which has since been reduced to synonymy with *L. lacteus* (Sparrow, 1960). *Saprolegnia libertiae* cannot be placed in either the genus *Saprolegnia* or the family because it is too sketchily circumscribed.

*Saprolegnia minor* Kützing  
Phycologia generalis, p. 157. 1843

Perhaps *Saprolegnia minor* is, as Seymour (1970) thought, an *Entomophthora*. In their account of *E. culicis* (Braun) Fresenius, D. M. MacLeod *et al.* (1976) remarked that there was little evidence to suggest that *S. minor* was identical to this entomophthoraceous fungus. The later descriptions of *S. minor* provided by Kützing in 1845 and 1849 give no clue to its actual identity. This species also was reported by Robin in 1853.

*Saprolegnia mixta* forma *agama* Lotsy  
Botanische Stammgeschichte, Vol. 1, p. 168, fig. 98. 1907

This is not a formally described taxon, and the name is merely Lotsy's designation of the apogamous form of *Saprolegnia mixta* used by B. M. Davis (1903a, b) in his study of sporogenesis and oogenesis.

*Saprolegnia monoica* Pringsheim var. *ocellata* Shkorbatov  
Bot. Mater. Inst. Sporov. Rast. Glavn. Bot. Sada RSFSR 2:34. 1923

It is impossible, from the brief descriptive matter provided by Shkorbatov, to determine the affinities of this variety, just as Seymour (1970) remarked. A very brief account of the taxon appears in a later paper by Shkorbatov (1927, 82). The description of the oogonial and antheridial apparatus suggests that the variety may have been near *Saprolegnia turfosa* or *S. uliginosa*.

*Saprolegnia monoica* Pringsheim var. *tortipes* Shkorbatov  
Bot. Mater. Inst. Sporov. Rast. Glavn. Bot. Sada RSFSR 2:35. 1923

The variety *tortipes* is so poorly described that it cannot be evaluated. Seymour (1970) thought it approached *Saprolegnia furcata*; Shkorbatov's later description (1927:82) of the variety strengthens this view.

*Saprolegnia mucophaga* Smith  
Gard. Chron. (N.S.) 22:245, figs. 49, 50. 1884

Although both Humphrey (1893) and Coker (1923) thought that *Saprolegnia mucophaga* was a *Pythium*, this seems very unlikely. The hyphae are illustrated by W. G. Smith (*loc. cit.*) as septate filaments, and two of the figures of reproductive structures alleged to be of this species are strongly suggestive of drawings of conidia. Possibly Smith's species was one of the Fungi Imperfecti; it is not a *Saprolegnia*. Ramsbottom (1915b) simply noted that the description and figures provided by Smith were unsatisfactory.

*Saprolegnia papillosa* (Humphrey) Apinis  
Acta Horti Bot. Univ. Latv. 4:218, pl. 2. 1929

In his treatment of *Achlya papillosa*, T. W. Johnson (1956b) was in doubt about the status of *Saprolegnia papillosa*, but Seymour (1970) rejected the latter species. The fungus which Apinis saw was assuredly not the same as Humphrey's *Achlya papillosa*. The oogonia of Humphrey's and Apinis' species are very different. In fact, were it not for oospore number in *S. papillosa*, a position for it near *S. blelhamensis* might be appropriate.

Apinis (1929a: pl. 2, figs. 1-4) illustrated saprolegnoid renewal and pyriform primary spores for *Saprolegnia papillosa*. It is not certain that Apinis (1929a, b) had in fact isolated the fungus on which the transfer to *Saprolegnia* was made.

*Saprolegnia parasitica* var. *kochhari* Chaudhuri  
In, Chaudhuri and Kochhar, Proc. Indian Acad. Sci. (Sect. B)  
2:139, pl. 5, figs. 1-6. 1935

This variety is known only from the original collection and a later report by Chaudhuri *et al.* in 1947 (p. 26, fig. 7). As the variety was described only from the asexual phase, its relationship to *S. parasitica* sensu Kanouse is purely conjectural. Indeed, the Indian specimens fall into precisely the same category as most specimens reported as *S. parasitica* Coker, that is, identifiable only as *Saprolegnia* sp. The name has no validity.

*Saprolegnia philomukes* Smith  
Gard. Chron. (N.S.) 22:245. 1884

The events surrounding the publication of this name are curious enough to warrant reporting. In his 1884 paper, W. G. Smith first published this name to attach to a fungus which he stated he had described and illustrated in 1882. There is no such description or figure applicable to this fungus in the 1882 paper. Also in the 1884 (p. 781) account, W. G. Smith stated that the December 22, 1883, issue of "Gardner's Chronicle" contained an illustration of a fungus (found on the side of a silo). This fungus, he said, he had named elsewhere as *Saprolegnia philomukes*. The 1883 account is

by Pim, not Smith, and what Pim describes (and Smith later is alleged to have named) is not saprolegniaceous, nor is it a *Pythium* as Coker (1923) concluded. At best guess, *S. philomukes* is a name applied to a *Zygorhynchus* or some allied form. According to Pim (1883), the organism he found on ensilage conjugated as in the Spirogyras, but was allied to *Pythium*.

*Saprolegnia prolifera* Braun

Betrachtungen über die Erscheinung der Verjüngung in der Natur..., p. 268. 1851

This is *Achlya prolifera* Nees von Esenbeck, and is so treated.

*Saprolegnia quisquiliarum* Roumequère

Fungi selecti exsiccati, cent. LX. 1891

We have not seen the specimens in this exsiccata. According to Humphrey (1893) there was nothing saprolegniaceous about them.

*Saprolegnia saccata* Kützing

Species algarum, p. 159. 1849

Kützing described this species as having filaments each with a saccate apex and a general mucronate aspect. There is nothing to identify the specimens (found in stagnant water, in slime) with the Saprolegniaceae.

*Saprolenia schachtii* Frank

In, Schenk, Handbuch der Botanik, Vol. 1, p. 477. 1879

Other than a brief description derived by Berlese and deToni (1888) apparently from Schacht's (1856: pl. 3, fig. 8) single illustration, there is no formal, published account of this species; Frank (1897) simply applied the name but saw no specimens so far as we can determine. Both Minden (1912) and Coker (1923) considered Frank's species to be a *Pythium* (A. Fischer, 1892, believed it was synonymous with *P. debaryanum*), but curiously neither cited Schacht's illustration to support that view. The fungus which Schacht (1856) depicted cannot be identified; the one terminal swelling (Berlese and deToni called it an oogonium) figured is pythiaceous, but not far removed from the configuration of a small, immature sporangium of a *Pythiopsis*.

*Saprolegnia siliquaeformis* Reinsch

Jahrb. Wiss. Bot. 11:293, pl. 15, figs. 12, 13. 1878

Although Cornu (1877b) considered *Saprolegnia siliquaeformis* to be a *Monoblepharis* and named it *M. prolifera*, A. Fischer (1892) created the genus *Gonopodya*

to accommodate Cornu's species. Thaxter (1895) put Reinsch's species in *Gonapodya* -- as *G. siliquaeformis* -- but this name also is synonymous with *G. prolifera* (Sparrow, 1960).

*Saprolegnia spiralis* Cornu

Ann. Sci. Nat. Bot. (5<sup>e</sup> sér.) 15:10, pl. 6, figs. 10-12, 15-17; pl. 7, figs. 1-4, 10, 1872

Simultaneous with the report and description of the new taxa *Rozella septigena* and *Woronina polycistis*, Cornu (*loc. cit.*) described *Saprolegnia spiralis* as one of the host fungi. Since the species was based on obviously infected material, it is excluded.

Curiously, Cornu's *Saprolegnia spiralis* has been reported three times (since the original account) and evidently as a valid species. Höhnk (1935a), recorded *S. spiralis* in some collections from Germany. As *S. spiralis* Cornu *sensu* Minden, the species was reported from Czechoslovakia by Cejp (1959a:251, fig. 95). He thought Horn's *S. retorta* was possibly synonymous with Cornu's species. Neither the description nor illustration of *S. spiralis* Cornu *sensu* Minden published by Logvinenko and Meshcheryakova (1971:87, fig. 2) provide a clue as to what watermold species (from Russia) was actually at hand.

Johannes (1955a) transferred Cornu's *Saprolegnia spiralis* to *Cladolegnia* as a new combination, but evidently did not do so on the basis of a study and analysis of specimens. Cejp (1959a) cited *C. spiralis* (Cornu) Johannes as a synonym of Cornu's species.

*Saprolegnia spiralis* Cornu var. *Charkoviensis* Shkorbatov

This epithet appears in Cejp's compilation of the Oomycetes of Czechoslovakia, published in 1959(a). It is evidently a name resulting from a misinterpretation or an error in transcription. The variety described by Shkorbatov (1923, 1927) was applied to Minden's *Saprolegnia variabilis*.

*Saprolegnia tenuis* Kützing

Species Algarum, p. 159. 1849

The characteristics said to define this species -- branched, attenuate, flaccid, nonseptate filaments -- are too scanty to be useful in identifying its affinities. Possibly the organism which Kützing saw was not even saprolegniaceous.

*Saprolegnia toruloides* (Kauffman and Coker) Reed

*In*, thesis, An Illustrated Guide..., p. 43, fig. 17. 1973

Reed (*loc. cit.*) assigned *Isoachlya toruloides* (Kauffman, 1921) to *Saprolegnia*. The species had earlier been relegated to synonymy with *S. torulosa* (Howard *et al.*, 1970).

*Saprolegnia variabilis* Minden var. *Charkoviensis* Shkorbatov

Bot. Mater. Inst. Sporov. Rast. Glavn. Bot. Sada RSFSR 2:35. 1923

The description has nothing in the way of critical details to permit a decision on the taxonomic status of the variety. From Shkorbatov's later (1927:82) account, this variety is probably nothing more than a representative of *Saprolegnia ferax*.

*Saprolegnia xylophila* Kützing  
Phycologia Generalis, p. 157, pl. 2. 1843

It is very likely, if one may judge from illustrations, that Kützing had indeed observed a watermold (perhaps a mixture) to which he applied this name. The apices of some filaments, for example, are illustrated as containing spore-like bodies. The description does not convey the impression of a watermold, and nothing in later accounts (1845, 1849) by Kützing adds any information on which to base a decision on the affinities of the organism. The fasciculate nature of the filaments of *S. xylophila* recall some of the Fungi Imperfecti, and this is strengthened by taking into account the substratum on which the fungus was found: decaying wood (in stagnant water). Too ill-defined to be identified.

*Scoliolegnia depauperata* Dick  
J. Gen. Microbiol. 65:326. 1971

There are no illustrations or description of this species. The name first appears in Table 1 of Dick's 1971(c) publication, and in 1973 (p. 141), he refers to it as a *nomen nudum*.