

CHAPTER 37

PROTOACHLYA Coker Saprolegniaceae p. 90. 1923

Monoecious. Sporangia cylindrical, subcylindrical, clavate, or elongate-obpyriform; renewed in a sympodial, cymose, or basipetalous fashion, and also by internal proliferation, in which instances the secondary ones may be produced outside the exit orifice of the discharged ones. Spores dimorphic; flagellate at discharge, some or all swimming away upon release, or some encysting and remaining in a loose cluster in the vicinity of the exit orifice; occasionally dictyuchoid, rarely aplanoid. Gemmae usually present. Oogonia lateral, intercalary, or terminal; spherical or obpyriform, cylindrical or pyriform when intercalary. Oogonial wall pitted or unpitted; smooth. Oogonial stalks usually short; simple or once-branched. Oospores centric or subcentric; one to several per oogonium. Antheridial branches androgynous, monoclinal, or diclinous. Antheridial cells simple; apically or laterally attached.

Type species: *Achlya paradoxa* Coker, Mycologia 6:285, pl. 146. 1914.

Although species in this genus resemble the *Achlyas*, the spore behavior pattern is sufficiently distinct to maintain *Protoachlya* distinct from *Achlya*. The primary spores are equipped with flagella at discharge (in *Achlya* species they are not, or the flagella are so evanescent as not to be seen readily), and thus may swim away from the orifice at release. Often, however, even from the primary sporangia, some of the spores encyst at the exit orifice in the vicinity of this pore. The resulting cluster of spores is not a spherical, hollow ball of cells as is characteristic of the *Achlyas*. Dictyuchoid sporangia are not uncommon, but so far as we are aware only secondary ones exhibit this type of spore release.

In 1954, H. Meier and Webster published on the ultrastructure of the primary spore cysts in *Protoachlya paradoxa*. They found these to be smooth, and suggested on this basis that *Protoachlya* was more closely related to *Achlya* than to *Saprolegnia*.

Great caution and careful observation must be taken in identifying isolates of *Protoachlya* to distinguish them from members of *Pythiopsis*. The emerging spores of representatives of the latter genus may encyst swiftly in loose aggregations near the sporangium exit papilla, but these cells are only of the primary type (even in cases of repeated encystment and excystment). Spores of *Protoachlya* species may, as they leave the exit orifice, initially behave like those of representatives of *Pythiopsis*. Specimens of *Protoachlya*, however, produce both primary and secondary planonts (dimorphic).

Key to the species of *Protoachlya*

1. Oogonia smooth only *P. paradoxa* (p. 587)
1. Oogonia ornamented or both smooth and ornamented 2
 2. Antheridial apparatus generally hypogynous *P. hypogyna* (p. 588)

- 2. Antheridial apparatus not hypogynous 3
- 3. Oospores centric only; apex of oogonial stalk
sometimes flared at juncture with oogonial wall *P. benekei* (p. 591)
- 3. Oospores centric and subcentric; apex of oogonial stalk not flared 4
 - 4. Some oogonia smooth, others provided with one
to a few cylindro-conic or cylindrical projections,
these giving the oogonium an asymmetrical aspect;
predominantly 2-6 oospores per oogonium *P. polyspora* (p. 593)
 - 4. All oogonia densely or sparsely ornamented;
predominantly 1-2 oospores per oogonium *P. mucronata* (p. 596)

Protoachlya paradoxa (Coker) Coker
Saprolegniaceae, p. 91, pls. 26-28. 1923
(Figure 88 C-F)

Achlya paradoxa Coker, Mycologia 6:285, pl. 146. 1914.
Isoachlya paradoxa Kauffman, Amer. J. Bot. 8:231. 1921.

Monoecious. Mycelium diffuse, moderately extensive; hyphae slender to moderately stout, sparingly branched. Sporangia narrowly clavate to narrowly cylindrical, straight or slightly curved, but sometimes strongly curved near the apex; apical exit papilla prominent; generally renewed in a basipetalous fashion, less often in a sympodial manner or internally; 163-308 x 15-34 μm . Spores dimorphic; at discharge behaving in a saprolegnoid or basic achlyoid manner with some spores encysting in an ill-defined clump near the exit orifice and others swimming away for some distance before encysting; flagellated during discharge; infrequently behaving in a dictyuoid or aplanoid manner; primary spore cysts 8-12 μm in diameter. Gemmae spherical, subspherical, or obpyriform, infrequently cylindrical or irregular; terminal or intercalary, commonly catenulate. Oogonia lateral, occasionally terminal, infrequently intercalary; very rarely sessile; obpyriform or spherical, broadly oval when intercalary, rarely constricted or cylindrical; (28-) 40-60 (-100) μm in diameter. Oogonial wall sparsely and sometimes inconspicuously pitted; smooth. Oogonial stalks $1/2$ -1 (- $2^{1/2}$) times the diameter of the oogonium, in length; stout, often irregular and curved; unbranched. Oospores subcentric or centric; spherical or broadly oval; (1-) 4-8 (-22) per oogonium, and usually filling it; (18-) 26-32 (-41) μm in diameter; germination not observed. Antheridial branches abundant, and several often attending each oogonium; frequently dichinous, occasionally androgynous, infrequently monochinous; usually short, slender, twisted or irregular, and sometimes coiling loosely about the oogonial stalk; unbranched; dichinous ones sometimes not persisting. Antheridial cells clavate to irregular; stout; often sharply bent; persisting; laterally or apically appressed; fertilization tubes present, not persisting.

This is the only known *Protoachlya* with smooth oogonia, and it can be recognized easily by this characteristic. The sporangia are protoachlyoid in all respects, but in cultures aging in staling water the frequency of saprolegnoid discharge decreases markedly with time. As Coker (1923:91) observed, and Beverwijk (1948) so carefully chronicled, the sporangia originating by internal proliferation (as in *Saprolegnia*) develop outside the confines of the emptied sporangium. Accordingly, nested secondary sporangia are not to be seen in *P. paradoxa*. Spores emerging as in *Achlya* do not form a discrete, hollow sphere. Usually the planonts encyst a short distance from the exit orifice, but some swim away before settling into a poorly defined group with others. The loose cluster of cysts usually disperses soon after it is formed as the peripheral cells excyst and the secondary planonts emerge. Beverwijk found the oospores to be centric and subcentric, but Coker described them as centric.

Chaudhuri and Kochhar (1935:141) authored a new combination *Protoachlya paradoxa* (Coker) with *Achlya paradoxa* and *Isoachlya paradoxa* as synonyms. Twelve years previously Coker (1923) already had made this nomenclatural change (as Mundkur, 1938, noted).

CONFIRMED RECORDS: -- CANADA: Maestres (1977:150). CZECHOSLOVAKIA: Cejp (1959a:120, fig. 33). GERMANY: Richter (1937:244). INDIA: Chaudhuri and Banerjee (1942:216); Chaudhuri and Kochhar (1935:141, pl. 6, figs. 10-25); Chaudhuri *et al.* (1947:58, figs. 29, 30). LATVIA: Apinis (1929a:224). NETHERLANDS: Beverwijk (1948:235, fig. 5). SOUTH AMERICA: A. L. Rogers *et al.* (1970:102). UNITED STATES: Beneke (1948b:89); Coker (*loc. cit.*); Lounsbury (1930:215 *et seq.*, figs. 1, 2); Milanez (1966:99, pl. 10, figs. f, g).

RECORDED COLLECTIONS: -- CANADA: Maestres and Nolan (1978). DENMARK: A. Lund (1978). GERMANY: Höhnk (1956a); Schlösser (1929). UNITED STATES: Beneke and Schmitt (1961); R. L. Butler (1975(?); Cotner (1930b); Crane and Vermillion (1966); Klich (1980); Rooney and McKnight (1972); Slifkin (1964). USSR: Logvinenko and Meshcheryakova (1971).

SPECIMENS EXAMINED: -- UNITED STATES (1), TWJ. MWD (1). Centraalbureau (1).

Protoachlya hypogyna (Coker and Pemberton) Johnson and Seymour
Mycotaxon 92:11-32, figs. 40-50, 2005, and present fig. 89

Achlya hypogyna Coker and Pemberton, Bot. Gaz. (Crawfordsville) 45:194, figs. 1-6. 1908.
Basionym

Protoachlya hypogyna Shanor and Conover, Amer. Midl. Naturalist 28:748, pl. 1. 1942.

Monoecious. Mycelium limited, dense; hyphae slender, sparingly to moderately branched. Sporangia narrowly cylindrical to clavate, usually irregular, and occasionally strongly curved distally; discharge papilla prominent; renewed sympodially, in a cymose, or a basipetalous manner, and occasionally internally; 81-603 x 12-43 μm .

Spores dimorphic; at discharge some, most, or all swimming from the orifice, or some encysting after release, and remaining in a loose, undefined clump in the region of the exit pore; rarely released in a dictyocoid or aplanoid fashion; primary spore cysts 10-12 μm in diameter. Gemmae spherical, obpyriform, or cylindrical; terminal or intercalary, single or catenulate. Oogonia lateral, infrequently terminal or sessile, rarely intercalary and single or catenulate; spherical, subspherical, obpyriform, broadly apiculate, obovate, ovate, or angular; (20-) 40-50 (-90) μm in diameter, exclusive of wall ornamentations. Oogonial wall unpitted or rarely very sparsely pitted; smooth or provided sparsely with papillate or cylindro-conical projections, or merely sparsely crenulate; smooth or roughened on inner surface. Oogonial stalks ($1/8$ -) $1/2$ -1 (- $1\frac{1}{2}$) times the diameter of the oogonium, in length; stout, straight or curved; sometimes faintly irregular. Oospores centric or subcentric; spherical, ellipsoidal, or oval, sometimes pyramidal or flattened at one side due to mutual pressure; (1-) 2-6 (-12) per oogonium, and usually not filling it; (18-) 26-32 (-45) μm in diameter; at germination forming a slender, unbranched germ hypha bearing a small, terminal sporangium. Antheridial apparatus usually consisting of hypogynous or hemihypogynous cells, or of androgynous or monoclinal, or rarely diclinal antheridial filaments; antheridial branches moderately stout; usually short, often irregular and sparingly branched; persisting. Antheridial cells simple; clavate or tubular, unbranched, lobed, or branched; persisting; laterally or apically appressed; fertilization tubes present, persisting.

Protoachlya hypogyna differs from the other species in the genus by reason of its commonly occurring hypogynous antheridial cells (Fig. 89 A-C). Such cells may branch laterally (hemihypogynous) and the resulting short protuberance then often becomes appressed to the oogonial wall (Fig. 89 E). Oogonia lacking a hypogynous antheridial cell may (Fig. 89 J) or may not be attended by antheridial filaments of a monoclinal or diclinal origin.

The ratio of smooth (Fig. 89 G, I) to ornamented (Fig. 89 A, B, J) oogonia in *Protoachlya hypogyna* is by no means constant, judged either by the performance of our isolates or the various characterizations of this species that appear in the literature. The ornamentations are consistently sparse, and usually papillate (Fig. 89 B), but some are longer and more prominent than papillae (Fig. 89 A, J). Similarly, the predominant number of oospores may be noticeably different among individual specimens. Shanor and Conover (*loc. cit.*) used oospore number as one character separating their *P. hypogyna* (1-2 usually) from *A. hypogyna* (3-5 generally).

Clausz (1965, 1968), working on oospore germination in *Achlya hypogyna* gathered experimental evidence to show that the configuration of wall ornamentations and the number of oospores were influenced by temperature. Colonies grown at 15 °C formed oogonia with prominent wall projections and 2-6 oospores per oogonium. At 25 °C, however, the oogonia produced by the mycelium were nearly smooth, and generally contained only 1-2 oospores each.

The status of *Achlya hypogyna* is very difficult to reconcile with previous statements concerning the behavior of its asexual apparatus. We see no evidence from

the morphology of the sexual cells of *A. hypogyna* and the *Protoachlya hypogyna* of Shanor and Conover to contest our claim that the two are synonymous. Accounting for alleged differences in spore behavior and sporangium renewal, however, is critical to the merger of the two taxa.

In the original account of *Achlya hypogyna*, Coker and Pemberton (*loc. cit.*) illustrated the primary spores as biflagellate cells on emergence, and in Coker's later (1923) description of the species he called attention to the similarity in appearance of the sporangia of *A. hypogyna* to those in his *Protoachlya paradoxa*. In the description of *P. paradoxa*, however, Coker (1923:90) wrote that some sporangia were renewed internally as in species of *Saprolegnia*, and certainly Shanor and Conover (*loc. cit.*) noted this for their *P. hypogyna*. In the cultured specimens we have examined, sporangia may be renewed just as described for *Protoachlya* species, and the emerging spores are equipped with flagella. We have reexamined the single existing type specimen (preserved) of *A. hypogyna*, and are satisfied that the sporangia displayed are identical (shape and prominent terminal papilla) to those produced by *P. hypogyna*. We found no convincing evidence of internal sporangium renewal in the mycelium on the type slide. It is indeed curious why Coker (1923:104-106) did not assign *A. hypogyna* to his genus *Protoachlya* when he obviously saw cases of spore behavior in *A. hypogyna* exactly like those encountered in *P. paradoxa*.

Equally curious is T. W. Johnson's (1956b) retention of *Achlya hypogyna* in *Achlya* and his statement that the type specimen of this species, his isolate from Michigan, and *P. hypogyna* (seen as living material) were not synonymous. We have again examined the only two preserved specimens of Johnson's collection of *A. hypogyna* still in existence, and are now satisfied that on one point at least, he did not describe the fungus precisely. All of the sporangia in the preserved material of this *A. hypogyna* are clavate, and each has a noticeable exit pore at the end of a prominently raised exit papilla. Such sporangia are identical to those we find in *Protoachlya hypogyna*. None of the sporangia in Johnson's material shows internal proliferation, and notes taken on spore discharge at the time the Michigan isolate was characterized do not mention spore behavior. From our study of *P. hypogyna* we recognize that isolates often display a basically achlyoid spore discharge pattern. However, the emerging spores seldom cluster as compactly as is expected of an *Achlya*, and they are flagellate on discharge. In sum, Johnson simply failed to study spore discharge critically, and therefore A. W. Ziegler (1948b) was correct in concluding that the *A. hypogyna* of Coker and Pemberton was synonymous with *P. hypogyna* Shanor and Conover.

The characteristics chosen by Shanor and Conover (*loc. cit.*) to emphasize the difference between *Protoachlya hypogyna* and *Achlya hypogyna* are for the most part not constantly expressed, and thus are not reliable. As Clausz (1965, 1968) has demonstrated, for example, the number of oospores and prominence of the wall ornamentations are temperature-influenced. Some oogonia in our isolates of *P. hypogyna* have a smooth contour to the inner surface of the oogonial wall while others, often on the same hypha, are irregular in this region. In our specimens, catenulate oogonia are quite infrequently formed, but were reported by Shanor and Conover to be very

common in *P. hypogyna*. The hypogynous nature of the antheridial apparatus, motility of spores at discharge, and the development of wall projections by some oogonia are features common to both *A. hypogyna* and *P. hypogyna*. These features are much more important to the taxonomy of these species than are oogonium wall pigmentation or other characters singled out by Shanor and Conover.

Dick (1969c) has written that *Achlya hypogyna* might represent an aggregate species, that is, one defined as broadly as to include three other valid ones (*Protoachlya hypogyna*, *A. mucronata*, and *A. benekei*). We disagree with Dick's aggregate concept because of the very different sporangial behavior patterns among these taxa (see discussion of *Pythiopsis*).

The *Achlya hypogyna* reported from India by J. N. Rai and Misra (1976) is a doubtful record; there were no papillate oogonia in their specimens. Doubtful also is a second record by J. N. Rai and Misra (1977b) of this species. Although they reported the fungus to have hypogynous antheridia, none is illustrated. The form reported by Kobayasi and Konno (1971a) seems to have differed from the usual concept of *A.* (= *Protoachlya*) *hypogyna* only in having more densely ornamented oogonia.

CONFIRMED RECORDS: -- CZECHOSLOVAKIA: Cejp (1959a:176, fig. 58). JAPAN: Kobayasi and Konno (1971a:9, fig. 3F-H). PEOPLE'S REPUBLIC OF CHINA: Ou (1940:435). UNITED STATES: Beneke (1948b:90); R. L. Butler (1975: figs. 145-152); Clausz (1968: figs. 1-8); Coker (1923:102, pls. 29, 30); Coker and Pemberton (*loc. cit.*); Cooper (1929a: pl. 2); T. W. Johnson (1956b:26, pl. 2, figs. J-P); Shanor and Conover (*loc. cit.*); A. W. Ziegler (1948b:25, pl. 5, figs. 6-8; 1952:9, 10, pl. 4, figs. 2, 3). USSR: Naumov (1954:70).

RECORDED COLLECTIONS: -- BRITISH ISLES: H. Meier and Webster (1954)(?); R. E. Roberts (1963). GERMANY: Höhnk (1935a, 1956a). INDIA: J. N. Rai and Misra (1976:843; 1977a; 1977b:73, fig. 1b)(?). NEW ZEALAND: Karling (1966f). POLAND: Żebrowska (1976a). UNITED STATES: Barksdale (1960); Coker (1927); J. V. Harvey (1925a, b; 1927b; 1930); Monsma (1936); A. W. Ziegler (1958b). USSR: Domashova (1974b); Logvinenko and Meshcheryakova (1971).

MATERIAL EXAMINED: -- UNITED STATES (2), TWJ, RLS & W. C. Coker (preserved type of *A. hypogyna*). CENTRAL AMERICA (1), RLS. MWD (1).

Protoachlya benekei (Furtado) Johnson and Seymour

Mycotaxon 92:11-32, figs. 36-39. 2005, and present figs. 88 A, B; 90 G, H

Achlya benekei Furtado, Rickia 2:122, figs. 1-10. 1965. Basionym

Monoecious. Mycelium dense, limited; hyphae slender, moderately branched. Sporangia sparse; clavate, cylindrical; straight, curved, or bent; exit papilla prominent; renewed sympodially, infrequently in a cymose manner; 96-233 × 18-28 μm. Spores dimorphic; at discharge behaving in an achlyoid manner, but with many spores grouping only in an irregular, undefined clump and soon swimming away, but others

encysting or swimming away immediately from exit orifice in a saprolegnoid fashion and then encysting; motile during discharge; primary spore cysts 10-11 μm in diameter. Gemmae sparse; spherical, subglobose, broadly ovoid, or short-cylindrical; terminal or intercalary, single or catenulate. Oogonia lateral or terminal; spherical to subspherical or faintly hemispherical, occasionally broadly ovoid; (50-) 66-75 (-83) μm in diameter, including wall ornamentations. Oogonial wall unpitted; provided moderately densely or sparsely with papillate to short-cylindrical ornamentations. Oogonial stalks ($1/3$ -) 2-3 times the diameter of the oogonium, in length; stout, straight or curved; isodiametric or flaring outward conspicuously at the junction with the oogonial wall; unbranched. Oospores centric; spherical or broadly oval; (1-) 2-3 (-6) per oogonium, and often nearly filling it; (10-) 30-40 (-45) μm in diameter; germination not observed. Antheridial branches androgynous or monoclinal; slender, generally irregular; infrequently branched; persisting. Antheridial cells simple; short-clavate to large and irregular; persisting; laterally appressed; fertilization tubes not observed.

It is difficult to distinguish between *Protoachlya benekei* and *P. mucronata* since they deviate so little from one another. Furtado (*loc. cit.*) was aware of the close likenesses of the two when he described his species, and singled out certain characters that were prominently enough expressed to separate these taxa. In our specimen of *P. benekei* the ornamentations on most oogonia are more numerous and less variable in length than are those found generally in the material we have of *P. mucronata* (Figs. 88 A, 90 B, C). Commonly there are 2-3 oospores in the oogonia of Furtado's species, while a single one (or only two) usually is encountered in Ziegler's taxon. We have not found diclinous antheridial branches in *P. benekei*; these may be present in *P. mucronata*. So far as is known only centric oospores occur in the former, but both centric and subcentric ones are produced by the latter. In our specimen of *P. benekei* the oogonial stalks are commonly conspicuously flared (Fig. 88 A, B) at the junction with the oogonial wall; such oogonia are sometimes nearly hemispherical. *Protoachlya mucronata* lacks terminally expanded oogonial stalks.

The only previously published report of *Achlya benekei* since the discovery of the species by Furtado is that by Milanez (1970). His specimen (which we have not seen) had a larger oospore size range than Furtado's, and a predominance of monoclinal antheridial branches. In addition -- as Milanez clearly illustrates (1970: figs. 36, 38) -- the specimen he isolated from soil had oogonium wall ornamentations that were larger and more varied as to length than had been described for *A. benekei*. In this character, at least, Milanez' plant approached *P. mucronata*. This being so, our view that *P. benekei* has less variability in the prominence of oogonium wall ornamentations than *P. mucronata*, may well be called into question. Milanez reported that his Brazilian specimen of Furtado's species had centric oospores. However, in at least one figure (Milanez, 1970: fig. 37) the oospore is illustrated as subcentric. This fact also is contradictory to what we have found (see foregoing paragraph) with respect to *P. benekei* and *P. mucronata*. A comparative study of additional specimens, should these be recovered from various collections, is necessary before the status of the two taxa with respect to each other can

be decided. It is possible, of course, that Milanez had isolated *P. mucronata* rather than Furtado's species since the description does not mention the flaring of the oogonial stalk at its juncture with the oogonium proper. This characteristic strikes us as a very prominent recognition feature for *P. benekei*.

The spores of *Protoachlya benekei* behave in exactly the same fashion as those produced by *P. mucronata* (and other *Protoachlyas*). The spores are motile at release, some encysting in an ill-defined clump at or near the exit orifice, while others behave in a saprolegnoid manner. All functional spores are dimorphic.

CONFIRMED RECORDS: -- SOUTH AMERICA: Furtado (*loc. cit.*); Milanez (1970:26, figs. 36-41).

SPECIMENS EXAMINED: -- SOUTH AMERICA (1), RLS. MWD (1).

Protoachlya polyspora (Lindstedt) Apinis
Acta Horti. Bot. Univ. Latv. 4:224, pl. 3. 1929
(Figure 87 D-L)

Dictyuchus polysporus Lindstedt, Synopsis der Saprolegniaceen..., p. 19, pls. 2, 3. 1872.

Monoecious. Mycelium dense, moderately extensive; hyphae stout or slender, sparingly branched. Sporangia short- or long-cylindrical, narrowly clavate or fusiform, and usually slightly irregular; apical papilla prominent; renewed sympodially or in a cymose fashion; 150-300 × 20-50 μm. Spores apparently dimorphic; at discharge behaving in a saprolegnoid or basic achlyoid manner, with some spores encysting near the sporangial orifice; infrequently behaving in an aplanoid fashion, and some primary spore cysts evidently not producing secondary spores; primary spore cysts 12-15 μm in diameter. Gemmae absent. Oogonia predominantly terminal, occasionally lateral, seldom intercalary; spherical to occasionally obpyriform, infrequently oval, obovate, pyriform, or dolioform, sometimes irregular or asymmetrical; spherical ones (40-) 50-75 (-80) μm in diameter; nonspherical ones (51-) 60-70 (-93) × (3-8-) 40-58 (-67) μm, including any wall projections. Oogonial wall pitted or unpitted; smooth, or provided with one to a few papillate to cylindro-conical or cylindrical projections, these often giving the oogonium an irregular or asymmetrical appearance. Oogonial stalks of various lengths, stout, generally slightly irregular; unbranched. Oospores centric or subcentric; spherical; (1-) 2-6 (-32) per oogonium, and usually barely filling it; (18-) 22-26 (-35) μm in diameter; germination not observed. Antheridial branches sparse or moderately abundant; androgynous or monoclinal; usually short, arising near the base of the oogonium; curved, sometimes noticeably irregular; unbranched or branched; persisting. Antheridial cells short; broadly clavate, sometimes slightly irregular; persisting; laterally appressed; fertilization tubes not observed.

In 1929 (a, b) Apinis published a description and ample drawings of a fungus he identified with Lindstedt's (*loc. cit.*) *Dictyuchus polysporus*. The watermold Apinis

collected produced some dictyucoid sporangia, but because sporangia also released spores in the manner of members of *Achlya*, he assigned Lindstedt's species to *Protoachlya*. Apinis did not think it significant that his isolate generally produced slightly irregular or asymmetrical oogonia while Lindstedt (*loc. cit.*, pl. 3, figs. 1-3) had illustrated portions of what must be interpreted as spherical oogonia for his *D. polysporus*. Furthermore, some of the illustrations that Apinis provided of discharging sporangia of his *Protoachlya polyspora* showed aplanoid not dictyucoid behavior as he thought.

More than thirty-five years before Apinis "rediscovered" Lindstedt's species, A. Fischer (1892:364) expressed the opinion that the description and illustrations of *D. polysporus* were based on a conglomerate of two watermolds, one a *Dictyuchus* and the other a *Saprolegnia*. Evidently Apinis ignored Fischer's view, and even Migula's (1903) account of his own collection of *D. polysporus* did nothing to dispute what Fischer had published. Thus, the curious situation has developed where a properly isolated, recognizable watermold (Apinis, 1929a) has been identified with a species strongly suspected of having been circumscribed from a mixed culture (Lindstedt, *loc. cit.*). In retrospect, it probably was unwise for Apinis (*loc. cit.*) to equate his specimens with Lindstedt's, especially in view of the noticeable discrepancy in oogonial shape among the various specimens. Apinis chose to use the name applied by Lindstedt and as there are no specimens of Lindstedt's fungi, Apinis' decision on the synonymy of *D. polysporus* with *Protoachlya polyspora* must stand.

We have isolated three watermolds that produce both spherical, multioosporous oogonia -- as described for *Dictyuchus polysporus* -- and slightly irregular, asymmetrical ones much as Apinis (*loc. cit.*) reported for *Protoachlya polyspora*. The characteristics of the sexual apparatus of our specimens agree with those Apinis ascribed to the *Protoachlya* with one exception: in our specimens the oogonia may have either centric or subcentric oospores. *Protoachlya polyspora* was described as having centric ones, and it is not known for certain just what oospore type occurred in Lindstedt's *D. polysporus*. The discrepancy in the nature of the oospores is not particularly troublesome because some watermolds commonly have both centric and subcentric ones.

It is in the matter of spore release and subsequent behavior that our specimens are difficult to reconcile with *Protoachlya*. We have not seen directly the fate of the encysted primary spores in any of our specimens, although the presence of an occasional empty cyst suggests that motile spores may emerge from those cysts. Of course, such planonts could be either apically biflagellate -- in which case the affinity of the specimen is with *Pythiopsis* -- or laterally biflagellate, and thus ally the isolate to *Protoachlya*. We have observed that if water cultures of some specimens of *Pythiopsis* are not meticulously clean the emerging planonts quickly encyst outside the sporangium orifice in loose clusters that might be viewed as an expression of achlyoid discharge. Moreover, in some specimens of *Protoachlya* grown in staling water most of the planonts in a sporangium may fail to emerge at discharge but will encyst endogenously. If the mycelium bearing such sporangia is then flooded with fresh water, some of the endogenous, encysted spores may excyst, leaving a loose, incomplete network of cyst

walls within the sporangium. Such sporangia may be confused with those behaving in a dictyuoid manner.

Because his fungus from Latvia produced both achlyoid and dictyuoid sporangia Apinis (*loc. cit.*) assigned it to *Protoachlya*. As he did not detail the sequence of events in the release of spores of *P. polyspora*, there is no way to know whether the pattern was achlyoid or protoachlyoid. There is in any case no implied or direct evidence in Apinis' account that the spores in his specimens behaved like those of *Pythiopsis* species.

Two characteristics of the isolates we have identified as *Protoachlya polyspora* bring to mind at least a coincidental affinity to the genus *Pythiopsis*. Each sporangium in these fungi has a prominent apical papilla that, upon opening, leaves a conspicuously flared, tubular projection (Fig. 87 J-L). Sporangia of some representatives of *Pythiopsis* -- *P. irregularis*, for example -- display an identical discharge apparatus (Fig. 86 A-C). The antheridial branches in our cultures of *P. polyspora* are generally rather short, and regularly arise from the hypha directly below the oogonial septum (Fig. 87 D-F); such a near origin is of course very characteristic of such species of *Pythiopsis* as *P. cymosa* (Fig. 85 D) and *P. humphreyana* (Fig. 85 M-P).

Inasmuch as we have been unable to characterize fully the spore behavior in our isolates -- and this knowledge is essential to a decision -- we are obliged to retain the species in *Protoachlya*. A thorough analysis of spore behavior in a reasonable number of isolates of *Protoachlya polyspora* is necessary before a permanent assignment can be made.

Ritchie and Slovin (1974) collected several times from one site (New Jersey) a watermold which they believed was Apinis' *Protoachlya polyspora*. Their specimens commonly had more than 100 oospores in some oogonia -not only a remarkable number but also a condition quite unlike anything Apinis evidently saw in his collection. According to Ritchie and Slovin their watermolds had androgynous antheridial branches, but whether these filaments originated immediately below the oogonia (as is characteristic of species of *Pythiopsis*) is not known. While the oospores of the multioosporous fungi from New Jersey were said to be centric, in the one photograph of an oogonium (Ritchie and Slovin, 1974: fig. 2) at least two oospores appear to be subcentric.

The precise structure and behavior of the spores produced by the isolates described by Ritchie and Slovin (1974:362) is not known, but they stated that some sporangia produced "...*Achlya*-like masses of spores outside the sporangium mouth..." Other sporangia retained encysted spores. The one illustration of a sporangium in the account by these two investigators depicts a very prominent apical discharge papilla.

Protoachlya polyspora might well be considered intermediate among the species of the genus with respect to the oogonial wall configuration. In *P. paradoxa*, the oogonia are consistently smooth; by contrast, those of *P. mucronata* are ornamented. Like *P. hypogyna* and *P. benekei*, *P. polyspora* has both smooth and ornamented oogonia; the former is recognized by its hypogynous or hemihypogynous antheridial cells (none in

P. polyspora), and the latter is separated from *Apinis*' species by its exclusively centric oospores.

CONFIRMED RECORDS: -- CZECHOSLOVAKIA: Cejp (1959a:119, fig. 32).
LATVIA: *Apinis* (*loc. cit.*). MIDDLE EUROPE: Migula (1903:72).

RECORDED COLLECTIONS: -- GERMANY: Lindstedt (*loc. cit.*)(?). UNITED STATES: Ritchie and Slovin (1974:364, figs. 1, 2)(?). USSR: Logvinenko and Meshcheryakova (1971: fig. 5)(?).

SPECIMENS EXAMINED: -- SWEDEN (1), TWJ. UNITED STATES (6), RLS.

Protoachlya mucronata (Ziegler) Johnson and Seymour
Mycotaxon 92:11-32, figs. 51-56. 2005, and present fig. 90 A-F

Achlya mucronata Ziegler, Mycologia 50:403, figs. 1-8. 1958. Basionym
Achlya stellata var. *multispora* J. N. Rai and Misra, Curr. Sci. 46:28. 1977.

Monoecious. Mycelium extensive, moderately dense; hyphae moderately stout, sparingly branched. Sporangia sparse; short- or long-cylindrical to long-clavate, straight or irregular; apical exit papilla not prominent; renewed sympodially or in basipetalous succession; 106-703 x 15-28 μm . Spores dimorphic; at discharge behaving in an achlyoid manner, but with spores grouping in an irregular, undefined clump, and some soon swimming away but others encysting, or swimming away immediately from the orifice in a saprolegnoid fashion and then encysting; motile during discharge; primary spore cysts 9-12 μm in diameter. Gemmae sparse; obpyriform to dolioform; terminal or intercalary, usually single. Oogonia lateral, infrequently terminal or intercalary; spherical to obovoid or oval, broadly dolioform when intercalary; (23-) 30-40 (-66) μm in diameter, exclusive of wall ornamentations. Oogonial wall unpitted; usually provided moderately with short or long papillae and elongate cylindro-conical ornamentations, occasionally only sparsely ornamented; projections straight or curved. Oogonial stalks ($1/2$ -) $1-2^{1/2}$ (-4) times the diameter of the oogonium, in length; stout or slender, straight, curved, or irregular; unbranched, or occasionally sparingly branched. Oospores centric or subcentric, occasionally containing a conspicuous pellucid spot; usually broadly oval, asymmetrical, or broadly ellipsoidal, occasionally spherical; 1-2 (-5), and usually not filling it; (20-) 24-30 (-39) μm , in diameter; at germination forming a short, stout germ hypha bearing a small, terminal sporangium. Antheridial branches generally monoclinal, infrequently or occasionally androgynous and declinal as well; slender, usually irregular; not persisting. Antheridial cells simple; tubular or clavate, and often irregularly so; persisting; laterally or apically appressed; fertilization tubes not observed.

Because of its protoachlyoid spore discharge pattern, this species must be removed from *Achlya*. The spores of *Protoachlya mucronata* emerge as flagellated cells, and then may behave basically as occurs in *Achlya* species except that the encysted spores do not aggregate into a compact or hollow sphere or cluster. Alternatively, the

planonts may leave the sporangium in a saprolegnoid manner (although moving rather sluggishly) only to encyst in a poorly-defined, loose mass at some distance from the orifice. In a few cases, some of the discharging planonts encyst while others from the same sporangium swim away.

There is no mention in A. W. Ziegler's (*loc. cit.*) paper of spore behavior in the two specimens he had collected, and he did not illustrate the sporangia, hence there is no direct evidence that his water molds were protoachlyoid. However, the very close resemblance in sexual apparatus configuration among the specimens he described and the ones we have examined convinces us that these fungi represent a single species.

Spore behavior in *Protoachlya mucronata* may be difficult to determine because the sporangia are very sparse (developing in very young cultures, then being quickly masked by the growing mycelium). Moreover, there is much variation in *P. mucronata* in the extent to which an achlyoid (or pseudoachlyoid) configuration will occur. The full expression of protoachlyoid discharge is rarely observed in standard wet mount preparations under a coverslip.

Our specimens of *Protoachlya mucronata* differ from those described by Ziegler (*loc. cit.*) in oospore type: there are both centric and subcentric ones in our material, but Ziegler reported only the subcentric type. This is not an important difference since it has been demonstrated repeatedly that some Achlyas (as in *Saprolegnia*) may produce both types of oospores in the same oogonium.

Protoachlya mucronata differs substantially from *P. hypogyna* in the nature of the antheridial apparatus. Additionally, the oogonia of *P. mucronata* are more prominently ornamented than are those of *P. hypogyna*. See remarks under *P. benekei*.

Shibuya's *Achlya* sp. (1959:150, 151, fig. 5) cannot be identified with certainty with any of the ornamented Achlyas having centric or subcentric oospores. The illustrations accompanying the description of *Achlya* sp. suggest that its oogonia are characteristic of both *Protoachlya mucronata* and *Achlya crenulata*. Thus, it is possible that Shibuya's *Achlya* was in fact not in unifungal culture when described.

Provisionally we are merging *Achlya stellata* var. *multispora* with *P. mucronata* chiefly on the basis of the illustrations published by J. N. Rai and Misra (1977b) in a separate paper from that in which the variety was first described. We are in any case satisfied that the fungus described by them is not allied to de Bary's *A. stellata*.

Achlya stellata var. *multispora* evidently has achlyoid spore discharge, but J. N. Rai and Misra (1977a) made no mention of emergence of planonts. In one figure (J. N. Rai and Misra, 1977b) illustrating sporangia of the variety, the discharged spore mass is depicted as a loose agglomeration of cells. The sporangia of the variety *multispora* have a very distinct exit papilla. The oogonial wall ornamentations of *A. stellata* var. *multispora* are somewhat more robust than is usually encountered in *Protoachlya mucronata*, but this one difference alone does not exclude the variety as a representative of this species. Oogonium and oospore sizes in these two taxa are not radically different. Three to five oospores per oogonium are commonly produced by *A. stellata* var. *multispora*, and this number, to be sure, is slightly more than is usual (1-2) in *P. mucronata*. A small difference in oospore number, however, is not particularly

noteworthy in separating most taxa in the family. The evidence favors a merger of the variety *multispora* with *P. mucronata*, pending a study of additional specimens that might in the future be recovered and isolated.

CONFIRMED RECORDS: -- INDIA: J. N. Rai and Misra (*loc. cit.*). UNITED STATES: A. W. Ziegler (*loc. cit.*).

RECORDED COLLECTION: -- UNITED STATES: A. W. Ziegler (1958b).

SPECIMENS EXAMINED: -- AUSTRALIA (2), OCEANIA (1), UNITED STATES (12), RLS.

Protoachlya sp.

CANADA: Chong (1973; collected on fish). GERMANY: Höhnk (1956a). INDIA: Khulbe (1977, 1980a); Khulbe and Bhargava (1977). UNITED STATES: Beneke (1948b:91).

EXCLUDED TAXON

Protoachlya parasitica

In Thesis, S. Y. Chong, Univ. British Columbia, Vancouver, p. 17. 1973

This name appears in Chong's dissertation in reference to a watermold parasitic in *Oncorhynchus kisutch* (Walbaum) from Canada. There is no such species described under this name in *Protoachlya*.