

CHAPTER 41

Aphanomyces de Bary
Jahrb. Wiss. Bot. 2:178. 1860

Hydatinophagus Valkanov, Jahrb. Univ. Sofia 27:215. 1931.

Monoecious. Mycelium consisting of slender, delicate, branched hyphae. Sporangium filamentous, of same diameter as vegetative hyphae; renewed occasionally from lateral branching below a terminal one. Spores dimorphic. Primary spores arranged in a single row in the sporangium; emerging as elongate cells, often connected tenuously by a thin, hyaline, cytoplasmic strand at each end; encysting in a spherical or irregular mass at the terminal exit orifice of the sporangium; releasing the secondary planont through a pore, a papilla, or in a schistose fashion. Secondary spore laterally biflagellate, reniform. Gemmae absent. Oogonia lateral, terminal, or intercalary; usually spherical or subspherical. Oogonial wall unpitted; smooth or ornamented on the outer surface, and smooth or irregular on the inner. Oogonial stalks of various lengths, branched or unbranched. Oospores at maturity containing a single, conspicuous, centric or subcentric refractive globule surrounded by cytoplasm; single, and filling the oogonium or not; germinating to form mycelium directly, or producing a germ tube bearing a terminal, filamentous sporangium. Antheridial branches, when present, androgynous, monoclinous, or diclinous. Antheridial cells, when produced, tubular, or clavate to subglobose; attached laterally or apically.

Lectotype: *Aphanomyces stellatus* de Bary, Jahrb. Wiss. Bot., 2:178, pl. 19. 1860.

De Bary (1860) did not designate a type species for the genus, and so far as we are aware, the first to do so were Coker and Matthews (1937). They selected *Aphanomyces stellatus*, and were followed in this by Scott (1961a) and Sparrow (1960). As there are no specimens of *Aphanomyces* in the de Bary collections deposited in the British Museum (Natural History), a holotype cannot now be specified. To avoid confusion, we accept the decision by Coker and Matthews, and merely change the designation from type to lectotype.

In the single extant monograph of the genus, Scott (1961a) proposed three subgenera, *Aphanomyces*, *Axyromyces*, and *Asperomyces*, separated chiefly on the nature of the oogonial wall of the species included. Dick (1973:131) discarded these taxa as illegitimate because the type species of the genus was not included in the subgenus *Aphanomyces*. Much earlier than Scott, Schröter (1893) had recognized two subgenera, *Euaphanomyces* and *Acanthomyces*, and in 1954, Naumov followed this separation. Dick's criticism of Scott's subgenera would also seem to apply to the two taxa proposed by Schröter.

Scott's (1961a) disposition of Valkanov's (*loc. cit.*) *Hydatinophagus* as a synonym of *Aphanomyces* needs no further elaboration. Cejp (1959a:86) recognized Valkanov's genus as a valid one, and placed it in the subfamily Saprolegnioideae.

A number of species in the genus *Aphanomyces* are parasitic and pathogenic on vascular plants and on freshwater animals. The chief ones are *A. euteiches* (Chapter 27), *A. cochlioides* (Chapter 28), *A. raphani* (Chapter 28), and *A. astaci* (Chapter 30). In the listings of records of collections of these species we seldom include host names; these are noted in the host range tables in the foregoing chapters. In addition, there are numerous references in issues of the Review of Applied Mycology and the Plant Disease Reporter (mimeographed) to records of some of the phytopathogenic species: Cassell (1945), D. E. Ellis and Garriss (1943), McWhorter *et al.* (1943), Mix (1945a, b), Sprague *et al.* (1948), Tervet (1943), Tidd (1945), and Ware (1943), to name a few. These two journals may be consulted for additional records. Drechsler (1943a) and J. N. Couch have reported cases of antagonism or parasitism by species of *Aphanomyces* on other fungi.

Many specimens of *Aphanomyces* do not reproduce sexually. Dogma (1966) attempted to induce the sexual apparatus in 32 isolates by modifying temperature and nutrient sources (natural product and chemically defined media). He was unsuccessful, but did not rule out the possibility of dioecism in members of this genus.

Some members of the genus are rarely collected, and then only as invaders of algae or freshwater plankters, for example. Few species will grow on hempseed in gross cultures, but are most often collected on some chitinous (shrimp exoskeleton) or keratinized (snake skin, hair) bait. Whether this is the result of a substrate "preference" or a matter of absence of competing water molds is not known. In our experience, the saprotrophic species of *Aphanomyces* are more likely to occur in wet mud (but not that approaching anaerobic conditions), or water and organic debris. The three commonest plant pathogens in *Aphanomyces* have been collected from agricultural soils that support plantings of the principal host species. Although *A. astaci* is not an obligate parasite, we have searched for it in Sweden in bottom sediments and shoreline waters known to harbor infected *Astacus astaci*, but have not once collected it by the usual gross culture techniques. The species that grow on chitinous or keratinized substrates easily can be isolated into unifungal culture on the same type of bait on which they first grew in gross culture. A few individuals, such as some of those invading plankters, have never been brought into culture.

Representatives of the genus are readily recognized by the filamentous sporangia that evacuate spores in an achlyoid fashion. It is possible to mistake specimens of *Aphanomyces* in very old cultures for representatives of the genus *Pythium* having filamentous sporangia, if the sexual apparatus is not evident. In such aged cultures, the spherical masses of spores that aggregate at the orifice at discharge fall away, leaving a slender, empty sporangium. Depauperate forms of *Aphanomyces* that sometimes develop when pollen is used as a substratum also resemble pythiaceous fungi. The spores of *Aphanomyces* species are fully formed endogenously, and are not discharged into an exogenous vesicle. Species of *Leptolegnia* also have filamentous sporangia bearing spores in a single row, but at discharge, the spores are motile and do not encyst at the exit orifice as in *Aphanomyces* species.

Key to the species of *Aphanomyces*

1. Oogonia present, usually abundant; outer surface of oogonial wall smooth or ornamented, or becoming roughened with age; parasitic or saprophytic (saprotrophic) 2
1. Oogonia absent (not known); parasitic on crayfish *A. astaci* (p. 722)
2. Oogonial wall smooth on outer surface, smooth or irregular on inner surface 3
2. Oogonial wall ornamented (projections), or becoming minutely roughened with aging 13
3. Oogonial wall smooth on outer and inner surfaces 4
3. Oogonial wall smooth on outer surface, irregular on inner surface 9
4. Parasitic in copepods and protozoans; antheridial filaments branched or unbranched, but not coiling profusely about the hyphae or oogonial stalks or both 6
4. Saprotrophic on cellulosic substrates, or on chitinous or keratinized materials; antheridial filaments sometimes coiling profusely about the oogonia, their stalks, and adjacent hyphae 5
5. Colonizing chitinous or cellulosic substrates; antheridial branches sometimes coiling about the oogonial stalks and subtending hyphae, but not branching and wrapping profusely about the oogonia; antheridial branches predominantly diclinous, rarely androgynous *A. laevis* (p. 681)
5. Colonizing keratinized substrates; antheridial hyphae branching and wrapping profusely around the oogonia but not the oogonial stalks or subtending hyphae; antheridial branches predominantly monoclinal or androgynous *A. keratinophilus* (p. 686)
6. Parasitic in protozoans (*Akineta* sp.); oogonia small (up to 24 μm in diameter), oospores small (up to 22 μm in diameter) and with homogenous contents *A. acinetophagus* (p. 688)
6. Parasitic in copepods; oogonia large (up to 39 μm in diameter), oospores large (up to 35 μm in diameter), contents homogeneous, or containing a single centric or subcentric refractive

oil globules surrounded by cytoplasm	7
7. Parasitic in species of <i>Bosmina</i> ; antheridial branches absent	<i>A. bosminiae</i> (p. 689)
7. Parasitic in species of <i>Daphnia</i> ; antheridial branches present	8
8. Oospore 33-35 μm in diameter; extramatrical portion of sporangium tapering toward the apex; primary spore cyst opening in a poroid fashion	<i>A. daphniae</i> (p. 689)
8. Oospores 21-31 μm in diameter; sporangium isodiametric; primary spore cyst opening in a schistose fashion	<i>A. patersonii</i> (p. 691)
9. Antheridial branches declinous	10
9. Antheridial branches declinous, monoclinal, and androgynous	12
10. Oogonia small, predominantly 22-26 μm in diameter; parasitic primarily in sugar beets (<i>Beta vulgaris</i>) but also occurring in other Chenopodiaceae, or in <i>Avena sativa</i>	11
10. Oogonia large, predominantly 28-34 μm in diameter; parasitic principally in peas (<i>Pisum sativum</i>) but also occurring in other legumes	<i>A. euteiches</i> (p. 692)
11. Parasitic in <i>Beta vulgaris</i>	<i>A. cochlioides</i> (p. 696)
11. Parasitic in <i>Avena sativa</i>	<i>A. camptostylus</i> (p. 699)
12. Oogonial stalks consistently short, generally equal in length to the oogonial diameter; antheridial branches not coiling about the hyphae and oogonial stalks; parasitic principally in <i>Raphanus sativus</i> , but also occurring in other Cruciferae	<i>A. raphani</i> (p. 701)
12. Oogonial stalks generally longer than the diameter of the oogonium; antheridial branches coiling about the hyphae and on some long oogonial stalks; parasitic principally in <i>Lycopersicon esculentum</i> , but also occurring in <i>Viola tricolor</i> and other plants	<i>A. cladogamus</i> (p. 703)
13. Outer surface of oogonial wall at first smooth then becoming minutely roughened with age	<i>A. acinetophagus</i> (p. 688)
13. Outer surface of oogonial wall ornamented from early stages in maturation	14
14. Antheridial cells very large, inflated and conspicuous	<i>A. amphigynus</i> (p. 705)

- 14. Antheridial cells not conspicuously inflated 15
- 15. Basal portion of the oogonium tapering broadly to its junction with the cylindrical oogonial stalk; oogonia commonly obpyriform *A. volgensis* (p. 706)
- 15. Basal portion of the oogonium tapering abruptly to its junction with the cylindrical oogonial stalk; oogonia commonly spherical 16
 - 16. Oogonial wall projections conical, narrowly or broadly cylindrical, or papillate, but terminating in a truncate, rounded, or umbonate apex 17
 - 16. Oogonial wall projections short- or long-conical, or tapering, but terminating in a sharp, narrow apex 19
- 17. Wall projections papillate, scattered or dense *A. scaber* (p. 708)
- 17. Wall projections long-conical or cylindrical, the apex rounded or truncate, or infrequently umbonate; dense 18
 - 18. Saprotrophic; ornamentations predominantly cylindrical, and usually with a rounded, truncate or infrequently umbonate apex *A. stellatus* (p. 711)
 - 18. Parasitic in filamentous algae (*Spirogyra* spp., *Zygnema* spp., *Mougeotia* spp.); ornamentations generally long-conical, and occasionally slightly curved, but usually with a rounded apex *A. norvegicus* (p. 713)
- 19. Wall projections consisting predominantly of long, sharply pointed, curved or straight spines that are occasionally bifurcate; parasitic in *Nitella flexilis*, or saprotrophic *A. sparrowii* (p. 715)
- 19. Wall projections consisting predominantly of short, strongly tapering, sharply-pointed spines that are not bifurcate; parasitic in filamentous, zoosporic fungi 20
 - 20. Parasitic in *Pythium* species; oospores predominantly 24-32 μm in diameter *A. exoparasiticus* (p. 717)
 - 20. Parasitic in species of Saprolegniaceae, oospores predominantly 19-21 μm in diameter *A. parasiticus* (p. 718)

Aphanomyces laevis de Bary
Jahrb. Wiss. Bot. 2:179, pl. 20, figs. 17, 18.1860
(Figures 80 J-L, 81 A-E)

Aphanomyces helicoides Minden, Kryptogamenfl. Mark Brandenburg 5:559. 1912 (1915).
Aphanomyces balboensis Harvey, J. Elisha Mitchell Sci. Soc. 58:35, pl. 8, figs. 1-7. 1942.
Aphanomyces laevis var. *helicoides* (Minden) Cejp, Oomycetes I, Flora ČSR, Ser. B, Part 2,
p. 97. 1959.

Monoecious. Hyphae delicate or moderately stout; sparingly or densely branched; generally isodiametric, but occasionally twisted and contorted. Sporangia filamentous; straight, curved, bent, or irregular and sinuous; rarely tapering toward the apex; predominantly unbranched, infrequently once-branched; extremely variable in length, 77- 818 x 4-12 μm . Spores dimorphic. Primary spores cylindrical to oval; in a single row in the sporangium; usually connected by a thin, protoplasmic strand; rarely spherical, then not interconnected; at discharge, encysting in a loose or compact, spherical to irregular cluster at the exit orifice; cysts 6-12 μm in diameter; releasing the secondary planont through a pore. Secondary spores reniform, laterally biflagellate. Gemmae absent. Oogonia generally lateral or terminal, occasionally sessile; predominantly spherical or subspherical, infrequently obpyriform, rarely oval, broadly ellipsoidal, or irregular; (16-) 24-28 (-39) μm in diameter. Oogonial wall unpitted; smooth, but becoming quasi-roughened as antheridial cells disintegrate. Oogonial stalks $\frac{1}{8}$ - 4 times the diameter of the oogonium, in length, but usually about as long as the oogonial diameter; generally unbranched, infrequently once- or twice-branched, or bearing one or two lateral, conical, cylindrical, or papillate projections; straight or curved; usually somewhat irregular in outline. Oospores containing a centric or subcentric refractive globule in the cytoplasm; spherical; single, and usually not filling the oogonium; (12-) 20-26 (-31) μm in diameter; at germination forming an unbranched or sparingly branched germ hypha that occasionally produces a terminal sporangium, or forming a sparingly branched mycelium. Antheridial branches, when present, generally declinous or monoclinal, infrequently androgynous; varying greatly in extent and configuration, often twisted or moderately contorted; branched or unbranched, and frequently, rarely, or not at all coiling about the oogonial stalks or adjacent hyphae; when coiling, sometimes forming tight, dense wrappings (knots) about the hyphae; persisting. Antheridial cells simple; clavate, cylindrical, vermiform, often irregular, infrequently large and bulbous; straight, curved or bent; persisting; laterally appressed; fertilization tubes present or absent; persisting.

The original description of *Aphanomyces laevis* was extremely meager (de Bary, *loc. cit.*), but the illustrations accompanying the circumscription convey well the general aspect of the species as de Bary recognized it. Numerous morphological variants have since been found (Boedjin, 1923; Coker, 1923; J. N. Couch, 1926a; Dogma, 1966; Goldsmith, 1948, among others) as have various physiological "strains", (R. I. Smith,

1940; Nolard-Tintigner, 1974; O'Bier, 1960; G. C. Srivastava and R. C. Srivastava, 1977e; Vishniac and Nigrelli, 1957, for example). The chief morphological variation encountered in *A. laevis* is that of the extent to which the antheridial branches develop. An evaluation of this characteristic requires a prior analysis of Minden's (1912) *A. helicoides*.

Unfortunately, Minden (*loc. cit.*) failed to illustrate his *Aphanomyces helicoides*, but explicitly mentioned the coiling nature of the antheridial branches (associated with oogonia), and, additionally, their development into localized tangles of hyphal branches. Minden himself was not satisfied that his fungus was more than a variety of *A. laevis*, but nevertheless chose to accord it species rank. Since his time, there have been several reports of isolates of *A. laevis* in which (occasionally or rarely) antheridial branches tended to coil about hyphae and oogonial stalks (J. N. Couch, 1926a; Coker, 1923). In 1941, Cutter provided the most detailed account of *A. helicoides* up to that time. His specimens produced oogonia in clusters, and also formed short, intertwined branches (hyphal knots) at intervals along the mycelium. He concluded that *A. helicoides* was a valid species and should be retained separate from *A. laevis*.

Howard and his associates (1970) discussed *Aphanomyces helicoides* as a taxon doubtfully distinct from *A. laevis*. The hyphal knots alleged to be characteristic of Minden's species were absent in some of their specimens, or of variable occurrence in others during culturing. Since some isolates retained some degree of antheridial branch coiling, Howard and his associates did not merge *A. helicoides* with *A. laevis*. One isolate studied by T. W. Johnson (1974b) retained the coiling antheridial structure when cultured in either soil extract or pond water. Moreover, in specimens identified as *A. laevis*, he found that less than 11% of the oogonia were attended by coiled antheridial branches.

What was at the time judged to be "typical" *Aphanomyces helicoides* is known from one collection in Sweden (T. W. Johnson, 1977c). The isolate, recovered from a bog water sample, had a particularly pronounced coiling pattern to the antheridial filaments (Fig. 80 L). At the time, Johnson concluded that whether *A. helicoides* and *A. laevis* were indeed separate species was unresolved.

While the world literature on *Aphanomyces helicoides* is rather sparse, that on *A. laevis* is not. An analysis of the descriptions, discussions, and illustrations of the two taxa permits only one conclusion: they are representatives of a single, broadly definable taxon. At one extreme are specimens in which there is no antheridial branch coiling or clustering; at the other are ones having very pronounced and abundantly produced, coiled and tangled filaments. Between these are a range of individuals showing a wide degree of variation in the occurrence and frequency of these two characteristics (as, for example, the specimens examined by J. N. Couch, 1926a). Thus, to be sure, there are specimens clearly representing Cutter's (1941) and Scott's (1961a) concept of *A. helicoides*. On the other hand, there are individuals in which branch coiling, for instance, is absent, in very low frequency, or appears only occasionally. Moreover, coiling of the antheridial filaments may be very dense and extensive, or restricted to a single coil about an oogonial stalk (Fig. 81 C) or to a few loosely wrapped turnings about the stalk

and its subtending hypha (Fig. 81 D). In our experience with isolates identified as *A. laevis*, we have been unable to suppress (by culture manipulation) the formation of coiled branches if such were produced in gross cultures from which the isolates were obtained. Similarly, by modifying the conditions of incubation (temperature and source of water, for instance) we failed to eliminate coiled antheridial filaments from isolates characteristic of the *helicoides* type. At best, culture condition manipulation modified only the frequency of occurrence of the coiling antheridial hyphae. Admittedly, our experimental work hardly is in strict accord with our disposition of Minden's species.

We see in the *Aphanomyces laevis*-*A. helicoides* complex a precise taxonomic parallel to the *Saprolegnia ferax*-*S. mixta* problem ultimately resolved by Seymour (1970). In both of these complexes, specimens "typical" of each member are extant. Equally abundant, however, are individuals undeniably intermediate between the extremes. Establishing a broad species concept is preferable to a course that narrows species limits such that the components can be recognized confidently only in some individuals.

From time to time, major structural variants of *Aphanomyces laevis* have been described; certain of these accounts are worthy of mention.

Specimens of *Aphanomyces laevis* with larger oogonia and oospores than previously had been recorded were reported by J. N. Couch (1926a:215). In his plants, the oogonia tended to cluster at points along the hyphae, and occasionally the oogonial walls appeared to be ornamented because of the adhering remnants of disintegrating antheridial cells. We have found in some isolates of *A. laevis* that oogonia developed on hyphae growing directly on keratinized substrates also are irregular or distinctly roughened in general configuration. Oogonia on the same filaments growing in water, however, are consistently spherical and smooth. Representatives of *A. laevis* collected by Dogma (1966) exhibited some coiled antheridial branches, but none of the hyphal knots such as Cutter (1941) had described for *A. helicoides*. Some oogonia, Dogma found, were lobed because of indentations in the wall. In this same Philippine material, the oogonia and oospores were intermediate in diameter between those characteristic of *A. laevis* and those of *A. helicoides* (both *sensu stricto*). Goldsmith (1948) identified some African specimens of *Aphanomyces* as *A. laevis*, even though antheridial filament coiling was common. There were no hyphal knots (Cutter, 1941) in his material. According to Fox and Wolf (1977a:101), coiling of antheridial branches around hyphae and oogonial stalks was "... practically universal..." in some specimens they identified as *A. laevis*.

Whether Cutter's (1941:227, fig. 15A, B) form of *Aphanomyces laevis* can be properly aligned with de Bary's species is open to debate. The fungus, collected on nymphs of a species of *Odonata*, produced declinous, abundantly lobed or branched antheridial filaments, but did not form androgynous ones. The oogonial stalks were extremely short, Cutter reported, and the diameters of the oogonia and oospores were somewhat smaller than is usually encountered in *A. laevis*. We have recovered similar variants of de Bary's species on chironomid exuviae and on keratinized baits used in gross cultures.

With considerable reservation, we are referring to *Aphanomyces laevis* the unidentified *Aphanomyces* sp. 2894 described by T. W. Johnson (1974b:21, figs. 87-93).

Certain differences in the characteristics of the isolate and de Bary's species are readily apparent. In all instances the primary spore cysts in *Aphanomyces* sp. 2894 released the secondary planont through a papilla; in *A. laevis*, the cysts are consistently poroid. More than 70% of the oospores in isolate 2894 were 15-18 μm in diameter, a size less than the predominating range found in de Bary's species. Chiefly, however, the Iceland specimens had broadly obovate to obpyriform, laterally expanded, or bulged and somewhat angular oogonia (Fig. 80 J) and few spherical ones. The oospore was distinctly aplerotic. The asymmetrical nature of the oogonia (T. W. Johnson, 1974b: figs. 87-92) is quite unlike the spherical ones found in *A. laevis*. We provisionally assign Johnson's fungus to *A. laevis* until such time as additional material is available for analysis.

Some of the pioneer and contemporary investigators of blackroot of beets (*Beta vulgaris*) have identified the causal agent as *Aphanomyces laevis*: Edson (1915a), Peters (1906, 1911), Härle (1951), Klemm *et al.* (1957), and Terényi (1928-29), for example. While it is impossible to be certain that some of these authors were in fact dealing with *A. cochlioides*, we are assuming that this was the case. As has been noted (Chapter 28), Edson's *A. laevis* was a species of *Pythium*. Naumov (1954) reduced *A. laevis* to synonymy with *A. cochlioides*, but retained *A. lévis* [*sic*] de Bary as a valid taxon.

Aphanomyces laevis var. *helicoides* Cejp (1959a) is simply a new combination according varietal status to Minden's species (not a record for Czechoslovakia). Scott (1961a:26, 27) quite correctly treated J. V. Harvey's (*loc. cit.*) *A. balboensis* as a representative of *A. laevis*. It is likely that Harvey's illustration of gemmae in *A. balboensis* was in error. He did not mention them either in the description or discussion of his species.

In his monograph of *Aphanomyces*, Scott (1961a) refers to records in a 1958 publication of collections of *A. laevis* and *A. helicoides*. As there is no such paper cited in the bibliography to his account, we assume that 1958 refers to his dissertation. Dangeard's publication of 1890-91 also is cited by Scott as a record of *A. laevis*. To be sure, Dangeard commented on this species, but seems not to have himself collected it. According to Milanez (1970), *A. laevis* was reported in Brazil by Beneke and Rogers (1962); they in fact listed only *A. stellatus* and *Aphanomyces* sp. among the water molds they recovered.

CONFIRMED RECORDS:--AFRICA: Alabi (1967: pl. 13, figs. d, e); Goldsmith (1948:141, pl. 16, figs. 11, 12); Paul (1983:464, pl. 1, figs. 1-3). BRITISH ISLES: R. A. Couch (1951:93, pls. 14, 15). CANADA: Maestres (1977:152). CZECHOSLOVAKIA: Cejp (1959a:96, fig. 21). DENMARK: Petersen (1909a:386, fig. 3c; 1910: 525, fig. 3c). EAST GERMANY: Borkowski (1972: fig. 1c). GERMANY: de Bary (*loc. cit.*); Bock (1956:39); Minden (1912:558, 559); Richter (1937:253); Schäufele and Beiss (1973: fig. 1). ICELAND: Howard *et al.* (1970:64, figs. 5-8); T. W. Johnson (1974b:15,16; figs. 74-86). INDIA Khulbe (1980c:78; 1987:55, pl. 1, figs. 4, 5); Prabhuji (1979:74, pl. 8, figs. 10, 11); G. C. Srivastava (1967a:290, pl. 4, figs. 4-6). JAPAN: T. Ito (1942:128, fig. 2d-h; 1944:54); Kobayashi and Ôkubo (1954:562, fig. 2). MIDDLE EUROPE: Migula (1903:74). NETHERLANDS:

Boedijn (1923:86, 87, figs. 1, 2, and 1 unnumbered fig.). NORWAY: T. W. Johnson (1977c: 360). PEOPLE'S REPUBLIC OF CHINA: Er (1973:39); Shen and Siang (1948:195). PHILIPPINES: Dogma (1966:77). POLAND: Stpiczyńska (1962:109, fig. 9); Szwanke (1938:12, pl. 4, figs. 8-10). REPUBLIC OF CHINA: Chien (1980:96, figs. A, B; 1981: figs. 9, 23, 24). Chiou *et al.* (1975:171, pl. 3, fig. 33); RUMANIA: Toma (1971:16, pl. 5). SOUTH AMERICA: Milanez (1970:29). SWEDEN: T. W. Johnson (*see* Norway). UNITED STATES: Beneke (1948b:94); R. L. Butler (1975: figs. 61-68); Coker (1923:16, pl. 50, fig. 17; pl. 55); J. N. Couch (1926a:215); Cutter (1941:226, 227, figs. 1, 2, 13G-L); Fox and Wolf (1977a:101); J. V. Harvey (*loc. cit.*); Holland (1958:19); Humphrey (1893:128, pl. 20, figs. 105-107); Milanez (1966:90, pl. 9, figs. a-d); O'Bier (1960:36, pl. 6, figs. b-d); Overman (1970:28); Rose (1932:45, pl. 5, figs. 44,45); Scott (1961a:25, 27, pl. 2, figs. A-R; pl. 3, figs. A-J); Wolf (1944:31, pl. 3, fig. 19); A. W. Ziegler (1948b:25, pl. 5, fig. 11; 1952:11, pl. 5, fig. 1). USSR: Kasanowsky (1911: pl. 10, fig. 1); Milovtsova (1935a:34); Morochkovs'kiĭ *et al.* (1967:124, fig. 101); Naumov (1954:62).

RECORDED COLLECTIONS:--AFRICA: Alabi (1971a, b; 1973); Fajola *et al.* (1978); AUSTRALIA: Karling (1988). BRITISH ISLES: Cook and Morgan (1934); Perrot (1960); R. E. Roberts (1963); Sparrow (1937). BULGARIA: Valkanov (1931a). CANADA: Dick (1970, 1971c); Maestres and Nolan (1978). CUBA: Sparrow (1952a). CZECHOSLOVAKIA: Jesenoská and Prandlová (1983) DENMARK: A. Lund (1934); Obel (1910a); Petersen (1903); Sparrow (1937). DOMINICAN REPUBLIC: Sparrow and Dogma (1973). GERMANY: Busse and Ulrich (1908); Busse *et al.* (1911); Edson (1915a; a doubtful record -- possibly a *Pythium*); Höhnk (1935a, 1956a); Stoll (1936). HAITI: Scott (1960a). ICELAND: Howard and Johnson (1969); Howard *et al.* (1970). INDIA: E. J. Butler and Bisby (1931); Chaudhuri *et al.* (1947); Chowdhry (1985); Chowdhry and Agarwal (1980a); Chowdhry and Aggarwal [*sic*] (1980b); Dayal and Thakur Ji (1965, 1966); Khulbe (1977; 1979; 1980a, b, d; 1981; 1982b); Khulbe and Bhargava (1977; 1983); Manoharachary and Ramaro (1981); Mekrani (1980); Mer *et al.* (1980); Nolard-Tintigner (1974); Prabhuji and Srivastava (1977); Prabhuji *et al.* (1984); Sati and Khulbe (1980); G. C. Srivastava (1967, b); G. C. Srivastava and R. C. Srivastava (1976b, 1977e); R. C. Srivastava (1976; 1980d; 1985); Sydow *et al.* (1907). JAPAN: Okane (1981); Suzuki (1960e-g; 1961f, l; 1962b-e; 1964); Suzuki and Hatakeyama (1960); Suzuki and Nishita (1963); Suzuki and Tatsuno (1965a, b); MEXICO: Céspedes and Castillo (1982).

NETHERLANDS: Beverwijk (1948). NEW ZEALAND: Karling (1966f). PANAMA: Karling (1987; as *Aphanomyces laevis*). PEOPLE'S REPUBLIC OF CHINA: Yu and Liang (1983). PHILIPPINES: Dogma (1975). POLAND: Staniak (1971); Stpiczyńska-Tober (1965). SRI LANKA: Karling (1981c). TOBAGO AND TRINIDAD: Karling (1987; as *Aphanomyces laevis*). UNITED STATES: Clausz (1970, 1974); Coker (1927); W. B. Cooke and Bartsch (1960); J. N. Couch (1926a); J. V. Harvey (1925a, 6; 1930; 1942); Höhnk (1935a); Jensen (1912); F. R. Jones and Drechsler (1925); Karling (1977); Kauffman (1906, 1908); Klich (1980); Klich and Tiffany (1985); C. E. Miller (1965); Schmitt (1967); Schmitt and Beneke (1962); Scott (1960b, 1962); Scott and O'Bier (1962); Scott, Seymour and Warren (1963); Slifkin (1964); R. I. Smith (1940); Sorenson (1962); Sparrow (1937, 1952b); Vishniac and Nigrelli (1957); Wolf and Wolf (1941); A. W. Ziegler (1958b). USSR:

Domashova (1974b); Dudka (1966); Florinskaya (1969); Logvinenko (1970, 1971); Logvinenko and Meshcheryakova (1971); Mil'ko (1965); Mil'ko and Belyakova (1968); Mil'ko and Dudka (1968); Mil'ko and Zakharova (1976); V. Miller (1906); Osipyan *et al.* (1974). VENEZUELA: Karling (1981a). YUGOSLAVIA: Ristanović (1970a, 1973).

MATERIAL EXAMINED:-- ICELAND (61), NORWAY (103), SWEDEN (88), UNITED STATES (141), TWJ, RLS, W. W. Scott, F. K. Sparrow (preserved specimens). CENTRAL AMERICA (6), RLS.

Aphanomyces keratinophilus (Ookubo and Kobayasi) Seymour and Johnson
Mycologia 65:1317, figs. 1-11. 1973
(Figures 80 I, 81 F-H)

Aphanomyces laevis forma *keratinophilus* Ookubo and Kobayasi, Nagaoa 5:5, figs. 4, 5. 1955.

Monoecious. Hyphae occasionally sinuate or contorted. Sporangia long, filamentous, unbranched or sparingly branched, 57-301 x 6-13 μm . Spores dimorphic. Primary spores elongate; in a single row in the sporangium, connected by a thin, protoplasmic strand; at discharge encysting in a loose, nearly spherical cluster at the exit orifice; cysts 6-11 μm in diameter, releasing the secondary planont through a pore. Secondary spores reniform, laterally biflagellate. Gemmae absent. Oogonia lateral or terminal; sometimes intercalary, then single or in chains of two or three; usually spherical or obpyriform, occasionally irregular; (18-) 25-28 (-43) μm in diameter. Oogonial wall unpitted; smooth, infrequently sparingly papillate; wall sometimes having an irregular or warted aspect because of the enwrapping antheridia. Oogonial stalks short or long; usually 1-1 $\frac{1}{2}$ times the diameter of the oogonium, in length; unbranched or once-branched, straight or irregular. Oospores containing a single, large, subcentric refractive globule in the cytoplasm and, rarely, a pellucid spot; spherical; single, and occasionally filling the oogonium; (16-) 23-26 (-31) μm in diameter; germination not observed. Antheridial branches usually androgynous or monoclinous, but sometimes diclinous; unbranched or branched, often contorted and irregular, commonly wrapping profusely about the oogonium, but not about their stalks or adjacent hyphae; persisting. Antheridial cells, when delimited, small, simple, clavate; persisting; attached laterally; may not be formed (or visible) in some specimens; fertilization tubes not observed.

A thorough treatment of this species (not included in Scott's monograph of 1961 (a) was published in 1973(b) by Seymour and Johnson. Primarily there are two features that separate *Aphanomyces keratinophilus* from *A. laevis* (which it resembles). In the former the antheridial filaments may be only sparingly branched, but they tend to wrap closely and profusely about the oogonium (Fig. 80 I) sometimes obscuring the shape of this structure. The degree to which the ends of the antheridial filaments in *A. laevis*

enwrap the oogonium is considerably less (Fig. 81 D). Antheridial branches in *A. keratinophilus* are predominantly monoclinal or androgynous (Fig. 81 F, G), while in *A. laevis*, diclinal ones are most commonly produced, and androgynous ones are rare. *Aphanomyces keratinophilus* is strongly keratinophilic, but can be cultivated on YpSs agar.

Neither Ookubo and Kobayasi (*loc. cit.*) or Seymour and Johnson (*loc. cit.*) saw antheridial cells in their specimens of *Aphanomyces keratinophilus*. In the Scandinavian material at hand, some antheridial filaments have such cells, although they are often obscured by the profuseness of the branches themselves. The same may be said for Icelandic specimens (T. W. Johnson, 1974b).

Aphanomyces keratinophilus exhibits certain variations of note. Some specimens produce sessile oogonia (T. W. Johnson, 1973b), or very short-stalked ones (Seymour and Johnson, *loc. cit.*; T. W. Johnson, 1974b: 21, figs. 8-14). In unifungal culture the short-stalked forms always develop some long-stalked oogonia. A second form recovered from an Iceland soil sample by T. W. Johnson (1974b) produced oogonia and oospores (12-16 μm in diameter) that were much smaller than is usual for this species. An unnamed *Aphanomyces* collected on human hair baited in soil from a sheep enclosure in Iceland tentatively was allied (T. W. Johnson, 1974b:21) with *A. keratinophilus*. Specimens in this collection (TWJ 6422) seldom produced antheridial branches, but when such filaments occurred, they were terminated by nonfunctional antheridial cells (that is, cut off from the filament by a septum, but still containing cytoplasm even after the oospore in the oogonium had matured). In a few instances, antheridial cells of isolate 6422 terminated filament apices even though these branches did not actually contact an oogonium.

Karling (1976) recovered from African soil baited with snakeskin and human hair an *Aphanomyces* in which the antheridial branches were very rare (96 of 1700 oogonia had attendant antheridial filaments). He thought the fungus resembled Scott's (1961a) *A. bosminae*--which indeed it did. As the fungus was keratinophilic and could not be cultured, Karling could not identify it with certainty, and therefore did not name it. The oogonia and oospores of Karling's *Aphanomyces* sp. were smaller than those generally produced by *A. keratinophilus*. We have not observed the latter to be particularly sparse in antheridial branches, although Howard and Johnson (1969:496, figs. 28-38) collected on human skin (used as bait) an *Aphanomyces* devoid of antheridial branches. Their isolate had papillate or roughened oogonia; Karling's unnamed species had only smooth ones. Whether Karling's *Aphanomyces* sp. is a variant of *A. keratinophilus* -- as the substratum suggests -- cannot be determined from the available descriptive matter. Study of additional specimens is necessary before the fungus can be placed properly. Retaining it, as we do, in *A. keratinophilus* is solely a convenience.

CONFIRMED RECORDS:--AFRICA: Karling (1976:760, pl. 4, figs. 74-96) -- provisional. BRITISH ISLES: Tribe and El-Souod (1979: figs. 14-160. GUATEMALA: Seymour and Johnson (*loc. cit.*). HAWAIIAN ISLANDS: Seymour and Johnson (*loc. cit.*).

ICELAND: T. W. Johnson (1973b:294; 1974b: 21, figs. 8-14); Seymour and Johnson (*loc. cit.*). JAPAN: Kobayasi and Konno (1971a:11, fig. 4F, G); Ookubo and Kobayasi (*loc. cit.*). NORWAY: T. W. Johnson (1977c: 362, fig. 2A-F). OCEANIA: Kobayasi and Konno (1973: fig. 9A-C); Ookubo and Kobayasi (*loc. cit.*), Seymour and Johnson (*loc. cit.*). SWEDEN: T. W. Johnson (*op. cit.*).

RECORDED COLLECTIONS: -- CUBA: Sparrow (1965). DOMINICAN REPUBLIC: Sparrow and Dogma (1973). HAWAIIAN ISLANDS: Sparrow (1965). JAPAN: Suzuki (1961f). LIBERIA: Sparrow (1965). MEXICO: Céspedes and Castillo (1982). OCEANIA: Karling (1968b).

SPECIMENS EXAMINED: -- AFRICA (3), AUSTRALIA (6), CENTRAL AMERICA (26), HAWAIIAN ISLANDS (8), OCEANIA (19), RLS. ICELAND (7), NORWAY (3), SWEDEN (9), TWJ.

Aphanomyces acinetophagus Bartsch and Wolf
Amer. J. Bot. 25:394, figs. 1-9. 1938
(Figure 84 D)

Monoecious. Hyphae slender, much branched and contorted; intramatrical. Sporangia filamentous, sinuous and ramifying within the host; isodiametric. Spores dimorphic(?). Primary spores not observed; primary spore cysts forming an irregular cluster at the exit orifice; cysts 4-7 μm in diameter, releasing the secondary planont through a pore. Secondary spores reniform, laterally biflagellate. Gemmae absent. Oogonia lateral; spherical, but often becoming subspherical with age; 18-24 μm in diameter. Oogonial wall unpitted; smooth, but with age becoming irregularly and faintly roughened on the outer surface. Oogonial stalks of various lengths, usually shorter in length than the diameter of the oogonium; straight or slightly curved or sinuous; unbranched. Oospores homogeneous throughout; spherical; single, not(?) filling the oogonium; 15-22 μm in diameter; germination not observed. Antheridial branches declinuous; usually short, somewhat sinuous; unbranched. Antheridial cells, when formed, simple, cylindrical; laterally attached; fertilization tubes present. (Adapted from Bartsch and Wolf, *loc. cit.*; Scott, 1961a: 34, pl. 6, figs. A-D.)

Scott (1961) examined specimens provided by the authors of the species, and we have had a portion of that material for study (courtesy W. W. Scott). We can add nothing -- based on our examination of the preserved specimens at hand -- to the circumscription of this species.

Cleavage and emergence of the primary spore has not been seen. According to Scott (1961a: pl. 6, fig. C), antheridial cells were not cut off from the filaments by septa, but one of the illustrations he provides shows such a cell. We found few antheridial branches in the preserved specimens we examined, and none had a terminal antheridial cell (Fig. 84 D).

CONFIRMED RECORD: -- UNITED STATES: Bartsch and Wolf (*loc. cit.*).

SPECIMENS EXAMINED: -- UNITED STATES (1), A. F. Bartsch and F. T. Wolf (preserved specimens).

Aphanomyces bosminae Scott

Virginia Agric. Exp. Sta. Techn. Bull. No. 151, p. 33, pl. 4, figs. D-F. 1961
(Figure 82 R, S)

Monoecious. Hyphae delicate, profusely branched, forming a dense, entangled intramatrical system. Sporangia filamentous; tapering toward the extramatrical apex, 5-6 μm in diameter in intramatrical portion, tapering to 3.5 μm in diameter; short, unbranched; not constricted at the point of penetration through the host wall. Spores dimorphic. Primary spores cylindrical, few in number; in a single row in the sporangium, but not connected by a protoplasmic strand; at discharge encysting in a spherical or subspherical cluster at the exit orifice; cysts 6-8 μm in diameter, when empty showing a poroid configuration. Secondary spores not observed. Oogonia lateral or sessile; spherical; 20-28 μm in diameter. Oogonial wall unpitted; smooth. Oogonial stalks short, unbranched, stout; usually less than the diameter of the oogonium, in length. Oospores containing a single centric or subcentric refractive globule in the cytoplasm; spherical; single; 17-22 μm in diameter; at germination producing a long, filamentous, branched germ tube. Antheridial branches not observed. (Adapted from Scott, *loc. cit.*)

Aphanomyces bosminae has been found only in *Bosmina* sp. and in *Cyclops* sp. (Scott, *loc. cit.*). The species seems unique among those of *Aphanomyces* having smooth oogonia: small, spherical, short-stalked to sessile oogonia without attendant antheridial filaments. The extramatrical portion of the sporangium tapers toward the apex, and while this is not exclusively characteristic of *A. bosminae*, it is unusual. According to Scott, *A. bosminae* is distinguished from *A. daphniae* and *A. patersonii* by having smaller primary spore cysts. The absence of antheridial branches in Scott's species, however, is a more marked difference between it and the other two taxa.

Since there has been only a scanty collection of *Aphanomyces bosminae*, nothing is known of its variability.

CONFIRMED RECORD: -- UNITED STATES: Scott (*loc. cit.*).

SPECIMENS EXAMINED: -- UNITED STATES (1), W. W. Scott (holotype; preserved specimens).

Aphanomyces daphniae Prowse

Trans. Brit. Mycol. Soc. 37:22, figs. 1-3. 1954

Monoecious. Hyphae intramatrical; branched; 10-20 μm in diameter. Sporangia filamentous; unbranched, or provided with short lateral branches; constricted passing

through the host exoskeleton; tapering toward the apex; in the intramatrical portion, 150-200 μm long by 10 μm in diameter. Spores dimorphic. Primary spores cylindrical; in a single row in the sporangium and its branches, and connected by a thin, protoplasmic strand; at discharge (at 18 °C, or lower), encysting in a loose, irregular cluster at the exit orifice, or (above 20 °C) swimming as in *Leptolegnia* species; cysts 18 μm in diameter, releasing the secondary planont through a pore. Secondary spores reniform, laterally biflagellate. Gemmae absent. Oogonia lateral; spherical or subspherical; 36-38 μm in diameter. Oogonial wall unpitted; smooth, but sometimes with a broad, short, papillar extension at the point of attachment of the antheridium. Oogonial stalk unbranched, short, straight, or irregularly swollen or tapering. Oospores lacking a well-defined refractive globule, but provided internally with small oil droplets forming an irregular central mass; spherical; single; 33-35 μm in diameter; germination not observed. Antheridial branches declinuous; unbranched or branched, and lying closely appressed to the oogonium. Antheridial cells simple; apically attached; fertilization tubes not observed. (Adapted from Prowse, *loc. cit.*)

Aphanomyces daphniae was described from parasitized specimens of *Daphnia hyalina* var. *lacustris*, and subsequently propagated in a nutrient solution. The fungus produced oogonia in invaded crustaceans, and in culture, according to Prowse (*loc. cit.*), but no subsequent collectors of the species (Seymour *et al.*, 1984; Seymour and Briggs, 1984) have seen the sexual apparatus. We have on occasion found specimens of *Aphanomyces* in *Daphnia* species, but none reproduced sexually. Accordingly, there is no way to be certain that our material was in fact of Prowse's species. Scott (1961a) failed in attempts to induce the sexual apparatus in his subcultures of *A. daphniae*.

Prowse described the antheridial filaments as unbranched structures; the illustrations he provided, however, show beyond doubt that some could be branched. Although Prowse clearly stated that the cylindrical, endogenous primary spores were connected to each other by a protoplasmic strand (and illustrated this condition), Scott (1961a:30) found no such strands between "... fully formed zoospores..."

Prowse (*loc. cit.*) called attention to an unusual behavior pattern of the primary spores. At incubation temperatures of 18 °C or less, the spores emerged from the sporangium and encysted at the orifice in the fashion characteristic of species of *Aphanomyces*. When the temperature exceeded 20 °C, however, the primary spores emerged as elongate cells that swam away from the orifice. Subsequently, each spore bent at its mid-point to become a triangular cell with two apically attached flagella. There were no flagella visible on the spores as they emerged from the exit orifice. After release, the motile spores became pyriform in a manner precisely like that in species of *Leptolegnia*, then (with time) encysted. Prowse (1954:27) concluded from this behavior that the genus *Aphanomyces* "... may be regarded as having been derived from *Leptolegnia* by suppression of the primary (spore) stage."

In the structure and sizes of the components of its sexual apparatus, *Aphanomyces daphniae* is little different from *A. laevis*. Prowse maintained that his species could be separated from de Bary's species by reason of its habitat (parasitic as opposed to

saprotrophic in insect exuviae), and the absence, in *A. daphniae*, of a prominent refractive globule in the mature oospore. He was unable to culture *A. daphniae* on insect exuviae, suggesting that it differs from *A. laevis* nutritionally. It should be emphasized, moreover, that putative specimens of *A. laevis* are not known to have a leptolegnoid behavior pattern in the emerging primary spores.

Sparrow (1960), and Scott (1961a) remarked that the fungus Fritsch (1895) described as *Ancylistes cladocerarum* -- in *Bosmina cornuta* and *Daphnia* sp. -- might well have been an *Aphanomyces*. Perhaps so, but there is nothing either in the original description or illustration of Fritsch's (1895: fig. 5) species to link it to de Bary's genus, let alone to *A. daphniae*.

CONFIRMED RECORD: -- SCOTLAND: Prowse (*loc. cit.*).

RECORDED COLLECTIONS: -- UNITED STATES: Seymour *et al.* (1984).

Aphanomyces patersonii Scott
Virginia J. Sci. (N.S.) 7:171, figs. A-E.1956
(Figure 82 O-Q)

Monoecious. Hyphae intramatrical, sparingly branched. Sporangia filamentous, unbranched; isodiametric throughout; long, up to 15 μm in diameter. Spores dimorphic. Primary spores cylindrical, few; in a single row in the sporangium, connected by a thin, protoplasmic strand; containing a small, conspicuous refractive droplet; at discharge (below 20 °C), encysting in a compact, irregular cluster at the exit orifice, or (above 20 °C) swimming as in *Leptolegnia*; cysts 10-15 μm in diameter, releasing the secondary planont in a schistose fashion. Secondary spores reniform, laterally biflagellate. Gemmae absent. Oogonia lateral; spherical; 26.5-39 μm in diameter. Oogonial wall unpitted, smooth. Oogonial stalks generally $1/2$ the diameter of the oogonium, in length, or equal to it; unbranched; straight or slightly irregular. Oospores containing a single, subcentric, refractive globule in the cytoplasm, or a cluster of several small globules; spherical; single not filling the oogonium; 21.5-30.5 μm in diameter; germination not observed. Antheridial branches declinuous; unbranched, usually irregular in outline. Antheridial cells simple; swollen distally, clavate and slightly irregular; laterally attached; fertilization tubes not observed.

We have not seen living material of Scott's species, but have examined preserved specimens, on slides. Although he cultured *Aphanomyces patersonii* in the absence of the host, *Daphnia* sp., isolates have not survived.

The distinction between *Aphanomyces patersonii* and *A. daphniae* is enigmatical indeed. In the general configuration of the sexual apparatus the two species are alike, and on the basis of oogonium and oospore diameters cannot be separated. Moreover, just as in *A. daphniae*, the discharged primary spores of *A. patersonii* respond in a leptolegnoid fashion (swim away at emergence, and then bend to become pyriform with apically attached flagella) to incubation temperatures above 20 °C. Unlike *A.*

daphniae, *A. patersonii* has elongate-irregular antheridial cells, schistose primary spore cysts, and isodiametric sporangia.

In view of the similarity between Scott's species and Prowse's *Aphanomyces daphniae* in the primary spore discharge pattern, it is possible that the two species are the same in spite of the few aforementioned minor structural differences. Until colonies of both taxa are propagated in culture under a variety of conditions and their variability analyzed, they can be retained only provisionally as separate entities.

The illustrations of this species cited by Scott on page 31 of his monograph are incorrect; the figures depicting *Aphanomyces patersonii* are G-J, on plate 4. Figures D-F, as cited, refer to *A. bosminae*.

CONFIRMED RECORDS: -- INDIA: Dayal and Thakur Ji (1965:318, pl. 7) [as *Aphanomyces petersonii*, an obvious orthographic error]. UNITED STATES: Scott (*loc. cit.*).

RECORDED COLLECTIONS: -- INDIA: Thakur Ji (1967). UNITED STATES: C. E. Miller (1965).

SPECIMENS EXAMINED: UNITED STATES (1). W. W. Scott (preserved specimens).

Aphanomyces euteiches Drechsler

In, F. R. Jones and Drechsler, J. Agric. Res. 30:311, pls. 2-6. 1925

(Figure 82 D-H)

Monoecious. Hyphae slender; in culture infrequently branched, inconspicuously irregular or contorted in outline, and often isodiametric for considerable distances; *in vivo*, very abundantly branched, or provided with short, irregular, lateral protrusions, and conspicuously contorted or irregular and twisted. Sporangia filamentous, usually very long and unbranched or sparingly branched, the lateral branches generally tapering toward the apex, and often sinuous and contorted; unbranched sporangia, or main sporangial axis up to 2.8 mm long, and 4-11 μ m in diameter. Spores dimorphic. Primary spores cylindrical or oval, infrequently spherical; in a single row in the sporangium, and often connected by a thin, protoplasmic strand; at discharge, encysting in a loose or compact, globose or irregular cluster at the exit orifice; cysts (7-) 9-11 (-18) μ m in diameter, releasing the secondary planont through a papilla. Secondary spores reniform, laterally biflagellate. Gemmae absent. Oogonia lateral, rarely terminal, frequently sessile (*in vivo*); spherical or subspherical, (16-) 28-34 (-41) μ m in diameter. Oogonial wall unpitted; smooth on outer surface, but rarely displaying an inconspicuous depression at the points of antheridial cell attachment; noticeably irregular or sinuous on inner surface; wall occasionally conspicuously thickened. Oogonial stalks $1/8 - 1^{1/2}$ times the diameter of the oogonium, in length, but predominantly shorter than the diameter; stout, straight or curved, infrequently strongly bent; rarely once-branched. Oospores containing a single, conspicuous,

spherical, centric or eccentric refractive globule in the cytoplasm; pellucid spot not evident; spherical or subspherical; single, often filling the oogonium, or nearly so; (16-) 21-23 (-28) μm in diameter; at germination forming one or more hyphae directly, or producing an irregular, sinuous hypha, tapering gradually toward the apex, and converting directly into a sporangium. Antheridial branches predominantly diclinous, occasionally monoclinal; usually short; branched or unbranched, often irregular in outline; usually persisting; Antheridial cells simple or compound; predominantly large and clavate or expanded conspicuously apically; usually curved or bent; generally provided with one or two lateral branches or lobes; persisting; infrequently intercalary; apically appressed; fertilization tubes present.

Before discussing this and the subsequent four species, it is appropriate that we comment generally on the published descriptive matter.

Drechsler (1929; in F. R. Jones and Drechsler, 1925) provided exceptionally detailed accounts of the structure of the plant pathogenic species of *Aphanomyces*; *A. euteiches*, *A. raphani*, *A. camptostylus*, *A. cladogamus*, and *A. cochlioides*. In spite of his meticulous attention to details of descriptive characters, the practicality of distinguishing these taxa from one another was not served. The general morphological configurations of these taxa are so remarkably similar that precise, objective distinctions seem all but nonexistent. The differences among these species are subtle and often Drechsler couched these in subjective terms emphasizing only degrees of dissimilarity in one or two characters. Our treatment must necessarily follow this same pattern because Drechsler himself evidently could find no clear-cut, unambiguous differences among the taxa he described. To be sure, the five species were known by Drechsler to attack very different host plants; later evidence (see Chapters 27 and 28) was to show that host range was much broader than he suspected, and there is substantial overlap in this regard.

In our account of *Aphanomyces euteiches* and the obviously closely allied species, we have attempted to single out objective morphological differences. They are scanty, and perhaps with further study could prove untrustworthy. In the final analysis, identification of the particular fungi must rely heavily on the determination of the vascular plant species most commonly invaded.

Aphanomyces euteiches was the first of the phytopathogens to be described by Drechsler (*loc. cit.*), and subsequently has been studied more extensively than his other species. The fungus is so familiar to phytopathologists that it is often simply identified *in situ*, without benefit of isolation and culture. Boosalis and Scharen (1959), for example, recovered (by sieving) samples of plant debris from soil planted in peas (*Pisum sativum* L.), and reported that they could identify *A. euteiches* in the material solely by relying on its oospore characteristics. We are satisfied, however, from a study of living specimens and an analysis of the descriptive literature that the oospores of all of Drechsler's phytopathogenic species of *Aphanomyces* are indistinguishable from one another (except, perhaps, in their predominating diameters).

On the mycelium produced *in vivo*, the oogonia of *Aphanomyces euteiches* are sessile or nearly so (Fig. 82 E), and the wall of each is thin but noticeably irregular on the inner surface. The antheridial branches are usually very short, originating near the oogonium to which they are attached. Moreover, in the pea root tissue, the oogonia are often subspherical or depressed-globose. *In vitro*, the mycelium produces oogonia that are generally short-stalked, but in contrast to ones formed *in vivo*, the wall is conspicuously thickened (Fig. 82 F-H), though still sinuous on the inner surface.

On the basis of cultures we have examined, it appears that *Aphanomyces euteiches* most nearly resembles *A. raphani*, yet the two appear to have subtle differences as well. In both, the antheridial branches and oogonial stalks are generally short, and there are no sporangial characteristics which the two do not have in common. Drechsler (1929:325) recorded measurements showing that on the average the oogonia and oospores of *A. euteiches* are smaller than those of *A. raphani*. The differences are exceedingly slight and therefore not of first-order significance taxonomically. The antheridial cells in cultures of *A. euteiches* usually are more irregular (Fig. 82 D-F) than those of *A. raphani*, and the oogonial walls are substantially thicker also (at least in individuals grown *in vitro*). Some antheridial cells are countersunk into the oogonial wall in both species, but there are far fewer instances of this structural feature in *A. euteiches* than in *A. raphani* (Fig. 82 B). We have found that the mycelium of the latter is perceptibly coarser and the hyphae stouter than in the former, but this is not an impressive difference.

The characteristics that separate *Aphanomyces euteiches* morphologically from *A. cochlioides*, *A. cladogamus*, and *A. camptostylus* are discussed in the accounts of these latter taxa.

It appears that it is necessary -- because the species is not structurally unique -- to recognize *Aphanomyces euteiches* largely on its host range, even though this "characteristic", too, is not entirely dependable. The primary host, of course, is *Pisum sativum*, but *A. euteiches* seems to be able to invade many other vascular plants (Chapter 27), even some rather unusual ones such as *Echinodorus brevipedicellatus* (Ridings and Zettler, 1973) and conifer seedlings (Eliason, 1928). Indeed, the fungus even attacks the primary hosts that are known to be invaded by *A. cochlioides* and *A. raphani*. As we have emphasized in the account of the pathology of pea root rot (Chapter 27) the host range of *A. euteiches* in part reflects artificial inoculations that resulted in the subsequent invasion of a variety of test plants grown under laboratory or greenhouse conditions. Such a host range cannot be judged entirely reflective of a natural virulence.

Aphanomyces euteiches occurs in soil (Alconero and Hagedorn, 1968; Burke, Hagedorn, and Mitchell, 1969, 1970; Burke, Mitchell, and Hagedorn, 1969, among others). Domashova (1971) reported its recovery from a water sample, and so far as we are aware, hers is the only published record of the fungus from an aquatic habitat.

It is very likely that *Aphanomyces euteiches* had been discovered in association with diseased pea roots (but thought to be a *Pythium*) prior to being identified by F. R. Jones and Drechsler (1925). Clinton (1920) found oogonia of a filamentous fungus in pea roots, but could not induce sporulation. The oogonia of the fungus Clinton collected

were (24-) 27-33 (-36) μm in diameter, and became wrinkled with age. The oospores were (20-) 22-27 (-30) μm in diameter. He concluded that the fungus was *Pythium debaryanum* Hesse, but recognized that the oogonia and oospores were larger than those encountered in species of *Pythium*. It is evident that the sex cell diameters reported by Clinton would readily apply to *A. euteiches*.

Schmitthenner (1964) described an "alfalfa *Aphanomyces*" that resembled *A. euteiches*. The oogonia of the watermold in *Medicago sativa* L. averaged 30 μm in diameter (33 μm in *A. euteiches* according to Schmitthenner), and characteristically were attended by 2-3 antheridial cells, as opposed to 4-5 such cells on the oogonia of Drechsler's species. Schmitthenner found that his isolate was a very weak pathogen in red clover, but otherwise was limited to alfalfa. On the other hand, he noted that *A. euteiches* caused very little damage to postemergence alfalfa seedlings, and concluded that his isolate could have been simply a strain of *A. euteiches* only slightly virulent to peas. Because *A. euteiches* has such a broad host range, and the fungus found in alfalfa was not substantially different structurally from Drechsler's species, we concur with Schmitthenner's supposition. However, the *A. euteiches* reported by Coker and Braxton (1926) was in all likelihood *A. cladogamus*. Similarly, *Aphanomyces euteiches* P.F. 2 (in *Viola tricolor* var. *hortensis*, Buisman, 1927), which Drechsler (1954b) thought was not that species, was probably also *A. cladogamus* (see discussion of this latter taxon).

There are numerous references to *Aphanomyces euteiches* (sometimes merely as the "pea root rot fungus") in mimeographed accounts and general governmental reports (such as Ministry of Agriculture publications in the United Kingdom). Such records are excluded from the listings of citations to follow. General distribution maps published by Kreisel (1975) contain reports of *A. euteiches*. Doran *et al.* (1942) stated that *A. euteiches* was the cause of damping off in *Apium graveolens* L., but gave no source or locality for the species. Similarly, Drechsler (1938) failed to cite the source of his material of *A. euteiches* in which the oospores were parasitized by *Dactylella spermatophaga* Drechsler. These -- and papers of a similar nature, as, for example, Ayers and Papavizas (1965) and Hoch and Mitchell (1972) -- are not included as records of the species. A substantial body of literature was published on *A. euteiches* prior to the division of the taxon into the two form species proposed by Pfender and Hagedorn (1982a). It is not possible to be certain which form species was intended by authors of reports prior to 1982, although one might surmise either f. sp. *pisi* or f. sp. *phaesoli* from host records. In view of the uncertainty, however, post-1982 reports of the form species are simply included as recorded and confirmed reports of *A. euteiches*.

CONFIRMED RECORDS: -- JAPAN: Fukunishi *et al.* (1976: fig. 1 E, F); Yokosawa and Kuninaga (1977: pl. 1); Yokosawa *et al.* (1974: figs. 1, 3-6). NEW ZEALAND: Manning and Menzies (1980: fig. 2). NORWAY: Sundheim and Wiggen (1972:5, fig. 1). SWEDEN: Olofsson (1967: fig. 4; 1968: figs. 1-4). UNITED STATES: Boosalis and Scharen (1959: fig. 1A); F. R. Jones and Drechsler (*loc. cit.*); King and Cho (1962: figs. 1, 2); Reinking (1942:25, figs. 5,6); Ridings and Zettler (1973:292, fig. 2); Scharen (1960b:

figs. 1-3); Schäufele and Beiss (1973: fig. 3); Schmitthenner (1964:1014). USSR: Domashova (1971: fig. 1); Kotova (1969: 440, figs. 2,3).

RECORDED COLLECTIONS: -- AUSTRALIA: Greenhalgh *et al.* (1985). BRITISH ISLES: Alcock and Foister (1931); Dennis and Foister (1942); Beaumont (1951, 1954?); P. H. Gregory (1951); W. C. Moore (1959). CANADA: Lamari and Bernier (1985); Tu (1985, 1986). FRANCE: Labrousse (1934). JAPAN: Yokosawa and Kuninaga (1979, 1983); Yokosawa *et al.* (1986). NEW ZEALAND: Manning and Menzies (1984). NEPAL: S. C. Singh (1986b). NORWAY: Jørstad (1928); Solberg (1925, 1926); Sundheim (1971, 1972). POLAND: Tomashevski and Furgal (1975). TASMANIA: Geard (1961); Wade (1955), identified merely as *Aphanomyces* root rot. UNITED STATES: Alconero (1967); Alconero and Hagedorn (1967, 1968); Beneke and Schmitt (1961); Beute and Lockwood (1967); Blume and Harman (1979); Burke, Hagedorn, and Mitchell, 1969, 1970; Burke, Mitchell, and Hagedorn (1969); Carley (1969); Cassell (1945); Cho and King (1963); Clinton (1920, 1934); Coker (1927); Delwicke *et al.* (1987); Drechsler (1925, 1927); Eliason (1928); D. E. Ellis and Garriss (1943); Fenwick (1969); Grau (1975, 1977); Grau and Reiling (1977); Haenseler 1924, 1925, 1926, 1928); Haglund (1960); Haglund and King (1961a, b; 1962); R. G. Harvey *et al.* (1975); H. G. Johnson (1953); KenKnight (1944); Linford (1927, 1929); Linford and Vaughn (1925); Llanos and Lockwood (1960); Lloyd and Lockwood (1961); Lockwood (1960b, 1961); McWhorter *et al.* (1943); W. H. Martin (1931); V. D. Matthews (1927); J. E. Mitchell and Hagedorn (1966, 1969); Mix (1954b); Morrison (1972); Morrison *et al.* (1971); Oyekan and Mitchell (1972); Pfender and Hagedorn (1982a, 1983), Pfender *et al.* (1984); Schmitt and Beneke (1962); Sharvelle *et al.* (1942); Shehata, Grau *et al.* (1976); Sherwood (1958); Sherwood and Hagedorn (1962); Starr (1932); Teasdale *et al.* (1978); Temp (1966); Temp and Hagedorn (1967); Tidd (1945); Walker and Musbach (1939); Ware (1943). USSR: Domashova (1974b); Kotova (1971, 1977, 1979).

SPECIMENS EXAMINED: -- UNITED STATES (6), TWJ, R. Emerson (unnumbered culture)

Aphanomyces cochlioides Drechsler
J. Agric. Res. 38:326, figs. 1-4. 1929
(Figure 81 I-K)

Monoecious. Hyphae slender, sparingly to moderately branched. Sporangia filamentous, long; straight, sinuous, or irregular; often extensive and branched; frequently narrowing toward the apex; provided with ramifying branches that function in spore release; 4-11 μm in diameter, branches up to 3 mm long. Spores dimorphic. Primary spores cylindrical; in a single row in the sporangium, connected by a thin, protoplasmic strand; varying in number depending upon the length and extent of branching of the sporangium; at discharge, encysting in a loose, irregular cluster at the exit orifice; cysts (6-) 7-10 (-15) μm in diameter, releasing the secondary planont through a papilla. Secondary spores reniform, laterally biflagellate. Gemmae absent. Oogonia lateral; spherical to subspherical, but occasionally slightly irregular in outline; (18-) 22-26 (-31) μm in diameter. Oogonial wall unpitted; smooth on outer surface, but

frequently marked with hemispherical depressions at the point of attachment of the antheridial cells; noticeably irregular on the inner surface. Oogonial stalks $1/2$ to twice the diameter of the oogonium, in length, but usually about as long as the diameter; straight, curved, or bent; generally irregular or twisted; unbranched or with a single branch. Oospore containing a single, conspicuous, centric or subcentric refractive globule in the cytoplasm, and generally also exhibiting a pellucid spot; spherical; single, occasionally nearly filling the oogonium; (16-) 18-21 (-27) μm in diameter; germination not observed. Antheridial branches declinous, rarely monoclinal, and then of distant origin; long, branched, irregular and contorted; usually closely wrapped about the oogonium, and then often in a cochleate fashion; occasionally contacting the oogonial stalks, but not coiling about them; persisting. Antheridial cells simple; clavate and curved or bent, or clavate and provided with a short, apical protrusion; sometimes noticeably irregular in outline; apically attached, with the broad end often partially countersunk into the oogonial wall; fertilization tubes present.

The name *Aphanomyces cochlioides* first appeared in abstract form (Phytopathology, 18:149. 1928). The validating formal description and illustrations were published by Drechsler in 1929. Drechsler's (1934) description of *Pythium scleroteichum* [causing necrosis in *Ipomea batatas* (L.) Lam.] is remarkably similar to that of his *A. cochlioides*. The *Pythium* is not known to have a sporangial stage; hence its identity with Pringsheim's genus is suspect.

Aphanomyces cochlioides is primarily a pathogen in the roots of sugar beet (*Beta vulgaris* L.). It occurs in other vascular plants, and invades a variety of artificially inoculated hosts: *Amaranthus retroflexus* L., *Beta vulgaris* var. *rapa* Dumont, *Chenopodium album* F., *Lathyrus odoratus* L., *Medicago sativa* L., *Melilotus alba* Desf., *Spinacia oleracea* L., *Vicia atropurpurea* Desf., *V. monanthos* Desf., *V. angustifolia* L., and *Pisum* spp., to name a few (Coulombe, 1975; Geach, 1936; W. E. McKeen, 1949). The fungus has also been recovered from soil (Schneider and Robertson, 1975; Schneider and Safir, 1975; Whitney and Doney, 1970, among others.) In Chapter 28 a further account of the host range of *A. cochlioides* is provided.

It is abundantly clear from the accumulated literature that *Aphanomyces cochlioides* has been misidentified on occasion, and in particular, mistaken for *A. laevis*. Peters (1906, 1911) studied an *Aphanomyces* (in sugar beet roots) that he reported as *A. laevis*. His accounts do not substantiate this identification, but neither do they present any evidence that the specimens he had were not *A. cochlioides*. The *A. laevis* reported by P. A. Murphy (1927) to occur in sugar beets may also be treated as Drechsler's species. Naumov (1954) cited de Bary's *A. laevis* as a synonym of *A. cochlioides*, but at the same time recognized as valid de Bary's (1860) *A. levis* (note orthography). Both Schaufele and Beiss (1973), and Steudel (1968, 1969) identified the beet root water molds they isolated from infected beet roots as *Aphanomyces* "type *cochlioides*" but Beiss and Schaufele (1973) concluded that these fungi indeed represented Drechsler's species. Winner (1962, 1966a-c) likewise designated as "type *cochlioides*" the fungus he recovered from diseased sugar beets, but also referred to the *Aphanomyces* associated with that

disease simply as "sp." While it is evident from his 1966(a) paper that Winner recognized the proper name of the beetroot pathogen as *A. cochlioides*, even later he and Schäufele (1968) continued to refer to the fungus as *Aphanomyces* sp. It is very likely that the *Aphanomyces* discovered by Winner in 1952, in Chile, was Drechsler's species.

Edson (1915a) corrected his earlier (1913, abstract; not cited) misidentification (*A. laevis*) of a beet root invader he collected and named *Rheosporangium aphanidermatus* (Edson, 1915b). Curiously, Peters confirmed that a fungus Edson had isolated from sugar beets in Germany was the same as the *A. laevis* that he (Peters, 1906) had studied. However, Edson (1915a) asserted that the *A. laevis* he had discovered in the United States was not the same species as the one he had collected in Germany. According to J. R. Warren (1948:884), *R. aphanidermatus* (Edson) Fitzpatrick subsequently was assigned to *Pythium* "... and is now known as *Aphanomyces cochlioides* Drech." This of course is in error.

Aphanomyces cochlioides can be distinguished from *A. laevis* only with the greatest difficulty, and at times not satisfactorily. So far as we have been able to determine from an examination of more than 200 collections of *A. laevis* (saprotrophic on various bait types), the oogonial walls are never depressed to receive the antheridial cell as is of common occurrence in *A. cochlioides*. Furthermore, the oogonial walls in all of our specimens of *A. laevis* are smooth on the inner surface, whereas that surface is noticeably irregular (universally?) in *A. cochlioides*. The antheridial branches in Drechsler's species are only rarely monoclinal, and we have never seen androgynous ones in our cultures. In *A. laevis*, on the other hand, monoclinal branches are common, and androgynous filaments also are produced.

Separating *Aphanomyces cochlioides* from *A. euteiches*, *A. raphani*, *A. cladogamus*, and *A. camptostylus* is very difficult and the results are uncertain. The general configuration of the asexual and sexual apparatus is remarkably similar among these taxa, and the species expressly form a progressive series with respect to oogonium and oospore diameters as Drechsler (1929: table 2) circumscribed them.

Our analysis of our specimens of *Aphanomyces cochlioides*, in conjunction with Drechsler's (1929:321-326) account, suggests that the species may be distinguished from his other taxa on only a few subtle points. *Aphanomyces cochlioides* has predominantly smaller oogonia and oospores than either *A. euteiches* or *A. raphani*. The oogonial wall is not as noticeably irregular on the inner surface in *A. cochlioides* as it is in *A. euteiches*. In general, the antheridial branches of *A. raphani* are much shorter and stouter than those usually present in *A. cochlioides*, but such a characteristic may prove to be variable among isolates. The overt coiled nature of the antheridial branches and oogonial stalks so readily seen in *A. cladogamus* and *A. camptostylus* sets these species apart from *A. cochlioides*.

Practicality seems to dictate that the best scheme for the recognition of *Aphanomyces cochlioides* is to rely on determining the commonly invaded host. Strong arguments otherwise can be made to assemble *A. cochlioides*, *A. euteiches*, and *A. raphani* into a single broadly defined taxon. The obvious overlapping in host ranges among these species certainly supports a merger of them. We are retaining these taxa,

however, however, because we are not satisfied that host ranges have been properly established, and morphological and pathological variability among these species thoroughly analyzed.

CONFIRMED RECORDS: -- BRITISH ISLES: Byford and Stamps (1975:158, pl. 32, fig. 4). CANADA: W. E. McKeen (1949:288 *et seq.*, figs. 6-15). EAST GERMANY: Böttcher (1979: figs. 1, 2). GERMANY: Peters (1911:239 *et seq.*, fig. 9); Schäufele and Beiss (1973: fig. 2). SOUTH AMERICA: Steeger (1965: fig. 1, in part). UNITED STATES: Drechsler (*loc. cit.*). USSR: Naumov (1954:62).

RECORDED COLLECTIONS: -- AUSTRALIA: Hutton and O'Brien (1986). BELGIUM: Ernould (1949a); a doubtful record since reference is only to common name of disease, that is, "black leg." BRITISH ISLES: Byford (1975; Byford and Prince (1976); W. C. Moore (1959); P. A. Murphy (1927). CANADA: Coulombe (1975); A. A. Hildebrand *et al.* (1949). EAST GERMANY: Klemm *et al.* (1957); Kühnel (1978). GERMANY: Bartels (1971); Härle (1951); Peters (1906); Schäufele and Winner (1979); Steudel (1968, 1969, 1979); Winner (1966a). HUNGARY: György (1957); Terenyi (1928-29). INDIA: Chowdhry and Agarwal [1980a; Chowdhry and Aggarwal (*sic*), 1980b]. JAPAN: H. Abe (1975); Akashi *et al.* (1986); Chikuo and Sugimoto (1985); Chikuo *et al.* (1982); Lee *et al.* (1985); Narita (1983a, b); Yokosawa and Kuninaga (1977); Yokosawa and Ui (1969); Yokosawa *et al.* (1986). SOUTH AMERICA: Gonzalez (1975); Winner (1966a). TASMANIA: Geach (1936). UNITED STATES: Afanasiev (1948a, b, 1962); Afanasiev and Morris (1949); Afanasiev and Sharp (1961); Bockstahler and Reece (1948); Bockstahler *et al.* (1950); Buchholtz (1944a, b); Buchholtz and Meredith (1944); Deems and Young (1956); Delwiche *et al.* (1987); Downie (1942); Downie, Schuster, and Oldenmeyer (1952); Downie, Doxtator *et al.* (1952); Doxtator and Downie (1948); Doxtator and Finkner (1954); Fink and Buchholtz (1954); Gaskill *et al.* (1948); Henderson and Bockstahler (1946); Herr (1973); Lyda (1958); Melhus *et al.* (1939); Rush (1988); Schmitthenner and Hilty (1962); Schneider (1959); Schneider and Robertson (1975); Schneider and Safir (1975); Warren (1948); Whitney and Doney (1970). USSR: Chulkina (1967); Pidoplichko (1970); Tverskoï (1954).

SPECIMENS EXAMINED: -- UNITED STATES (3), TWJ, R. Emerson (unnumbered culture).

Aphanomyces camptostylus Drechsler
J. Agric. Res. 38:342, figs. 9-11. 1929
(Figure 81 L-N)

Monoecious. Hyphae sparingly or moderately branched. Sporangia filamentous, long, often extensive and branched, and provided with multiple branches functioning in spore release; 6-7.5 μm in diameter, branches up to 2 mm long. Spores dimorphic. Primary spores spherical to oblong or cylindrical, in a single row in the sporangium, and sometimes connected by a thin protoplasmic strand; varying in number from a few to over 300; at discharge encysting in a loose cluster at the exit orifice; cysts 7-10 μm in

diameter, releasing the secondary planont through a papilla. Secondary spores reniform, laterally biflagellate. Gemmae absent. Oogonia lateral or terminal; spherical or subspherical; (19-) 22-24 (-26) μm in diameter. Oogonial wall unpitted; smooth on outer surface, faintly irregular on inner surface. Oogonial stalks of various lengths; unbranched or branched; the main axis and lateral branches sometimes coiling about adjacent antheridial filaments. Oospores containing a slightly subcentric refractive globule in the cytoplasm, and some also containing a pellucid spot; spherical; single, generally nearly filling the oogonium; (16-) 18-21 (-24) μm in diameter; germinating to produce a mycelium directly, or a hypha that converts into a sporangium. Antheridial branches mostly declinous; short or long, usually branched or provided with short, lateral protrusions; often irregular or sinuous in general configuration; frequently wrapping about the oogonia and its subtending stalk; usually persisting. Antheridial cells simple; irregularly cylindrical to inflated; branched or unbranched, curved, bent, or straight; persisting; laterally or apically appressed; fertilization tubes present.

The foregoing description is in part based on the characteristics of a specimen recovered and isolated from an agricultural soil sample (with associated debris), and in part derived from Drechsler's (*loc. cit.*) circumscription. We have not seen the species growing *in situ* in plant roots. Drechsler characterized the fungus in roots of *Avena sativa* L., and experimentally inoculated it into seedlings of *Beta vulgaris* L., with infection subsequently developing (*see* Chapter 28).

There are no pronounced characteristics of *Aphanomyces camptostylus* that patently set it off sharply from the other phytopathogenic forms. This being so, on what structural basis did Drechsler (*loc. cit.*) recognize the species? He characterized *A. camptostylus* as having a more delicate overall appearance (its mycelium) than *A. cladogamus*, but our isolates of these two species do not differ at all in this regard. Drechsler also held that the helicoid nature of the oogonial branches was more pronounced in *A. camptostylus* than in *A. cladogamus*. In *A. euteiches*, as Drechsler defined that species, dorsal extensions or prolongations were developed on some antheridial cells (Fig. 82 F), but were absent in *A. cladogamus*.

So far as we can determine from our very limited material of *Aphanomyces camptostylus*, its habitat -- roots of *Avena sativa* -- may well be one of the chief features by which it can be recognized. We have found only declinous antheridial branches in our specimen of *A. camptostylus*, but monoclinal and androgynous ones in an isolate of *A. cladogamus*. It must be recalled, however, that Drechsler reported the antheridial branches of *A. camptostylus* to be "mostly" declinous, implying thereby that other origins also were to be seen.

In subcultures we have made of our isolate of *Aphanomyces camptostylus* the oogonial stalks are more frequently coiled (but not about the antheridial branches as Drechsler emphasized) than are those of *A. cladogamus*. This is hardly a substantive feature on which to maintain these as separate species. Both taxa are in need of extensive study to establish their status.

Scott's (1961a:39, pl. 5, figs. J-K) account of *Aphanomyces camptostylus* differs little from the analysis prepared by Drechsler. The description provided by F. T. Wolf (1944: 35) was based on Drechsler's (*loc. cit.*) publication.

CONFIRMED RECORD: -- UNITED STATES: Drechsler (*loc. cit.*).

RECORDED COLLECTIONS: -- UNITED STATES: Sprague (1938, 1950); Sprague *et al.* (1948).

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

Aphanomyces raphani Kendrick

Purdue Univ. Agric. Exp. Sta. Bull. No. 311, p. 19, figs. 6-13. 1927

(Figure 82 A-C)

Aphanomyces brassicae Pavgi and Singh, in S. L. Singh and Pavgi, Mycopathologia 61:171, figs. 1-12. 1977.

Monoecious. Hyphae coarse or delicate, abundantly branched, the filaments often twisted and irregular. Sporangia filamentous, long; straight, sinuous, or irregular; abundantly branched, the lateral filaments usually tapering toward the apex, and generally very irregular or sinuous in outline; main axis of sporangium may or may not taper toward apex; unbranched sporangia 70-488 × 4-16 μm. Spores dimorphic. Primary spores cylindrical, oval, or spherical; in a single row in the sporangium, connected by a thin, protoplasmic strand; at discharge, encysting in a loose or compact, spherical or irregular cluster at the exit orifice; cysts 5-14 μm in diameter, releasing the secondary planont through a papilla. Secondary spores reniform or oval, laterally biflagellate. Gemmae absent. Oogonia lateral, rarely terminal; spherical or subspherical; (23-) 28-33 (-46) μm in diameter. Oogonial wall unpitted; smooth on outer surface, but frequently marked with hemispherical depressions at the points of antheridial cell attachment; faintly to noticeably irregular on inner surface. Oogonial stalks (1/4-) 1/2 - 1 (-3) times the diameter of the oogonium, in length; stout, usually straight or curved, occasionally irregular; unbranched or provided (infrequently) with one to a few short, cylindrical or papillate evaginations. Oospores containing a single, spherical, centric or subcentric refractive globule in the cytoplasm, and usually also a pellucid spot; spherical; single, and usually not filling the oogonium; (15-) 22-27 (-31) μm in diameter; at germination producing 1-2 unbranched or branched germ tubes which may or may not produce an apical sporangium. Antheridial branches predominantly declinuous, rarely monoclinal; branched or unbranched, or provided with one to a few short, lateral, papillate to cylindrical outgrowths; generally short, usually irregular or twisted; persisting. Antheridial cells simple; short, clavate, often bent or curved; the apex often expanded and rarely provided with an apical prolongation; occasionally forming one lateral, papillate protrusion; persisting; generally apically appressed, occasionally laterally attached; the broad end occasionally countersunk into a corresponding depression in the oogonial wall; fertilization tubes present.

There is little in the way of easily identifiable characteristics on which to base separation of *Aphanomyces raphani* from other plant pathogens in the genus. It is very closely akin to *A. euteiches* and *A. cochlioides* (see discussions of these species). The predominating diameters of the oogonia and oospores of *A. raphani* serve to separate it from *A. cladogamus* and *A. camptostylus*, but it must be admitted that these three species form a close series, indeed, in sizes of these structures. From a practical standpoint, much reliance must be placed on host range in attempting to identify *A. raphani*. The species was first discovered in roots of *Raphanus sativus* L., but has since been recovered from roots of other vascular plants, notably in the genus *Brassica* [see Chapter 28; also, Ghafoor (1964), and Ogoshi, Sakai, and Yokosawa 1972)].

The characteristics of the one isolate available for our examination are in reasonable agreement with Kendrick's (*loc. cit.*) and Drechsler's (1929) circumscriptions of *Aphanomyces raphani* (the name of the taxon first appeared in an abstract: *Phytopathology*, 17:43. 1927). The oogonial stalks of our specimen generally are very short and stout, and the antheridial branches originate in close proximity to the oogonia to which they are attached. In subcultures of our material, the hemispherical depressions in the oogonial wall (at the sites of antheridial cell attachment) are particularly prominent.

The most extensive study of the growth and nutrition of *Aphanomyces raphani* is that published by Ghafoor (1964). He failed to record the source of his material, but did cite several hosts (Chapter 28) for the fungus in addition to radish, as did Humaydan and Williams (1975). Kendrick's species has also been found in soil (Humaydan *et al.*, 1976), but we have not succeeded in recovering it from soil in sugar beet fields (Colorado).

In 1969, Pavgi and Singh provisionally identified as *Aphanomyces raphani* a fungus recovered from diseased specimens of *Brassica oleracea* var. *botrytis* (cauliflower). Subsequently, S. L. Singh and Pavgi (1977a) concluded that the causal fungus was a new species -- which they named *A. brassicae* -- distinguished from *A. raphani* by its more slender hyphae, absence of tapering sporangia, attachment of only one antheridium to each oogonium, and the production of smooth oospores. In reference to the nature of the oospore wall in their species, Singh and Pavgi wrote that those of *A. raphani* (among others) had a sinuous, irregular contour. We suggest that they mistook the oogonial wall for that of the oospore. The oogonia of *A. raphani* are irregular on the inner surface, and the oospores are smooth-walled.

None of the characters singled out by S. L. Singh and Pavgi (*loc. cit.*) are in fact limited to their *Aphanomyces brassicae*. Drechsler (1929:349) reported that a single antheridial cell (and filament) attendant to an oogonium was not rare in *A. raphani*, and our isolate of this species certainly conforms to that characterization. Since some sporangia produced by *A. raphani* do not taper toward the apex, the fact that those in *A. brassicae* are isodiametric is not useful taxonomically. As Ghafoor (1964) demonstrated, *A. raphani* invades *Brassica oleracea* var. *botrytis*, and Ogoshi, Sakai, and Yokosawa (1972) report Kendrick's species on several other species and varieties of *Brassica*. There is no significant host difference, then, between *A. brassicae* and *A. raphani*.

There is one characteristic of *Aphanomyces brassicae* that does not coincide with the circumscription of *A. raphani*. The oospores of the Indian fungus are smaller (16.5-21.5 μm) than is usual for *A. raphani*. The illustrations provided by S. L. Singh and Pavgi suggest that they observed immature oospores principally if not exclusively.

The evidence from our characterization of *Aphanomyces raphani*, in comparison with the circumscription of *A. brassicae*, does not single out any substantial morphological differences between the two. Accordingly, we are reducing the latter to synonymy.

CONFIRMED RECORDS: -- CZECHOSLOVAKIA: Cejp (1959a:94, fig. 20). GERMANY: Böning (1932-33:209, fig. 8). JAPAN: Ogoshi, Sakai, and Yokosawa (1972: figs. 6-9); Ogoshi, Yokosawa, and Sakai (1972:133, fig. 4); Yokosawa *et al.* (1972: pl. 1). INDIA: Pavgi and Singh (1969:990); S. L. Singh and Pavgi (*loc. cit.*). NEW ZEALAND: Wenham (1960:182, figs. 3,4). RUMANIA: Dumitraş and Bontea (1979:77, fig. 2). SOUTH AMERICA: Herold (1964) figs. 2C, D; 3). UNITED STATES: Drechsler (1929:345 *et seq.*, figs. 12-14); Kendrick (*loc. cit.*).

RECORDED COLLECTIONS: -- GERMANY: Böning(1935-36); Herold (1952). JAPAN: Yokosawa and Kuninaga (1979); Yokosawa *et al.* (1974). UNITED STATES: Clinton (1934); Hosford (1961); Humaydan and Williams (1975, 1978). Humaydan *et al.* (1976); Rich (1959); Weber (1932).

SPECIMEN EXAMINED: -- One unnumbered culture, R. Emerson (locality unknown).

Aphanomyces cladogamus Drechsler
J. Agric. Res. 38:335, figs. 5-7. 1929
(Figure 81 O, P)

Monoecious. Hyphae sparingly or moderately branched. Sporangia filamentous, long, often extensive and branched, and provided with ramifying branches that function in spore release; 7-9 μm in diameter, branches up to 2 mm long. Spores dimorphic. Primary spores spherical, oblong, or cylindrical; in a single row in the sporangium, sometimes connected by a thin, protoplasmic strand; varying in number depending on the length and extent of branching of the sporangium; at discharge encysting in a loose, irregular cluster at the exit orifice; cysts 7-11 μm in diameter, releasing the secondary planont through a papilla. Secondary spores reniform, laterally biflagellate. Gemmae absent. Oogonia lateral or terminal; spherical or subspherical; (18-) 24-28(-31) μm in diameter. Oogonial wall unpitted; smooth on outer surface, noticeably roughened or irregular on inner surface; sometimes slightly indented at point of antheridial cell attachment. Oogonial stalks of various lengths but generally longer than the diameter of the oogonium; usually irregular or contorted, occasionally coiled; branched or unbranched; sometimes coiling around attendant antheridial branches. Oospores containing a single, conspicuous, centric or subcentric, refractive globule in the cytoplasm, and frequently also exhibiting a pellucid spot; spherical;

single, generally not filling the oogonium; (14-) 18-23 (-29) μm in diameter; germination not observed. Antheridial branches predominantly declinous, occasionally monoclinal or androgynous; usually irregular or contorted; sometimes coiled or wrapping around the oogonial stalk, but only infrequently and sparingly around the oogonium; persisting. Antheridial cells simple; clavate, irregularly clavate, or cylindrical; infrequently lobed or with a lateral, papillate evagination; persisting although not formed on some antheridial filaments, when present, laterally appressed, or laterally or apically positioned in a slight depression in the oogonial wall; fertilization tubes present, not persisting.

Drechsler (*loc. cit.*) did not go to great lengths to discuss features by which *Aphanomyces cladogamus* could be distinguished from the other major phytopathogens in the genus. Indeed, Drechsler himself (1927) first identified *A. cladogamus* as *A. euteiches*. He cited the helicoid entwining of oogonial and antheridial filaments as a characteristic of *A. cladogamus*, but not of *A. euteiches*. His treatment of the dissimilarities among *A. cladogamus*, *A. raphani*, and *A. cochlioides* does not demonstrate convincingly that there are readily discernible differences.

We agree with Scott's (1961a) analysis that the most distinctive feature of *Aphanomyces cladogamus* is that of its patterns of antheridial branch origin. This is the only structural feature that we found to separate the species from the others described by Drechsler (1929; 1925, in F. R. Jones and Drechsler). Whether this difference will prove to be sufficiently constant (as determined by study of additional isolates) remains to be seen.

Our specimens support to some degree Drechsler's contention (1929: table 2) that the oogonia and oospores of *Aphanomyces cladogamus* are smaller (predominantly) than those in either *A. euteiches* or *A. raphani*, but generally larger than the ones produced by *A. cochlioides*. We find no convincingly apparent cochleate arrangement of antheridial branches and cells -- as is of occasional occurrence in *A. cladogamus* according to Drechsler (*loc. cit.*) -- in our two isolates. *Aphanomyces cladogamus* is very closely allied to *A. camptostylus*, structurally, as we have noted in our account of the latter.

It is evident from the information pertinent to the pathology of *Aphanomyces cladogamus* (Chapter 28) that this fungus differs little in host range from *A. euteiches*. The species may, in fact, have been mistaken for the latter. The *Aphanomyces euteiches* isolated by Buisman (1927) from the roots of *Viola* species possibly was *A. cladogamus*. The same may be said for *A. euteiches* P. F. 2 collected by Muers (1928), although it should be recognized that species of *Viola* are listed by Papavizas and Ayers (1974) as hosts for *A. euteiches*, the pea root rot pathogen. If Scott (1961a:36, pl. 5, figs. F, G) was correct in considering Mix's (1945a) *Aphanomyces* sp. to be *A. cladogamus*, then *Lactuca sativa* L. must be added to the host list for this pathogen. However, C. D. McKeen (1952) concluded that Mix's isolate was some species other than *A. cladogamus*, and we are in accord with that decision (*see records of Aphanomyces* sp.).

CONFIRMED RECORDS: -- CANADA: C. D. McKeen (1952:704 *et seq.*, pl. 1, figs. 2-5; pl. 2). INDIA: Dayal and Thakur Ji (1965:318, pl. 6), evidently recovered from soil and water. REPUBLIC OF CHINA: Chiou *et al.* (1975:171, pl. 3, figs. 34, 35), collected in soil. UNITED STATES: Coker and Braxton (1926: pl. 12, figs. 8,9), as *A. euteiches*; Drechsler (*loc. cit.*; 1954a:214, 216, figs. 1-4; 1954c:337 *et sqq.*, pls. 13-16). USSR: Logvinenko and Meshcheryakova (1971: fig. 6); Morochkovs'kiĭ *et al.* (1967:124, fig. 107).

RECORDED COLLECTIONS: -- INDIA: Chowdhry (1985); Chowdhry and Agarwal (1980a); Thakur Ji (1967). NETHERLANDS: Buisman (1927). USSR: Logvinenko (1971).

SPECIMENS EXAMINED: -- UNITED STATES: (2), TWJ, and one unnumbered culture, R. Emerson (locality unknown).

Aphanomyces amphigynus Cutter
Mycologia 33:230, figs. 7-11, 13 A-F. 1941
(Figure 83 A-E)

Monoecious. Hyphae slender, sparingly branched. Sporangia filamentous; unbranched; straight or curved; isodiametric; 60-187 x 3-6 μm . Spores dimorphic. Primary spores cylindrical or oval; in a single row in the sporangium, connected by a thin, protoplasmic strand; at discharge, encysting in a compact, spherical or subspherical cluster at the exit orifice; cysts 5-8 μm in diameter, releasing the secondary planont through a papilla. Secondary spores reniform, laterally biflagellate. Gemmae absent. Oogonia generally lateral, infrequently sessile; spherical or subspherical; (9-) 15-22 (-38) μm in diameter, exclusive of the wall ornamentations. Oogonial wall unpitted; provided with short or long spines, or with long or short, conical papillae, occasionally with a few truncate or indented-truncate tubercles. Oogonial stalks ($\frac{1}{4}$ -) $\frac{1}{2}$ -1 (-2) times the diameter of the oogonium, in length: straight or curved, unbranched; usually slightly irregular in outline. Oospores containing a small, centric or subcentric refractive globule in the cytoplasm; spherical; single, noticeably aplerotic; (9-) 12-15 (-20) μm in diameter; germination not observed. Antheridial branches predominantly declinous, infrequently monoclinal or androgynous; short and unbranched, rarely long, and then irregular or coiled loosely around oogonial stalks; usually persisting. Antheridial cells usually large, bulbous, bell-shaped, occasionally small and clavate or irregularly oval; persisting; often applied basally to the oogonial wall, and appearing amphigynous, but applied elsewhere as well; apically or laterally appressed; fertilization tubes not observed.

We have collected this species on onion skin bait, and also on insect exuviae, but have not succeeded in growing specimens either in unifungal or axenic culture.

Two characteristics single out *Aphanomyces amphigynus* from other saprotrophic species, namely aplerotic oospores (Fig. 83 A, D) and large, inflated, often basally applied antheridial cells (Fig. 83 A, B). There are some individuals of the species with small antheridial cells (T. W. Johnson, 1974b) hardly distinguishable from those

generally produced by *A. laevis* or *A. scaber*, for example. In such cases, the characteristic of the aplerotic oospore, coupled with the tapering, sharply pointed, or rounded projections on the oogonium (Fig. 83 B, C) are diagnostic for *A. amphigynus*.

Unlike the wall ornamentations in *Aphanomyces sparrowii* -- always sharply pointed spines -- those of *A. amphigynus* are spiny or papillate. There is a very close similarity between the sexual apparatus of Cutter's species and *A. parasiticus* (Coker, 1923), particularly in specimens of the latter possessing enlarged antheridial cells (Fig. 83 G). Aside from the fact that *A. parasiticus* occurs in water molds -- and *A. amphigynus* is free-living -- Coker's species almost always has spiny ornamentations rather than papillate ones. In *A. amphigynus*, both types of wall elements occur, although Cutter (1941:236) defined them as "... blunt spines or tubercles ..." Like Cutter's species, *A. parasiticus* has been found to have some of the antheridial cells applied to the oogonial wall in the vicinity of its juncture with the stalk (Cutter, 1941). In neither *A. amphigynus* nor *A. parasiticus* is this a constant feature, but Scott (1961a:53) in his discussion of the latter stated that the antheridial cell was "... applied in all cases to the base of the oogonium."

Some specimens of *Aphanomyces amphigynus* from Iceland (T. W. Johnson, 1974b: fig. 73) digress from the usual circumscription of this species in two characters. The oogonia are extremely short-stalked, or are sessile, and are provided with attendant monoclinal antheridial branches.

According to Cutter (*loc. cit.*), Sparrow had found *Aphanomyces amphigynus* in Denmark. As we have not seen specimens from this collection, we cannot be certain of the record. The *A. exoparasiticus* reported by Sparrow in 1933 is referable to *A. amphigynus*, just as Cutter concluded. Scott (1961a:55) cites a 1952 publication by Sparrow as providing a record of *A. amphigynus* from New York; such a record does not appear in either of Sparrow's papers published in 1952(a, b).

CONFIRMED RECORDS: -- ICELAND: T. W. Johnson (1974b:15, figs. 69-73).

UNITED STATES: Cutter (*loc. cit.*); Scott (1961a:54, pl. 7, figs. M-S).

RECORDED COLLECTIONS: -- UNITED STATES: Sparrow (1933).

SPECIMENS EXAMINED: -- ICELAND (3), TWJ. UNITED STATES (2), F. K. Sparrow, W. W. Scott (preserved specimens).

Aphanomyces volgensis Domashova
Mikol. i Fitopatol. 8:369, figs. a, b. 1974
(Figure 82 I-M)

Monoecious. Hyphae tenuous, flexuous, sympodially branched. Sporangia filamentous, simple or once- to twice-branched; up to 2.5 mm long, 5-11 μ m in diameter. Spores dimorphic. Primary spores cylindrical or allantoid; in a single row in the sporangium, connected by a thin, protoplasmic strand; at discharge encysting in a loose, nearly spherical cluster at the exit orifice; cysts 9-11 μ m in diameter, releasing the secondary planont through a pore. Secondary spores reniform, laterally biflagellate.

Gemmae absent. Oogonia terminal or lateral, rarely intercalary; single or catenulate; obpyriform and tapering broadly to the juncture with the subtending hypha or branch, or spherical; (21-) 28-36 (-51) μm in diameter, inclusive of wall ornamentations. Oogonial wall unpitted; thickened in distal, expanded portion, and there also papillate or tuberculate; thin and smooth in proximal portion. Oogonial stalks usually $\frac{1}{4}$ to as long as the diameter of the oogonium, in length; unbranched or once-branched; straight, curved, once-coiled, or irregular. Oospore containing a single centric or subcentric refractive globule in the cytoplasm, or several small, scattered droplets, and usually provided with a pellucid spot; spherical; single, not filling the oogonium; (17-) 24-28 (-36) μm in diameter; germination not observed. Antheridial branches usually absent; sparse when present, then androgynous or monoclinal, unbranched or branched; persisting. Antheridial cells, when delimited, simple, cylindrical or clavate; persisting; laterally attached; fertilization tubes not observed.

This species, isolated by Domashova (*loc. cit.*) from stagnant water in a fishpond, is very easily recognized by reason of the pattern of wall thickening in the oogonium. The wall in the distal, spherical portion of the oogonium is thick, but that of the lower portion that tapers broadly to the subtending stalk is thin (Fig. 82 I-K). Externally, this thickened portion of the oogonial wall is also provided with tubercles or short or somewhat elongate papillae (Fig. 82 M).

One of our isolates (from soil adjacent to a fish rearing pond in southwestern Iceland) of *Aphanomyces volgensis* differed slightly from that described by Domashova (1974a). Her specimens lacked antheridia; the Iceland material occasionally produced androgynous and monoclinal ones very sparingly, but in some subcultures did not form any such filaments.

An unidentified species of *Aphanomyces* resembling *A. volgensis* in the general shape of its oogonia was reported by Howard *et al.*, in 1970. This fungus appeared on midge exuviae from a bog pool in southwestern Iceland (T. W. Johnson, 1973b, recovered the species on snakeskin bait), but although axenically cultured, none of the colonies produced oogonia.

Although the oogonium and the subtending stalk of *Aphanomyces* sp. has a pyriform aspect (Fig. 82 N), as does that of *A. volgensis* (Fig. 82 J), the pattern of wall thickening is very different in the two fungi. In the Iceland material, the oogonial septum is thickened, as is the wall, and the thickening extends part way down the subtending stalk (Fig. 82 N). The wall of the stalk of oogonia in *A. volgensis* is of course not so thickened (Fig. 82 I, J). In their diameters, the oogonia and oospores of *Aphanomyces* sp. are smaller than those in Domashova's species. With respect to the nature of the oogonial wall ornamentation, the two taxa are very much alike, as are the origin and sparseness of their antheridial branches.

While it is possible that the *Aphanomyces* sp. recovered by Howard and his associates (1970) is perhaps only an extreme variant of *A. volgensis*, this has not been explored through comparative morphological culture studies. A brief description of *Aphanomyces* sp. (Howard *et al.*, 1970) follows.

Monoecious. Hyphae delicate, branched, and occasionally contorted or irregular. Sporangia filamentous, simple or branched; sometimes renewed in a basipetalous fashion; 96-287 x 6-8 μm . Spores dimorphic. Primary spores elongate; in a single row in the sporangium, connected by a thin protoplasmic strand; at discharge encysting in a compact mass at the exit orifice; cysts 4-8 μm in diameter, releasing the secondary planont through a pore. Secondary spores reniform, laterally biflagellate. Gemmae absent. Oogonia lateral; spherical or subspherical, but together with the stalk having an obpyriform aspect; (15-) 18-27 (-41) μm in diameter, inclusive of wall ornamentations. Oogonial wall unpitted, tuberculate, papillate, rarely spiny; often somewhat irregular on inner surface. Oogonial stalk short, about equal to the diameter of the oogonium; expanded distally, and usually thickened except in the basal portion; unbranched. Oospore containing a single, small, subcentric refractive globule in the cytoplasm and sometimes a pellucid spot; spherical or oval; single, and not filling the oogonium; spherical ones (10-) 14-18 (-22) μm in diameter; germination not observed. Antheridial branches usually absent; when present, androgynous or monoclinal; unbranched, somewhat irregular; usually not persisting. Antheridial cells simple, irregularly cylindrical; persisting; laterally appressed; fertilization tubes not observed. -- Figure 82 N.

CONFIRMED RECORD: -- USSR: Domashova (loc. cit.).
SPECIMENS EXAMINED: -- ICELAND (2), TWJ.

Aphanomyces scaber de Bary
Jahrb. Wiss. Bot. 2:178, pl. 20, figs. 14-16. 1860
(Figure 82 T-X)

Aphanomyces irregulare Scott, Virginia Agric. Exp. Sta. Techn. Bull. No. 151,
p. 47, pl. 7, figs. A-D. 1961.

Monoecious. Hyphae delicate, sparingly branched. Sporangia filamentous; straight or curved, and occasionally slightly irregular in outline; predominantly unbranched, rarely once-branched; (67-) 180-279 (-348) x 5-11 μm . Spores dimorphic. Primary spores cylindrical to oval; in a single row in the sporangium, usually connected by a thin, protoplasmic strand; at discharge encysting in a compact or (infrequently) loose, spherical or irregular cluster at the exit orifice; cysts 7-12 μm in diameter, releasing the secondary planont through a pore. Secondary spores reniform, laterally biflagellate. Gemmae absent. Oogonia lateral or terminal; predominantly spherical, infrequently subspherical, occasionally obpyriform; (14-) 22-28 (-38) μm in diameter, inclusive of the wall ornamentations. Oogonial wall unpitted; generally papillate, varying to slightly roughened, crenulate, or papillulate, rarely tuberculate, not spiny; wall ornamentations usually dense, but sometimes sparse and inconspicuous. Oogonial stalks $\frac{1}{4}$ - $2\frac{1}{2}$ times the diameter of the oogonium, in length; straight or curved; often slightly irregular in outline; unbranched. Oospores containing a small, centric or

subcentric refractive globule in the cytoplasm; spherical; single, and generally not filling the oogonium; (12-) 18-22 (-27) μm in diameter; at germination producing a branched or unbranched hypha. Antheridial branches sometimes absent; when present, predominantly dichinous, occasionally monochinous or androgynous; unbranched or sparingly branched, often curved or bent, and generally irregular in outline; infrequently deliquescing. Antheridial cells simple; small, clavate to cylindrical, and occasionally somewhat irregular; infrequently deliquescing; fertilization tubes not observed.

In the paper in which he first described species of the new genus *Aphanomyces*, de Bary (*loc. cit.*) was careful to stress that the various species he collected could be recognized as distinct entities because no intermediate forms had been found, and the specimens maintained their morphological integrity in culture. If de Bary was correct, *A. scaber* and *A. stellatus*, similar in several ways, should be readily distinguishable from one another. That they have been confused and misidentified is abundantly clear from the literature (Scott, 1961a; T. W. Johnson, 1974b, 1977c; Howard *et al.*, 1970; Humphrey, 1893; Cutter, 1941, among others).

In particular, de Bary's *Aphanomyces scaber* has proven to be very difficult to define, and has suffered from widely divergent interpretations. The uncertainty concerning the morphological limits that circumscribe *A. scaber* and set it off from other taxa in the genus seems to reside solely in the interpretation of the nature of the projections from the oogonium wall. De Bary (*loc. cit.*) referred to these protrusions as "spitz," but they are depicted in the majority of illustrations accompanying the description as papillae, not spines. Neither Humphrey (1893) nor Coker (1923) illustrated spiny oogonia for *A. scaber*, but in the former's descriptive account there is an undeniably clear reference to a spiny-walled form of the species. Somewhat later, Scott (1961a:53) described the oogonial wall ornamentations as "... sharp-pointed spines...", yet the illustrations he provided do not consistently show such protrusions. Some of T. W. Johnson's specimens from Iceland (1974b) and Scandinavia (1977c) had papillulate or crenulate oogonia as well as papillate ones.

It is in T. W. Johnson's paper of 1974(b) that the confusion over the nature of *Aphanomyces scaber* reached its zenith. He described a number of isolates, from Iceland, under the rubric of the *A. scaber*-*A. stellatus*-*A. irregulare* complex. Moreover, he ignored a decision reached previously by Howard *et al.* (1970) that Scott's *A. irregulare* was synonymous with *A. scaber*. Subsequently, T. W. Johnson (1977c) characterized a number of Scandinavian isolates of *A. scaber* and *A. stellatus*, comparing and contrasting them with the earlier recovered Iceland specimens. The resulting analysis of all the accumulated information permitted a precise naming of the Iceland collections (Johnson, 1977c:365). The subsequent records of *A. scaber* and *A. stellatus* reflect these identifications.

The fundamental difference, Scott (*loc. cit.*) asserted, between *Aphanomyces irregulare* and *A. scaber* was that of the nature of the oogonial wall. The oogonium of *A. irregulare* was simply defined as being roughened, but it should be noted that the

illustrations by Scott show them to be papillulate and crenulate as well. Scandinavian specimens with a preponderance of papillate oogonia (characteristic of *A. scaber*) also had (T. W. Johnson, 1977c) papillulate and crenulate ones, as did some of the specimens from Iceland (T. W. Johnson, 1974b). Accordingly, the decision reached by Howard *et al.* (1970:66) and Johnson (1977c) to equate *A. irregulare* with the antedating *A. scaber* must stand.

The structural characteristics that separate *Aphanomyces scaber* and *A. stellatus* are treated in the discussion of the latter. As defined in the foregoing description, *A. scaber* is essentially retained in the sense in which it was established by de Bary (*loc. cit.*).

Scott (1961a:47, 53) cited a record of *Aphanomyces scaber* and *A. irregulare* in 1958. This citation appears to refer to his dissertation, which was later (1961) published.

Three accounts of some ornamented *scaber*-like fungi require special mention. Whether or not Willoughby's (1971b) report of an ornamented species of *Aphanomyces* should be included as a record of *A. scaber* has not been resolved. The characteristics of his specimens did not agree particularly well with the circumscription of either species. Figure h on plate 1 of Willoughby's paper recalls *A. stellatus*, but illustrations on plate 2 are best considered representative of *A. scaber*. With reservation, Willoughby's unnamed isolate is included as a record of *A. scaber*. Goldsmith's (1948) account of *A. stellatus* is similarly in doubt; the one figure he provided suggests that he was dealing with *A. scaber*. It is difficult to identify with any confidence the *Aphanomyces* sp. recovered by Kobayasi and his colleagues (1967:12, text fig. 4) from Alaskan soil. The oogonia were described as having bluntly conical tubercles, but the illustrations show wide variation in the prominence of these wall evaginations. Antheridial branches were described as "... hypogenous...." but were illustrated as androgynous. The general configuration of the sexual apparatus in the Alaskan fungus is that of *A. scaber*, and we are provisionally accepting the specimens as that species, although the sporangial stage was not seen by Kobayasi, and the specimens therefore could have been representative of a *Pythium*.

CONFIRMED RECORDS: -- BRITISH ISLES: R. A. Couch (1951:85, pl. 11-13). CANADA: Maestres (1977:152 *et seq.*, figs. 50-54). CZECHOSLOVAKIA: Cejp (1959a: 108, fig. 28; 1931: 100). GERMANY: de Bary (*loc. cit.*; 1881:281 *et seq.*, pl. 6, figs. 30-36); Minden (1912:559); Richter (1937: 252). ICELAND: Howard *et al.* (1970:65 *et seq.*, fig. 9); T. W. Johnson (1974b:17 *et seq.*, figs. 53-68). INDIA: Dayal and Thakur Ji (1968c:34, figs. 21-28). MIDDLE EUROPE: Migula (1903:74). NORWAY: T. W. Johnson (1977c:362 *et seq.*, fig. 1 A-K). ORKNEY ISLANDS: Willoughby (1971b:473, pl. 1, fig. h; pl. 2, figs. u-w). PEOPLE'S REPUBLIC OF CHINA: Shen and Siang (1948:195). POLAND: Kadłubowska (1968:364, fig. 8); Stpiczyńska (1962:110, fig. 10); Zaborowska (1965: fig. 9). SWEDEN: T. W. Johnson (*op. cit.*). UNITED STATES: Beneke (1948b:96); Coker (1923: 163, pl. 50, figs. 13-16; pl. 56, figs. 8-10); Cutter (1941:235 *et seq.*, figs. 6, 14 E-I); Humphrey (1893:130, pl. 14, fig. 17; pl. 20, figs. 108-111); Kobayasi *et al.* (1967:12, text fig. 4) -- provisional; Scott (*loc. cit.*; 1961a: 53, pl. 7, figs. I-L); Wolf (1944: 33, pl. 3, fig. 20). USSR: Morochkovs'kiĭ *et al.* (1967:125, fig. 108)(as *A. stellatus*).

RECORDED COLLECTIONS: -- AFRICA: Goldsmith (1948:142, pl. 16, fig. 13)(?). BRITISH ISLES: Apinis (1964); Cook and Morgan (1934); Hunter (1975). CANADA: Maestres and Nolan (1978). CZECHOSLOVAKIA: Jesenská and Prandlová (1983). DENMARK: Petersen (1903, 1909a, 1910). GERMANY: Höhnk (1935a); Remy (1950). ICELAND: Howard and Johnson (1969); T. W. Johnson (1968). INDIA: Khulbe (1977; 1980a, d; 1981); Thakur Ji (1967); Khulbe and Bhargava (1977). JAPAN: Suzuki (1961f). UNITED STATES: Beneke and Schmitt (1961); R. L. Butler (1975)(?); Coker (1927); W. B. Cooke and Matsuura (1969); J. N. Couch (1926a, 1927); J. V. Harvey (1942); Höhnk (1935a); C. E. Miller (1965); Schmitt (1967); Slifkin (1964); A. W. Ziegler (1958b).

SPECIMENS EXAMINED: -- CENTRAL AMERICA (2), RLS, ICELAND (7), NORWAY (9), SWEDEN (6), TWJ. UNITED STATES (13), TWJ, RLS.

Aphanomyces stellatus de Bary
Jahrb. Wiss. Bot. 2:178, pl. 19. 1860
(Figure 83 L-0)

Aphanomyces coniger Petersen, Bot. Tidsskr. 29:378, fig. 3b, f. 1909. (Also in Ann. Mycol. 8:525, fig. 3b, f. 1910.)

Monoecious. Hyphae delicate to stout; sparingly or densely branched (in contact with substratum). Sporangia filamentous; straight or curved, and occasionally irregular or wavy in outline; occasionally tapering inconspicuously toward the apex; predominantly unbranched, rarely once-branched; (88-) 155-191 (-263) x 6-14 μm . Spores dimorphic. Primary spores cylindrical to oval; in a single row in the sporangium, sometimes connected by a thin, protoplasmic strand; at discharge, encysting in a compact or loose, spherical or irregular cluster at the exit orifice; cysts 8-12 μm in diameter, releasing the secondary planont through a pore; in some specimens, enlarged, giant cysts intermingled with the smaller ones, or cysts remaining in the sporangium and germinating *in situ*. Secondary planonts reniform, laterally biflagellate. Gemmae absent. Oogonia lateral or terminal, occasionally sessile (on hyphae on some substrates); predominantly spherical, occasionally subspherical or obpyriform; (16-) 22-28 (-35) μm in diameter, inclusive of wall ornamentations. Oogonial wall unpitted; sparingly or densely provided with stout, conspicuous, cylindro-tuberculate, broadly papillate, truncate, or tuberculate ornamentations, and infrequently with furcate or indented, truncate ones, or (rarely) cylindro-clavate projections. Oogonial stalks $\frac{1}{3}$ - $3\frac{1}{2}$ times the diameter of the oogonium, in length, but usually about as long as the diameter; usually unbranched, infrequently once-branched, rarely with conical or papillate lateral projections; generally straight or curved, and usually slightly irregular in outline. Oospores with or without a centric or subcentric refractive globule in the cytoplasm; spherical; single and occasionally nearly filling the oogonium; (12-) 20-27(-31) μm in diameter; at germination producing a branched or unbranched hypha, the latter rarely forming a terminal sporangium. Antheridial branches, when present, declinous or monoclinal, rarely androgynous; short or long, unbranched or sparingly branched;

usually curved or twisted, and irregular in outline; infrequently coiling about the oogonial stalk; sometimes deliquescing. Antheridial cells simple; short-tuberos, short-clavate, cylindrical, or cylindro-clavate; unbranched; persisting; laterally appressed; fertilization tubes produced(?).

As is evident from the chosen epithet, de Bary (*loc. cit.*) characterized the oogonia of *Aphanomyces stellatus* as having a stellate configuration. He described the individual ornamentations as blunt or conical projections. Some of the illustrations de Bary (1860: figs. 11, 13c) provided of the oogonia show cylindro-tuberculate, broadly cylindrical or broadly papillate wall extensions, and large, truncate evaginations indented apically, or noticeably lobed.

Evidently because de Bary failed to emphasize variations in the nature of the wall ornamentations in *Aphanomyces stellatus*, the species has been misinterpreted (T. W. Johnson, 1974b, for example). *Aphanomyces stellatus* is distinguished with facility from *A. scaber* by its stout, broad, cylindrical or conical, often truncate wall ornamentations (Fig. 83 M, N) as opposed to the papillate ones in the latter (Fig. 82 T, X). In the very few instances where the walls of some oogonia of *A. stellatus* have broad, low papillae (T. W. Johnson, 1977c), the oogonia themselves are somewhat larger than those of *A. scaber*.

De Bary (*loc. cit.*) did not illustrate the pattern of oil deposition in the oospores of *Aphanomyces stellatus*, but Coker (1923:164) thought these cells were "... eccentric ... with an inconspicuous lunate series of droplets on one side..." Scott (1961a), in conformity with de Bary's statement, reported that the oospores of *A. stellatus* lacked a conspicuous oil droplet. In all specimens of this species that we have examined, some oospores are provided with a refractive globule (Fig. 83 N), but others are not. Additionally, the oogonia of *A. stellatus* on hyphae growing in direct contact with substrates such as roach wing or snakeskin are often subspherical or slightly oval (Fig. 83 O), and sessile or nearly so.

It has been reported (de Bary, *loc. cit.*; Scott, 1961a) that unusually large spores may emerge from some of the sporangia of *Aphanomyces stellatus*, but we have never observed such cells in any of the numerous specimens in which we have followed the spore discharge process. There is considerable variation to be found among individual specimens with respect to maximum, predominating, and minimum diameters of the oogonia and oospores of *A. stellatus*. Unfortunately, many investigators failed to state whether or not the measurements they recorded included the wall ornamentations, hence the sizes given may be only approximations.

Scott (1961a); reduced correctly Petersen's (1909a, b) *Aphanomyces coniger* to synonymy in *A. stellatus*. Petersen's species did not appear in A. Lund's (1934) collections in Denmark but the latter noted that it was difficult to separate *A. coniger* from *A. stellatus*. Cejp (1959a) retained *A. coniger* although he did not report that it had been found in Czechoslovakia. The several Iceland forms of *stellatus*-like members of the genus described by T. W. Johnson (1974b) were later identified. (T. W. Johnson, 1977c).

CONFIRMED RECORDS: -- CANADA: Maestres (1977:153, 154, figs. 31-34); C. L. Moore (1908-09:232, fig. 20). DENMARK: A. Lund (1934:29); Petersen (*loc. cit.*). GERMANY: de Bary (*loc. cit.*); Bock (1956:9, pl. 4); Minden (1912:560, fig. 5); Richter (1937:253). GREENLAND: Kobayasi *et al.* (1971:21, text fig. 10B). ICELAND: T. W. Johnson (1974b:17 *et seq.*, figs. 26-52). INDIA: Shah *et al.* (1977:143, fig. 1); G. C. Srivastava (1975b:192). JAPAN: S. Ito (1936:94, fig. 39); Nagai (1931:30 pl. 7, figs. 18-22); Okane (1977:5, figs. L, M). LATVIA: Apinis (1929a:226). MIDDLE EUROPE: Migula (1903:74, pl. 2B, fig. 6; pl. 2C, fig. 1). NORWAY: T. W. Johnson (1977c:364, fig. 1 L-X). POLAND: Staniak (1971:360); Szwanke (1938:13, pl. 4, fig. 11). REPUBLIC OF CHINA: Chiou *et al.* (1975:173, pl. 3, fig. 36). SOUTH AMERICA: Beneke and Rogers (1962:187). SWEDEN: T. W. Johnson (*op. cit.*) UNITED STATES: Beneke (1948b:98); R. L. Butler (1975: figs. 69-72); Coker (1923:163, pl. 56, figs. 1-7). USSR: Naumov (1954:62, fig. 30).

RECORDED COLLECTIONS: -- AFRICA: El-Hissy (1974). BRITISH ISLES: Cook and Morgan (1934); Dick (1963, 1966); Dick and Newby (1961); Hunter (1975); Perrot (1960); R. E. Roberts (1963); Sparrow (1957). CANADA: Dick (1971c); Maestres and Nolan (1978). DENMARK: Petersen (1903). EGYPT: El-Hissy and El-Nagdy (1983); El-Hissy *et al.* (1982). GERMANY: Höhnk (1935a). JAPAN: Suzuki (1960a, 1961f, 1962b). NEW ZEALAND: Karling (1966f). UNITED STATES: Coker (1927); Coker and Braxton (1926); Fowles (1967, 1976); J. V. Harvey (1925a, b; 1930); Höhnk (1935a); T. W. Johnson (1956a); C. E. Miller (1965); Scott (1960b; 1961a); Slifkin (1964); Whiffen (1945); A. W. Ziegler (1958b). USSR: Logvinenko and Meshcheryakova (1971); Mil'ko and Belyakova (1968). VENEZUELA: Karling (1981a).

SPECIMENS EXAMINED: -- ICELAND (34), NORWAY (11), SWEDEN (58), TWJ. UNITED STATES (22), TWJ, RLS.

Aphanomyces norvegicus Wille

Skr. Vidensk.-Selsk. Christiana, Math.-Naturvidensk. Kl. 1899:12, figs. 14-27. 1899
(Figure 83 P, Q)

Monoecious. Hyphae slender, branched, usually somewhat twisted or contorted; intra- and extramatrical, the latter forming haustorium-like branches penetrating into the host cell. Sporangia filamentous, straight, sinuous, or irregular, unbranched; distal portion emerging through the host wall from intramatrical hyphae, and usually tapering toward the apex; swollen at the juncture with the internal surface of host wall; extramatrical portion 57-179 μm long by 3-6 μm in diameter at the host wall. Primary spores cylindrical; in a single row in the sporangium; connected by a thin, protoplasmic strand; at discharge, encysting in a compact cluster at the exit orifice; cysts 6-12 μm in diameter, releasing the secondary planont through a pore. Secondary spores reniform, laterally biflagellate. Gemmae absent. Oogonia lateral or terminal, intra- or extramatrical; spherical or subspherical; (16-) 21-27 (-30) μm in diameter, exclusive of wall ornamentations. Oogonial wall unpitted; hyaline or brown; provided with papillae and straight or curved, conical projections with a rounded end. Oogonial stalks $1/4$ to

as long as the diameter of the oogonium, in length; twisted or irregular; curved or bent; unbranched or provided with one or two short, lateral, papilla-like projections. Oospores containing a single, nearly centric, refractive globule in the cytoplasm; spherical; single, and filling the oogonium or not; wall hyaline or brownish; (15-) 18-21 (-24) μm in diameter; germination not observed. Antheridial branches present or absent; when present, dichinous; unbranched or sparingly branched; usually irregular or twisted, and curved or sinuous; persisting. Antheridial cells simple; cylindrical, clavate, or irregularly cylindrical; straight, curved, or bent; persisting; laterally appressed; fertilization tubes not observed.

Three undeniably closely allied species, *Aphanomyces phycophilus*, *A. apophysii*, and *A. norvegicus*, have been discovered in conjugate algae. For obvious reasons, we treat *A. phycophilus* and *A. apophysii* as incompletely known taxa. The ornamented specimens we have found in species of *Spirogyra* are considered to be representative of *A. norvegicus*. Wille (*loc. cit.*) first collected the species in filaments of *Spirogyra* sp., *Zygnema* sp., and *Mougeotia* sp., and in members of the Desmidiaceae.

Wille's (*loc. cit.*) description of *Aphanomyces norvegicus* is incomplete, but the illustrations establish the general characteristics of the sexual apparatus rather well. He did not see spore formation or discharge, and failed to record the sizes of the oogonia and oospores. Measurements were first provided for this species by Linder (1947); the spore discharge process was for the first time described and illustrated by Howard *et al.* (1970).

Both Minden (1912) and Coker and Matthews (1937) reported (without examining any specimens) that the sporangia of *Aphanomyces norvegicus* were intercalary. However, this is incorrect, for these asexual cells are clearly lateral elements from intramatrical hyphae (Howard *et al.*, 1970: fig. 10). Wille (*loc. cit.*) stated that *A. norvegicus* produced "conidie" -- oval, thick-walled cells -- but such structures are not mentioned in any subsequent descriptions of this species. Certainly there were no "conidia" in the specimens we have examined from our Iceland collections.

Wille (*loc. cit.*) recognized the similarity of his species to *Aphanomyces phycophilus*, but separated *A. norvegicus* from de Bary's taxon on two characteristics. According to Wille, *Aphanomyces norvegicus* had brown oogonial walls, and extramatrical hyphae that encircled the host filament as well as producing intramatrical penetrations. Linder (1947) confirmed Wille's observations with respect to the orientation of the extramatrical hyphae.

An analysis of the literature on *Aphanomyces norvegicus* indicates that those who saw specimens were in rather close agreement as to the nature of the oogonial wall ornamentations. These projections usually are straight or curved, tapering or cylindrical, and rounded at the apex (Fig. 83 P; Howard *et al.*, 1970: fig. 11; Linder, 1947: pl. 13, fig. D). Occasionally, the ornamentations are papillate, or are broadly conical. Not all of Wille's (*loc. cit.*) illustrations of the oogonia of *A. norvegicus* illustrate such projections (he figures them generally as narrow papillae), but figure 27 in his publication leaves no doubt that elongate ornamentations were formed by his fungus.

De Bary's (1860) figures of the oogonial wall projections in *A. phycophilus* are undeniably more like those Wille provided for his specimens of *A. norvegicus* than later investigators evidently saw in individuals they identified as *A. norvegicus*.

The close similarity of *A. phycophilus sensu de Bary*, to *A. norvegicus sensu Wille* is suggestive evidence that the two are in fact one species. On the other hand, the oospores and oogonia of *A. norvegicus sensu Linder, 1947*, and Howard *et al.*, 1970) are smaller than those described for either *A. phycophilus* or *A. apophysii*. Inasmuch as the sporangia of *Aphanomyces phycophilus* are unknown, a meaningful comparison of it with Wille's species is not possible. Perhaps an analysis of numerous additional specimens of *Aphanomyces* in conjugate algae would provide clues to the actual relationship between the two taxa. It is unfortunate that no type material of either de Bary's or Wille's species exists.

Uncertainty as to the nature of *Aphanomyces norvegicus* and *A. phycophilus* has doubtless led to misidentifications. In our judgment, the *A. phycophilus* reported by Weatherwax (1914) in *Spirogyra* sp. probably was *A. norvegicus*, although the illustrations he provided recall *Leptolegnia ornata*. *Aphanomyces apophysii* justifiably might be considered synonymous with *A. norvegicus* if it were not for the errors extant in the description published by Lacy (1949). The fungus described by Richter (1937) as *A. norvegicus* may or may not have been this species. The illustrations of the oogonial wall ornamentations recall those of *A. phycophilus*, but the length (6-8 μm) is more nearly appropriate to Wille's species. We include Richter's record with reservation.

CONFIRMED RECORDS: -- CANADA: Linder (1947:244, pl. 13, figs. C-F). GERMANY: Richter (1937:253, fig. 254). GREENLAND: Kobayasi *et al.* (1971:20, fig. 10A). ICELAND: Howard *et al.* (1970:65, figs. 10, 11). NORWAY: Wille (*loc. cit.*). UNITED STATES: Weatherwax (1914:109, figs. 1-6).

SPECIMEN EXAMINED: -- ICELAND (1), TWJ.

Aphanomyces sparrowii Cutter
Mycologia 33:233, figs. 3, 15 C-G. 1941
(Figure 83 H-K)

Monoecious. Hyphae sparingly branched in *Nitella* cells, abundantly branched on cellulosic substrates. Sporangia filamentous, unbranched or once-branched, straight or sinuous; isodiametric or tapering toward the apex; (57-) 88-125 (-210) \times 3.5-11 μm ; not constricted or swollen at point of passage through the host wall. Spores dimorphic. Primary spores cylindrical; in a single row in the sporangium, connected by a thin protoplasmic strand; often few in number; at discharge encysting in a compact or loose cluster at the exit orifice; cysts 7-10 μm in diameter, releasing the secondary planont through a papilla. Secondary spores reniform, laterally biflagellate. Gemmae absent. Oogonia lateral or terminal; generally spherical, infrequently ovoid or cylindrical; (16-21-24 (-28) μm in diameter, exclusive of the ornamentations. Oogonial wall unpitted; densely or sparsely ornamented with straight, curved, or furcate, short or long spines,

these reaching 26 μm long. Oogonial stalks of various lengths, generally as long as the diameter of the oogonium, but infrequently up to three times longer; straight or slightly irregular, unbranched or with one to a few short, papilla-like, lateral protrusions. Oospores containing a single, centric or subcentric refractive globule in the cytoplasm; spherical; single, and not filling the oogonium; (14-) 19-22 (-26) μm in diameter; germination not observed. Antheridial branches usually present, predominantly diclinous, occasionally monoclinal or androgynous; unbranched or sparingly branched; often short; usually slightly irregular in outline; occasionally deliquescent. Antheridial cells simple; large, clavate to bell-shaped, and occasionally bent or slightly contorted; persisting, but tending to collapse as culture ages; laterally or apically attached; fertilization tubes not observed.

Aphanomyces sparrowii was reported by Sparrow, in 1930, as *A. phycophilus*. He retained this latter name in his 1932 account, but in 1933 (p. 532) called attention to the fact that the fungus was too small and delicate, and the oogonial wall projections too spine-like "... to be identical with *A. phycophilus*." Cutter (*loc. cit.*) reexamined Sparrow's collection of *A. phycophilus*, and concluded that the specimens (in *Nitella* sp.) represented a new species, which he named *A. sparrowii*. The account of *A. sparrowii* published by Scott (1961a:57, pl. 8, figs. A-E) also was based on Sparrow's material. The only other report of Cutter's species is that by T. W. Johnson (1977c), who recovered it (on cellophane bait) from Norwegian soil. The foregoing description is based in large part upon the characteristics of that collection.

Aphanomyces sparrowii differs from all other ornamented species in the genus in the nature of the oogonial wall projections. These are generally very long and prominent (Fig. 83 H, J) and sometimes bifurcate and curved (Fig. 83 I, J). Only infrequently are oogonia with short spines produced in culture. Cutter (*loc. cit.*) illustrated the ornamentations as projections rounded at the apex; in our specimens, these wall extensions are sharply-pointed only. The oogonial wall ornamentations in that portion of Sparrow's (1930) material which we examined are identical to those produced by the Norwegian specimens. Although Cutter saw only diclinous antheridial branches in *A. sparrowii*, there are androgynous (Fig. 83 I) and monoclinal ones as well.

The large, prominent spines readily separate *Aphanomyces sparrowii* from *A. norvegicus* and *A. phycophilus*. Some oogonia of *A. exoparasiticus* (Fig. 84 C) have prominent spines that approach some of the shorter ones of *A. sparrowii*. The substrates on which the two species occur are very different, however, and in *A. exoparasiticus* only diclinous antheridial branches are known to be produced.

CONFIRMED RECORDS: -- NORWAY: T. W. Johnson (1977c:365, fig. 2 G-O). UNITED STATES: Sparrow (1930:118 *et seq.*, fig. 1). [Scott (1961a) in reference to Sparrow's material, records the host species as *N. flexilis*, evidently assuming that the record cited by Sparrow (1932:98) is the one on which the 1930 publication was based. The record published by Sparrow in 1932, however, does not appear to be the same as that of the collection he referred to in his 1930 account (as *A. phycophilus*).]

SPECIMENS EXAMINED: -- NORWAY (1), TWJ. UNITED STATES, F. K. Sparrow (preserved specimen).

Aphanomyces exoparasiticus Coker and Couch
In, Couch, J. Elisha Mitchell Sci. Soc. 41:216, pls. 28-33. 1926
(Figure 84 A-C)

Monoecious. Hyphae coarse, sinuous, branched; intra- and extramatrical. Sporangia filamentous, simple, isodiametric; straight or sinuous to irregular; 61-237 x 5-10 μm . Spores dimorphic. Primary spores cylindrical; in a single row in the sporangium; connected by a thin, protoplasmic strand; at discharge, encysting in a loose, irregular cluster at the exit orifice; cysts 8-12 μm in diameter, releasing the secondary planont through a pore. Secondary spores reniform, laterally biflagellate. Gemmae absent. Oogonia lateral; spherical; extramatrical; (21-) 30-38 (-47) μm in diameter, exclusive of wall ornamentations. Oogonial wall unpitted; provided with scattered, prominent spines up to 16 μm long, rarely papillate. Oogonial stalks usually 1-3 times the diameter of the oogonium, in length; unbranched, straight, bent, or slightly irregular. Oospore containing a large, centric or subcentric refractive globule in the cytoplasm; spherical; single, occasionally nearly filling the oogonium; (19-) 24-32 (-38) μm in diameter; germination not observed. Antheridial branches declinous; unbranched or branched, often coiling about the oogonial stalk and adjacent hyphae; not persisting. Antheridial cells simple; short and clavate or long and cylindrical, then partially wrapping about the oogonium; persisting, but often collapsing as culture ages; laterally appressed; fertilization tubes not observed.

Our only specimens (the third record of collection) of this species appeared in a cornmeal agar plate seeded with mycelium of *Aplanopsis terrestris* that was heavily overgrown with an unidentified *Pythium*. The *Aphanomyces* did not yield to isolation in subculturing, hence was intramatrical in the mycelium of the *Pythium* sp. when it was characterized.

According to J. N. Couch (*loc. cit.*) his specimen of *Aphanomyces exoparasiticus* produced rhizoid-like hyphal branches that maintained an intimate contact with the host hyphae. In our cultures the fungus lacked such structures even though it grew intramatrically (though sparsely) in the *Pythium* hyphae.

Aphanomyces exoparasiticus produces some oogonia with very prominent spines approaching those of *A. sparrowii* (Figs. 84 C, 83 K), but in general the wall projections are not as prominent as those in Cutter's species. *Aphanomyces exoparasiticus* appears to be limited to growth in species of *Pythium* (J. N. Couch, *loc. cit.*), and in this respect differs from the other parasitic forms with ornamented oogonia: *A. norvegicus*, *A. phycophilus*, and *A. parasiticus*. Other characteristics, such as the tendency for antheridial branches to coil about the hyphae (Fig. 84 A, B), are diagnostic for *A. exoparasiticus*.

Scott's (1961a:56, pl. 8, figs. F-I) treatment of *Aphanomyces exoparasiticus* is taken from Couch's (*loc. cit.*) account.

CONFIRMED RECORD: -- UNITED STATES: J. N. Couch (*loc. cit.*).
RECORDED COLLECTION: -- UNITED STATES: Sparrow (1933).
SPECIMEN EXAMINED: -- SWEDEN (1), TWJ.

Aphanomyces parasiticus Coker
Saprolegniaceae, p. 165, pl. 57. 1923
(Figure 83 F, G)

Monoecious. Hyphae intramatrical; slender, somewhat irregular and becoming increasingly so with age, sparingly branched; occasionally becoming extramatrical. Sporangia filamentous, unbranched or branched, isodiametric; in part extramatrical; emergent portion straight or sinuous, 31-218 × 5-9 μm. Spores dimorphic. Primary spores cylindrical; in a single row in the sporangium, connected by a thin, protoplasmic strand; at discharge, encysting in a loose, irregular clump at the exit orifice; cysts 6-14 μm in diameter, releasing the secondary planont through a pore. Secondary spores reniform, laterally biflagellate. Gemmae absent. Oogonia lateral or terminal; spherical; usually intramatrical, but occasionally extramatrical; (18-) 24-31 (-38) μm in diameter, including wall ornamentations. Oogonial wall unpitted; provided with scattered or dense, short, sharply pointed spines, infrequently merely papillate. Oogonial stalks usually smaller than the diameter of the oogonium, but occasionally equal to it, in length; unbranched. Oospore containing a single, centric or subcentric refractive globule in the cytoplasm, and occasionally a pellucid spot; spherical; single, filling the oogonium or not; (12-)16-21(-25) μm in diameter; germination not observed. Antheridial branches declinuous; unbranched or sparingly branched; short or long; persisting. Antheridial cells simple, clavate, sometimes bulbous or swollen; persisting; laterally or apically attached; fertilization tubes not observed.

Coker (*loc. cit.*) contended that *Aphanomyces parasiticus* parasitized only *Achlya* species. As the records of this species show, however, the fungus grows as well in other water molds (*see* confirmed records), although *Achlya* species are clearly more likely to be invaded than are others.

According to Coker, the oogonia of his species were warted to spiny (*see* also, Scott, 1961a:52, pl. 7, figs. E-H), but most descriptions of *Aphanomyces parasiticus* published since the original are not entirely in agreement with Coker's account. Cutter (1941:231), examining the specimens collected by Sparrow in Massachusetts and England, reported that all the oogonia were spiny. The specimens found in *Achlya prolifera* by Milanez and Beneke (1968: pl. 2, figs. 3, 4) are illustrated as having short, broad, sharp spines. In our material from Scandinavia the oogonial ornamentations are consistently spiny (Fig. 83 F, G).

Aphanomyces stellatus was reported by Coker (1923) to occur also in hyphae of *Achlya* species. The oogonial wall ornamentations of *A. stellatus* are of course quite different from those of *A. parasiticus* in *Achlya* species (Figs. 83 M, N; 83 G), and the two

species thus can be distinguished from one another readily. Projections on the oogonia of *A. amphigynus* may on occasion be distinct spines (Fig. 83 C), but this species is not parasitic on watermolds, so far as is known. In the discussion of *A. parasiticus* Coker (*loc. cit.*) mentioned that some of the least spiny oogonia of the species resembled those of *A. scaber*. In the latter, however, the antheridial branches are not strictly declinous as in Coker's species. In sum, *A. parasiticus* is a recognizable taxon that seems to be restricted to growth in other watermolds.

Prowse (1954a:26, fig. 3d) reported an *Aphanomyces* in hyphae of *A. daphniae*, itself parasitic in specimens of a *Daphnia*. He thought the hyperparasitic form might have been *A. parasiticus*, but as he saw only preserved specimens he questioned this identification. The *A. parasiticus* (in *Achlya* sp.) reported by Wolf (1944) also must be regarded as a provisional identification. Although he illustrated the sexual apparatus of Coker's species, Wolf remarked that he had not observed the oogonia. Reports of the recovery of *A. parasiticus* from soil or water (K. B. Raper, 1928, for example) are questionable.

CONFIRMED RECORDS: -- CZECHOSLOVAKIA: Cejp (1959a:104, fig. 26). PEOPLE'S REPUBLIC OF CHINA: Shen and Siang (1948:196, fig. 8). REPUBLIC OF CHINA: Chiou and Chang (1976:51, pl. 6, figs. 6, 7). UNITED STATES: Beneke (1948b:99); Coker (*loc. cit.*); Cutter (1941:230, 231); Milanez (1966:91, pl. 9, figs. E-H); Milanez and Beneke (1968:17, pl. 2, figs. 3, 4).

RECORDED COLLECTIONS: -- BRITISH ISLES: Dick (1964, 1966); Prowse (1954a:26, fig. 3d), Sparrow (1936). UNITED STATES: W. B. Cooke and Bartsch (1959; 1960); K. B. Raper (1928); Sparrow (1932); Wolf (1944:34, pl. 3, fig. 23). USSR: Mil'ko and Belyakova (1968)

SPECIMEN EXAMINED: -- NORWAY (1), TWJ.

Aphanomyces sp.

Citations marked by an asterisk (*) denote reports of unidentified collections on fish or fish eggs. Records of the *Aphanomyces* sp. later named *A. astaci* are not included in the following listing.

AFRICA: Karling (1976); Nolard-Tintigner (1974); Seymour and Briggs (1985) in *Anopheles gambiae* Giles). AUSTRALIA: Allen *et al.* (1987). BRITISH ISLES: Beaumont (1954), possibly *A. euteiches*; McKeen and Traquair (1980; figs. 1, 2); Traquair and McKeen (1980). Byford (1972), possibly *A. cochlioides*; Comerford and Mangan (1964), possibly *A. cochlioides*; Park (1972a); Dick (1966); P. H. Gregory (1951); Hallett and Dick (1981); O'Sullivan (1965); Pickering and Willoughby (1977); Warcup (1957); Willoughby *et al.* (1984); Wood and Willoughby (1986); Willoughby (1962; 1970*: pl. 2, fig. C; 1978*); Willoughby and Collins (1966). CANADA: Dick (1970); Maestres (1977: figs. 35-42); CENTRAL AMERICA: Sörgel (1941). CZECHOSLOVAKIA: Jesenská and Prandlová (1983). DENMARK: Petersen (1909a, 1910). FRANCE: Volkonsky (1934), identified as *A.*

(?)*stellatus*. GERMANY: Bock (1956); Höhnk (1935a, 1956a, 1958); F. Müller (1911). INDIA: Dayal and Tandon (1962, 1963); Dayal and Thakur Ji (1966); Khulbe (1977; 1980a, d; 1981; 1982b; 1983c); Khulbe and Bhargava (1977); Manoharachary (1974, 1979c); Manocharachary and Ramarao (1978); Mer *et al.* (1980); Mer and Khulbe (1984:200); Murdia (1938); R. C. Srivastava (1976*: pl. 2, fig. 8; 1985); R. C. Srivastava and G. C. Srivastava (1978a*); G. C. Srivastava and R. C. Srivastava (1977e*); Thakur Ji and Dayal (1966). JAPAN: Egusa and Masuda (1971*:42 figs. 4, 5, 13-15); Naiki and Kanoh (1978); Okane (1967, 1968); Suzuki (1960a-c, h, e; 1961d, e, h-k; 1962a, b; 1981); Suzuki and Hatakeyama (1960, 1961); Suzuki and Nimura (1961a, b, d, e; 1962); Suzuki and Tatsumo (1964); Suzuki *et al.* (1960, 1961). MEXICO: Seymour and Briggs (1985; in *Anopheles albimanus* Wiedemann, and *A. gambiae*). NETHERLANDS: Brandenburg (1931a, b), involved in "reclamation" disease of oats, beets, peas; Buisman (1927), isolated from *Viola* sp. NORWAY: Solberg (1925), possibly were "races" of *A. euteiches*. PEOPLE'S REPUBLIC OF CHINA: Liang and Yu (1985); Yu and Liang (1983). PHILIPPINES: Dogma (1975). REPUBLIC OF CHINA: Volz *et al.* (1974: fig. 7). SOUTH AMERICA: Beneke and Rogers (1962, 1970); A. L. Rogers *et al.* (1970); SOUTH KOREA: So *et al.* (1981, 1982). SWITZERLAND: Maurizio (1899*). UNITED STATES: Beneke (1948b:100); Beneke and Schmitt (1961); Bretsnyder (1943:14); Clausz (1970, 1974); W. B. Cooke (1968; 1976a); W. B. Cooke and Matsuura (1969); Dykstra *et al.* (1986: fig. 7*); Farr and Paterson (1974); Fox and Wolf (1977a); Fowles (1976*); Fuller and Poyton (1964); Gaertner and Sparrow (1966); Gould (1949); J. V. Harvey (1942; 1952); G. C. Hughes (1959; 1962); Humphrey (1893: pl. 14, fig. 11); Jaffee (1986); Klich (1980); V. D. Matthews (1935:309), Mix (1945a), in seedling roots of lettuce, pepper, egg plant; Noga and Dykstra (1986*); O'Bier (1960*); Paterson (1967); Pfender *et al.* (1984); Rajagopalan (1963: 119, fig. 3 E-H); B. L. Richards (1925), causes root rot of peas; Schmitt and Beneke (1962); Schmitthenner (1964), probably *A. euteiches*; Schmitthenner and Hilty (1962); Scott (1962), Scott and O'Bier (1962*); Shanor and Saslow (1944*:413, fig. 1); Sorenson (1962: pl. 4, fig. D); Sparrow (1937, 1965); Tervet (1943), possibly *A. cochlioides*; M. W. Ward (1939); A. W. Ziegler (1952, 1958b). USSR: Florinskaya (1969:117, fig. 13); Kirgizbaeva *et al.* (1975); Kotova and Tsvetkova (1979). WEST INDIES: Sörgel (1941); Volz and Beneke (1972).

IMPERFECTLY KNOWN SPECIES OF APHANOMYCES

Aphanomyces apophysii Lacy

Indian Phytopathol. 2:136, 137, figs. 2D, 3. 1949

Monoecious. Mycelium intramatrical; swollen at the point of entry into the host wall. Sporangia filamentous, straight or curved; tapering toward apex; a portion becoming extramatrical; apophysate (swollen at point of juncture with the inner surface of the host wall); 300-500 x 8-12 µm. Spores dimorphic; primary spore elongate on emergence, then encysting at sporangial orifice. Secondary spore escaping through an

irregular tear in cyst wall. Gemmae lacking. Oogonia lateral, intramatrical; spherical; 35-40 μm in diameter. Oogonial wall unpitted, papillate, the projections up to 5 μm long. Oogonial stalks short, stout. Oospores coarsely granular or with oil droplets; single; brown; 20-24 μm in diameter; producing a small germ tube at germination. Antheridial branches declinous or monoclinal; unbranched. Antheridial cells simple; clavate; laterally appressed; fertilization tubes not observed. (Modified and adapted from Lacy, *loc. cit.*).

There is only a single record of this species, occurring in the filaments of *Spirogyra* sp. According to its author, *Aphanomyces apophysii* generally first invades the "male" filament (contributing thallus) of the susceptible *Spirogyra*, then attacks the receptive ("female") filament, and hyphae subsequently grow throughout the infected zygospores. Lacy did not cite any direct evidence for this "preferential" invasion pattern, and there is thus good reason to suppose that initial invasion could as well occur in the receptive thallus. Contrary to Lacy's contention, we do not regard this feature of invasion pattern to be of any importance taxonomically.

The presence of an apophysis at the juncture between a hypha (or sporangium) and the host wall was singled out by Lacy as one characteristic distinguishing *Aphanomyces apophysii* from de Bary's (1860) *A. phycophilus*; one such swelling depicted in an illustration in Lacy's account is referred to as an "hypophysis". In any event, we find such subsporangial or hyphal penetration swellings in the filaments of *A. norvegicus* (Wille, 1899), and do not regard them as limited solely to Lacy's species.

Evidently Lacy was unaware of Wille's *Aphanomyces norvegicus*, which his species very strongly resembles. The oogonial size (as we interpret the original description of *A. apophysii*) in Lacy's species is somewhat greater than that of *A. norvegicus*, although it must be recalled that Wille did not give measurements for his species. The specimens of *A. norvegicus* from Iceland (Howard *et al.*, 1970) had oogonia generally in the range of 28-40 μm in diameter, including the ornamentations. On the other hand, the oogonia of *A. apophysii* are smaller than those reported for *A. phycophilus* (Scott, 1961a). Our best judgment is that Lacy's species is intermediate in this character between Wille's and de Bary's taxa.

Lacy's (*loc. cit.*) illustrations of the oogonial wall ornamentations in *Aphanomyces apophysii* are not particularly revealing. Some are shown as short, papillate protrusions, rounded or pointed at the apex, while others are long, conical projections, or mere irregularities on the oogonial wall. The fact that the ornamentations seem not to be consistently papillate suggests the condition which we have found in our specimens of *A. norvegicus* (Howard *et al.*, 1970).

None of the four characteristics used by Lacy to separate his species from *Aphanomyces phycophilus* is limited to his fungus alone. We suspect that Lacy had collected *A. norvegicus*, but as the separation of that species from *A. phycophilus* is still unresolved, there is no way to be certain of this conjecture. It is quite possible, that a study of generous developments of *Aphanomyces* specimens in *Spirogyra* species will show that there is only single species rather than three as have been described.

We are retaining Lacy's *Aphanomyces apophysii* in the imperfectly known category solely as a convenience. There are very obvious errors in the application of terms in Lacy's description of his material (oogonia being smaller than the oospores, for example), and the species could be rejected on this fact alone.

CONFIRMED RECORD: -- INDIA: Lacy (*loc. cit.*)

Aphanomyces astaci Schikora
Fischerei-Zeitung (Neudamm) 9:552.1906

Aphanomyces magnusi Schikora, Verh. Bot. Vereins Prov. Brandenburg 63:87 *et seq.* 1922.

Mycelium intramatrical, coarse, abundantly branched. Sporangia filamentous, unbranched, isodiametric, terminal portion extramatrical; not constricted in its passage through host cuticle. Spores dimorphic. Primary spores cylindrical to oval; in a single row in the sporangium, connected by a thin protoplasmic strand; at discharge encysting in a loose, irregular mass at the exit orifice; cysts 7-10 μm in diameter, releasing secondary planont through a pore. Secondary spores reniform, laterally biflagellate. Gemmae produced in synthetic media. Oogonia and antheridia not observed. (In part adapted from Schikora, *loc. cit.*, and Rennerfelt, 1936:11, fig. 1.)

In his discussion of *Aphanomyces astaci*, Schikora (1922) used the name *magnusii* but without explanation. A *nomen rejiciendum*.

What was presumed to be the sexual apparatus of *Aphanomyces astaci* was described by Rennerfelt, but has not since been observed with certainty either *in vivo* or *in vitro* (Unestam, 1964, 1969a). Rennerfelt (1936:11) characterized the sexual structures as follows: oogonia spherical, terminal on short branches; 41.6-48.0 μm in diameter; oogonial wall covered with small, short, finely pointed spines; oospore single, 22.4-22.8 μm in diameter; antheridia (branches) rare, androgynous. The figures provided by Rennerfelt of the oogonia and oospores of *A. astaci* are not definitive and the same may be said for the illustrations of antheridial branches. He stated that the antheridia were androgynous, yet of the two illustrated (Rennerfelt, 1936: fig. li), neither shows a point of origin.

Only one structure alleged to be an oospore was illustrated by Rennerfelt, that being a germinating cell positioned in a spiny "case" lacking any attachment to a hypha (Scott, 1961a: pl. 6, fig. 0, did not accurately depict Rennerfelt's drawing). It is not at all clear from Rennerfelt's account precisely when the oogonia became ornamented; the two immature ones illustrated by him are in any case smooth. Schäperclaus (1935) also reported oogonia in specimens of *Aphanomyces astaci*, describing them as spiny and 16-20 μm in diameter. He evidently did not see oospores, but believed that the oogonia were similar to those of *A. scaber* or *A. stellatus*. The photograph accompanying Schäperclaus' account cannot be interpreted as depicting oogonia. Unestam (1964; 1969a: fig. 2) found enlarged, thick-walled, spherical or subspherical structures

positioned terminally or in an intercalary fashion on the hyphae of some isolates of *A. astaci*. He was not certain that these structures were part of the sexual apparatus, a decision quite clearly supported by the illustrations.

None of the evidence for a sexual apparatus in *Aphanomyces astaci* is persuasive. Moreover, we have not encountered any sexual structures in the specimens we have examined. It is extremely doubtful that the sex cells have ever been observed, and for this reason Rennerfelt's circumscription of the sexual apparatus in this species is not a part of the foregoing description.

Unestam (1969a) reported that gemmae developed in mycelium grown in shake culture on a synthetic medium containing either alanine or ammonium chloride as the sole nitrogen source. The sexual apparatus may as well be formed only under very particular environmental conditions.

According to Rennerfelt, the spores of *Aphanomyces astaci* are at first connected by a slender protoplasmic strand, but prior to their discharge the strand disappears, and the spores become spherical. Rennerfelt's account thus describes a very unusual event for species of *Aphanomyces*. In the instances of sporangium discharge that we have seen in *A. astaci*, the spores are elongate, not spherical, during emergence.

See Chapter 30 for a discussion of crayfish plague, caused by *Aphanomyces astaci*, and an account of the host range. The fungus has been found primarily in *Astacus astacus*, but is also known to occur in *A. leptodactylus* Esch. (Amlacher, 1954; Tsukeris, 1964) and *Pacifastacus leniusculus*. Benisch (1940) reported the infection of *Eriocheir sinensis* Milne-Edwards by artificial inoculation with an *Aphanomyces*; he did not name the fungus, but it was presumably *A. astaci*.

CONFIRMED RECORDS: -- DENMARK: Rennerfelt (1936:11, figs. 1, 2). GERMANY: Amlacher (1954: figs. 1, 2), Benisch (1940: figs. 1-7); Schäperclaus (1935:353 *et seq.*, figs. 6-8, 14-16); Schikora (1903:353, *et sqq.*; *loc. cit.*). LATVIA: Mannsfield [1942: figs. 5 (in part), 6, 8-10, 13, 14], Tsukeris (1964:79 *et sqq.*, fig. 4). NORWAY: Håstein and Unestam (1972: fig. 2). POLAND: Kozłowski (1968: figs. 1, 2). SWEDEN: Unestam (1964: figs. 1-5; 1969a:317 *et sqq.*, 5 text figs.).

RECORDED COLLECTIONS: -- BRITISH ISLES: Alderman *et al.* (1984). CANADA: Fürst and Boström (1978). DENMARK: Nybelin (1931, 1934). ESTONIA/LATVIA: Gabran (1939). FINLAND: Järvenpää *et al.* (198); Nylund and Westman (1983); Westman and Nylund (1978); Westman *et al.* (1973). FRANCE: Vey (1981). GERMANY: Schäperclaus (1927), Schikora (1903, 1906, 1913, 1922, 1926). NETHERLANDS: Geelen (1975). NORWAY: Håstein and Gladhaug (1972). SWEDEN: Abrahamsson (1966); Fürst and Boström (1978); Unestam (1965a); Vallin (1932, 1933). UNITED STATES: Fürst and Boström (1978).

SPECIMENS EXAMINED: -- SWEDEN (19). TWJ.

Aphanomyces hydatinae Valkanov
Arch. Protistenk. 74:6 *et sqq.*, figs. 1-16.1931

Hydatinophagus apsteinii Valkanov, Jahrb. Univ. Sofia 27:231, figs. 1-11. 1931.

Monoecious. Mycelium intramatrical. Sporangia filamentous, simple, becoming partially extramatrical. Spores dimorphic. Primary spores cylindrical, in a single row in the sporangium, connected by a conspicuous protoplasmic strand, and at discharge encysting at the orifice in a loose or compact mass. Secondary spores reniform, biflagellate. Oogonia terminal(?); spherical or subspherical. Oogonial wall unpitted, smooth. Oospores containing a single, conspicuous, centric or slightly subcentric oil globule; single; germination not observed. Antheridial branches declinuous; simple. Antheridial cells simple, clavate; laterally appressed; fertilization tubes not observed. (Adapted from Valkanov, *loc. cit.*)

This species name was first used by Valkanov (1931a) in reference to a doubtful member of the genus *Aphanomyces*, *A. hydatinae*. In a second account (1931b), he discussed some of the morphological characteristics of the fungus (in the rotatorian *Hydatina senta*), again under the binomial *A. hydatinae*. Valkanov published a third paper, also in 1931(c), in which he erected the new genus *Hydatinophagus* for the rotifer-inhabiting fungus. At this time, he renamed the parasite *H. apsteinii*. A cytological study of the sexual apparatus of *H. apsteinii* was published by Valkanov in 1932; he stated at this time that he had earlier referred to this species as *A. hydatinae*. According to Valkanov, host infection began within the body cavity, in contrast to the condition in some parasitic *Aphanomyces* species in which invasion allegedly begins at the body surface. This appears to be the single characteristic on which *Hydatinophagus* was based; in all other features, the fungus in rotifers was an *Aphanomyces*. Scott (1961a) held this one difference to be of no taxonomic value, and correctly reduced *Hydatinophagus apsteinii* to synonymy.

Nowhere in the descriptive matter in Valkanov's species (1931a-c, 1932) are measurements of the sexual and asexual structures of *Aphanomyces hydatinae* recorded, and the illustrations are not provided with any indication of magnification. The species is therefore incompletely described, and a firm decision as to its proper disposition cannot be made. From the figures and descriptive matter available, we suggest that *A. hydatinae* could easily be identified with *A. laevis*. The fungus in *Hydatina senta* is known only from Valkanov's collections, and much of what he wrote concerning the parasite needs further analysis based on study of additional material.

CONFIRMED RECORD: -- BULGARIA: Valkanov (*loc. cit.*; 1931a).

Aphanomyces phycophilus de Bary
Jahrb. Wiss. Bot. 2:179, pl. 20, figs. 19-24. 1860

Monoecious. Hyphae intra- or extramatrical; not swollen at point of exit from host cell or in traversing cell walls between host cells, or only slightly expanded. Sporangia unknown. Gemmae absent. Oogonia terminal on short lateral branches,

mostly extramatrical; spherical or subspherical; 20-55 μm in diameter, exclusive of ornamentations. Oogonial wall provided sparsely or densely with blunt, conical projections or papillae, reaching 10 μm long. Oogonial stalks short, stout. Oospores homogeneous throughout, or containing one or two rows of oil globules around the inner periphery, or a single, conspicuous, centric refractive globule; single; hyaline or brownish; 18-43 μm in diameter; germination not observed. Antheridial branches diclinous; simple, sometimes coiling about the oogonial stalks. Antheridial cells simple; large, clavate or tubular, sometimes irregular or curved; laterally appressed; fertilization tubes simple.

As is evident from the records of occurrence of *Aphanomyces phycophilus*, the species is not uncommon, occurring principally in species of *Spirogyra*. Moesz (1937-38) provided a record of the fungus in an unidentified species of *Mougeotia*, and de Bary (*loc. cit.*) found it in filaments of a *Zygnema*.

Neither de Bary (*loc. cit.*) nor anyone subsequent to him has described the sporangial stage of *Aphanomyces phycophilus*, and it is for this reason that we relegate the species to the imperfectly known category. Scott (1961a), on the contrary, considered de Bary's species to be a valid, recognizable one. In a 1930 paper, Sparrow described the asexual stage of *A. phycophilus*, but Cutter (1941) reexamined Sparrow's collection and believed the specimens represented a new species, *A. sparrowii*.

Whiffen (1938) succeeded in culturing *Aphanomyces phycophilus* from an unidentified *Spirogyra*. While the characteristics of the oogonia as Whiffen figured them agree well with the illustrations provided by de Bary, the growth pattern, *in vitro*, was not at all "typical" of species of *Aphanomyces*. Based on the large hyphal diameters of material grown in culture, Whiffen suggested that *A. phycophilus* was possibly not correctly assigned generically. The transverse measurements of hyphae --10-15 μm -- given by de Bary, certainly bear out Whiffen's comment. Cutter (1941), however, with the same species, found hyphal diameters to be 7-10 μm . In the preserved specimens from Couch's collections, the hyphae rarely exceed 10 μm .

The oogonia of *Aphanomyces phycophilus* are larger in some specimens at least, than is characteristic of most species of *Aphanomyces*. De Bary found them to be 50-60 μm in diameter (whether inclusive or exclusive of ornamentations is not known). Scott (1961a) measured oogonial diameters of 65-70 μm , including the wall projections, and in the description of the species stated that the oogonia were 29-55 μm in diameter, excluding the ornamentations. In the preserved specimens we examined, the oogonia were 31-48 μm in diameter (exclusive of the wall ornamentations), and the oospores were 23-30 μm in diameter.

Piecing together the brief descriptive notes on *Aphanomyces phycophilus*, we believe the papillate nature of the oogonial wall to be a distinguishing feature. So far as we can determine from extant illustrations, the short, conical projections of the oogonial wall in de Bary's species are rounded apically, as opposed to the more pointed, longer (but tapering) ornamentations of *A. norvegicus* (Howard *et al.*, 1970; fig. 11) and *A. sparrowii* (Cutter, 1941; T. W. Johnson, 1977c: fig. 2 H-0). There can be no doubt,

however, that the general aspect of wall ornamentations in *A. phycophilus* is not far removed from that of *A. norvegicus* (see discussion of the latter species and *A. apophysii*). Some of the wall ornamentations on the oogonia in the specimens we examined are certainly not "typical" of those of *A. phycophilus* as de Bary illustrated the species.

The oogonial wall of *Aphanomyces phycophilus* has been described (Cutter, 1941; Scott, 1961a) as being hyaline to deep brown. This is a variable feature of no taxonomic consequence, although Wille (1899) emphasized wall color in separating his *A. norvegicus* from de Bary's species.

In 1872, Cornu published, under the binomial *Achlyogeton solatium*, a description of a filamentous fungus in *Oedogonium obsidionale*. The spores of the fungus were said to discharge in an achlyoid manner, and on this basis, A. Fischer (1892) suggested that Cornu's specimens were closely allied to *Aphanomyces phycophilus*; Coker (1923) thought likewise. Sparrow (1960) retained *A. solatium* as an imperfectly known species in *Achlyogeton*. Cornu's description of his material is much too brief to support any decision as to a proper disposition for the fungus, and he did not illustrate the specimens. Perhaps Cornu had collected an *Aphanomyces* -- the fungus was said to produce 3-12 spores that encysted at the exit orifice -- but there is no way to be certain. Although Weatherwax (1914) did not find sporangia associated with the *Aphanomyces* (in *Spirogyra dubia* Kützing) he named *A. phycophilus*, the illustrations suggest he had at hand a collection of *A. norvegicus* (Wille, 1899), as Scott (1961a) concluded (but see discussion of *Leptolegnia ornata*). The *A. phycophilus* reported in *Spirogyra nitida* (from Poland) by Kadłubowska (1968:364, pl. 3, fig. 8) very likely was misidentified. The one illustration depicts an oogonium quite like ones encountered in de Bary's *A. scaber*. That Kadłubowska described the oogonial wall as being undulant supports the possible conclusion that she was dealing with *A. scaber*. We are including her record of "*A. phycophilus*" with de Bary's species.

CONFIRMED RECORDS: -- CZECHOSLOVAKIA: Cejp (1959a:102, fig. 25). GERMANY: de Bary (*loc. cit.*); Minden (1912:560). MIDDLE EUROPE: Migula (1903:75). UNITED STATES: J. N. Couch (1926a:214); Cutter (1941:235 *et seq.*, figs. 4, 5, 15H-J); Whiffen (1938:649 *et seq.*, figs. 1-7).

RECORDED COLLECTIONS: --BELGIUM: Bommer and Rousseau (1884); de Wildeman (1889-90). HUNGARY: Moesz (1937-38). NEW ZEALAND: Karling (1966f). UNITED STATES: J. N. Couch (1924b); J. J. Davis (1919); Kauffman (1915).

SPECIMENS EXAMINED: -- UNITED STATES (2), J. N. Couch, V. M. Cutter, Jr. (preserved specimens, unnumbered collection).

Aphanomyces pisci R. C. Srivastava
Mykosen 22:27, figs. 2-4. 1979

Hyphae delicate; profusely branched; 7.2-9 μm in diameter. Sporangia filamentous; unbranched; formed from undifferentiated vegetative hyphae; 7.2-9 μm in diameter. Spores dimorphic. Primary spores encysting at the exit orifice upon release;

cysts 7-7.5 μm in diameter. Secondary spores reniform, laterally biflagellate. Gemmae abundant (especially at 11-13 $^{\circ}\text{C}$); irregular and consisting of several long or short lobes or branches; terminal or intercalary(?); contents dark. Oogonia and antheridial apparatus not observed. (Adapted from R. C. Srivastava, *loc. cit.*)

Aphanomyces pisci was isolated from diseased individuals of *Cirrhinus mrigala* (Ham.), and found by inoculation and infection studies to be limited to invading adults of this species. Morphologically, the distinctive feature of the fungus is the development of gemma-like (R. C. Srivastava, *loc. cit.*) hyphal segments. On the basis of these two characteristics the fungus was described as a new taxon.

The sexual apparatus of this species remains unknown, and until these cells are discovered and characterized, the taxonomic status of the species is in doubt. Neither subcultures nor preserved specimens of the type were available for examination. The "gemmae" of *Aphanomyces pisci* are striking (R. C. Srivastava, *loc. cit.*, figs. 2, 3) in their length and highly irregular contour. We have observed numerous nonsexual specimens of *Aphanomyces* to form dense, contorted hyphal segments in mycelium growing undisturbed in staling water contaminated heavily by bacteria and ciliates.

EXCLUDED TAXA

Aphanomyces aculeatus Fowles
In, Dissertation, Univ. California, Berkeley, p. 48, fig. 9. 1967

Fowles (*loc. cit.*) isolated an *Aphanomyces* from the skin of a dolphin (*Inia geoffrensis*), and mistakenly thought it to have a sexual apparatus. This was corrected in publication (Fowles, 1976), where the specimens were simply referred to as *Aphanomyces* sp. (nonsexual). The name applied by Fowles has no validity.

Aphanomyces americanus (Bartsch and Wolf) Scott
Virginia Agric. Exp. Sta. Techn. Bull. No. 151, p. 36.1961

Bartsch and Wolf (1938) assigned this species to Valkanov's (1931b, c) *Hydatinophagus*, largely on the basis, it seems, of the means by which the host, *Monostyla* sp., became infected. Scott (*loc. cit.*) saw a strong resemblance between *H. americanus* and *Aphanomyces hydatinae*, and assigned the former to de Bary's genus. As the asexual stage of *A. americanus* is unknown, and the sizes of the oogonia (8.5–11.2 μm in diameter) and oospores (7-9 μm in diameter) recall a pythiaceous fungus, we are excluding this taxon from *Aphanomyces*. The illustrations by Bartsch and Wolf (1938: figs. 10, 11) give credence to this decision.

Aphanomyces gordejewi Skvortzow
Arch. Protistenk. 51:433, figs. 11-13.1925

This species is clearly a *Pythium*, as Drechsler (1929) and Sparrow (1930) concluded, and Scott (1961a:68) has correctly excluded it from the genus *Aphanomyces*.

Both S. Ito (1936:95) and Berczi (1940a:87, figs. 42, 43) have reported collections of Skvortzow's species (from Japan and Hungary, respectively). Neither author presents any data to confirm their specimens as an *Aphanomyces*, and from the brief descriptive matter (and Berczi's inadequate illustrations) it is obvious that they, too, had material of *Pythium* at hand.

Aphanomyces ovidestruens Gicklhorn
Lotos 71:146, 148, figs. 1-11, and text figs. A-C. 1923

As Scott (1961a:45) remarked, Gicklhorn's species was indeed a bizarre parasite. The illustrations provided by Gicklhorn include figures of secondary spore germination by the production of holdfasts, a most un-saprolegniaceous character! It seems likely that Gicklhorn was dealing with a mixture of fungi in describing *Aphanomyces ovidestruens*: the oogonia were probably of an *Aphanomyces* (perhaps *A. scaber*), while the sporulation phase was in all probability described from specimens of *Zoophagus* or perhaps *Harpochytrium*. Lichtwardt (communication) doubted that Gicklhorn's fungus was a Trichomycete. Although Scott (1961a) retained *A. ovidestruens* among the valid species in the genus, we are excluding it on the grounds that the description was compiled from mixed specimens.

Cejp (1959a:91, fig. 18) records *Aphanomyces ovidestruens* from Czechoslovakia, but the illustrations are redrawn from Gicklhorn's publication. The fungus reported from Russia by Logvinenko and Meshcheryakova (1971: fig. 3) as *A. ovidestruens* is not referable to any species; they took the diagnosis for this species directly from Cejp's compilation.

An *Aphanomyces* identified as *A. ovidestruens* was reported from New Zealand by Burns (1980), but had been mentioned earlier by Burns (1979:447) as an "aquatic phycomycetes." The watermold parasitized the eggs and adult females of the copepod *Boeckella dilatata*, and also had been found (Burns *et al.*, 1984) in *B. hamata* Brehm. and *B. triarticulata* (Thomson) in New Zealand. Because of the invalid nature of Gicklhorn's species, Burns' report is of extraordinary taxonomic value. Through her generosity, we have obtained for study specimens from the New Zealand collection.

As Burns noted, the New Zealand fungus lacks the appressoria described for *Aphanomyces ovidestruens*. Moreover, we find nowhere in the specimens available to us the branched hyphal systems and holdfasts alleged to be the result of the germination of secondary spore cysts in Gicklhorn's species. Burns recognized that features of her *Aphanomyces* digressed from the characteristics attributed to *A. ovidestruens* -- chiefly oogonium and oospore diameters, and the nature of the oogonial wall -- and the specimens we have examined bear out these differences. The oogonia and oospores in the fungus in *Boeckella dilatata* are predominantly larger than those reported for *A. ovidestruens* (see Scott, 1961a), and the oogonial wall ornamentations are generally

papillae or blunt tubercles rather than spines. However, a few oogonia of the New Zealand fungus are provided with spines, as Burns (1980: fig. 1d; 1985a: fig. 1f) illustrated. We have found only declinous antheridial branches in the specimens from Burns' collection; *A. ovidestruens* is alleged to have both declinous and monoclinal ones. Photographs provided us by Carolyn Burns show unmistakably that in some of her material, sickle-shaped or sigmoid cells with a basal holdfast were present. These cells have the same configuration as those figured by Gicklhorn.

Inasmuch as Gicklhorn's species must be excluded from the valid taxa of the genus, a new identity for Burns' specimens must be sought. The New Zealand fungus differs from all species of *Aphanomyces* known to occur in aquatic animals in that its oogonia are ornamented. The oogonial wall projections resemble those ordinarily found in *A. scaber*, although some ornamentations to be sure, are characteristic also of *A. parasiticus*, *A. phycophilus*, and *A. norvegicus*. Of the latter three, however, two species occur in filamentous algae, the third being parasitic in certain water molds. The range of size of the oogonia and oospores in Burns' specimens in the copepod is nearest that described for *A. phycophilus*. In general configuration the sexual apparatus of the New Zealand *Aphanomyces* resembles that of *A. scaber*, a species often recovered on insect exuviae. The oogonia and oospores of Burns' fungus, however, are slightly larger than those of this latter species.

The *Aphanomyces* in *Boeckella dilatata* must be brought into culture before its identity can be determined with certainty. It is not conspecific with *A. ovidestruens*, but if its major characteristics prove to be stable in culture, the fungus may well represent a form of *A. scaber*.

Aphanomyces polysporis Milovtsova

Trudy Inst. Bot. Kharkivs'kiĭ Derzhavniĭ Univ. 1:36, pl. 3, figs. K₁, K₂. 1935

The validating Latin diagnosis appeared in Milovtsova's 1935(a) paper, but a second description fortified with additional drawings was published in another account in the same year (1935b). It is in this latter paper that the illustrations convey the impression that Milovtsova was dealing with a mixed culture. Figure 3 in the 1935b edition depicts oogonia that could possibly be related to *Aphanomyces stellatus*, but figure 4 in the same publication illustrates *Achlya papillosa*. There is nothing in either of Milovtsova's papers (1935a, b) to suggest that he had prepared even unifungal cultures. The description (unaccompanied by figures) of *Aphanomyces polysporis* reported by Morochkovs'kiĭ *et al.* (1967) yields nothing that could be taken to confirm Milovtsova's species as a valid one.

Aphanomyces polysporis is excluded on the grounds that the description was compiled from cultures of more than one fungus.

Aphanomyces sp. Barthelmes

Z. Fischerei und deren Hilfswissensch., Mitt. Deutsch. Fischerei-Vereins
10:515 *et seq.*, figs. 1-9. 1962

The lack of a formal description and the absence of information on such critical characteristics as oospore structure and antheridial branch origin is a sufficient basis on which to exclude this unnamed species. Barthelmes (1962a) compared the diameters of the hyphae, encysted spores, and oogonia of his species with *Aphanomyces astaci*, *A. daphniae*, and *A. ovidestruens*. As *A. ovidestruens* is based on a mixed culture, and *A. astaci* is not known to produce oogonia, Barthelmes' comparisons are meaningless.

Aphanomyces sp. Barthelmes
Biol. Zentralbl. 81:321 *et sqq.*, figs. 1-6. 1962

This unnamed species is not provided with a formal, concise description. The descriptive information given in Barthelmes' (1962b) paper lacks an account of the basic characteristics (antheridial branch origin, for example) necessary to identify the specimens.

Neither this nor the previous unnamed species are cited in the host list in Table 49 (Chapter 30), because both are excluded from *Aphanomyces*. Barthelmes (1962a, b) collected his fungi on species of *Diaptomus* and *Asplanchna*.

Aphanomyces sp.
In, Kobayasi *et al.*, Annual Rep. Inst. Ferment. Osaka,
No. 3. p. 12, (text) fig. 4. 1967

This unnamed fungus cannot be identified with certainty, although the general configuration of the oogonia suggests that it might represent *Aphanomyces scaber*. Kobayasi *et al.* (*loc. cit.*) admit that since spore discharge was not observed, their material could be assigned to *Pythium* or *Aphanomyces*. The antheridial branches are Described as being "hypogenous".