Reprinted from MYCOLOGIA, Vol. XXVIII., No. 4, 363–389, July–August, 1936
Printed in U. S. A.

NEW CONIDIAL PHYCOMYCETES DESTRUCTIVE TO TERRICOLOUS AMOEBAE

CHARLES DRECHSLER

(WITH 7 TEXT FIGURES)

In several previous papers (1, 2, 3, 4) were described a series of conidial Phycomycetes often making their appearance on old agar plate cultures, where they subsist through the destruction of microscopic animals frequently introduced in plantings of decaying vegetable materials. Subsequent observations on laboratory cultures of the same sort have brought to light more than a dozen fungi intimately related to those dealt with before, and like them mainly parasitic or predacious on terricolous *Amoebae*. Most of the additional species are as yet only partially known. Some have been seen only as predacious mycelia devoid apparently of both conidial and sexual apparatus. Others have been observed properly only in their asexual reproductive phases, the delicate underlying mycelia at the time of observation having become largely invisible from the very evacuation of protoplasmic contents entailed in the production of the conidia. Perhaps mainly also because of such obliteration, and the consequent difficulty of tracing a connection to conidial apparatus, a few forms are familiar only through their zygosporangia and zygospores. To increase the difficulties a tract of substratum is very often occupied by a number of predacious fungi, rather than by a single predacious species; so that the hyphae and reproductive bodies of several related forms frequently occur intermingled confusingly in the same area.

Besides five fungi known in all three developmental phases—vegetative, asexual and sexual—two species are described herein, which from their consistent failure hitherto to exhibit zygosporangia and zygospores, will presumably not soon reveal such structures under the conditions of cultivation so far employed. The

seven forms do not extend materially the morphological scope of the Zoopagaceae, all being readily referable to genera previously defined. They afford, however, clarification of a few structural details. Thus the separation of zygospore wall into an outer stellate membrane and an inner spherical one, prevailing apparently throughout the genus *Endocochlus,* is shown especially clearly in the sexual apparatus of the species to be described as *E. gigas.* Again, the description of the development of catenulate conidia, as given earlier in the account of *Cochlonema verrucosum* Drechsl., is definitely confirmed in the unusually favorable material now provided by *Zoopage nematospora.* If the confirmation leaves the homologies of the conidial apparatus with the asexual reproductive structures in both the Mucorales and the Entomophthorales as problematical as ever, it makes more precise the morphological similarities to *Actinomyces* to which attention was directed earlier. Somewhat curiously, these similarities might perhaps be considered extended in the provoking even if only partial correspondence between the conspicuously simplified sexual development in *Zoopage cladosperma* and the development of the "Vierhyphensporen," which Lieske (**5**) observed in many species of *Actinomyces* and regarded as probably representing sexual structures.

ENDOCOCHLUS BRACHYSPORUS

On many old agar plate cultures that, after being found infested with various species of nematodes and protozoans, had been planted with pinches of leaf mold received from Ames, Iowa, was found on examination a week or two later, a display of arachnoid conidiiferous filaments having an unmistakable general similarity to the asexual reproductive apparatus of *Endocochlus asteroides* Drechsl. In accordance with expectations each separate system of filaments on being traced backward was found to originate from a partially or wholly evacuated cochleate thallus lying loosely within a membrane, often badly collapsed and wrinkled, that was readily recognizable as the persistent pellicle of an *Amoeba.* Living *Amoebae* bearing internally thalli in various stages of development abounded in some of the cultures (FIG. 1, *A, B*). These *Amoebae* were approximately of the same dimensions as

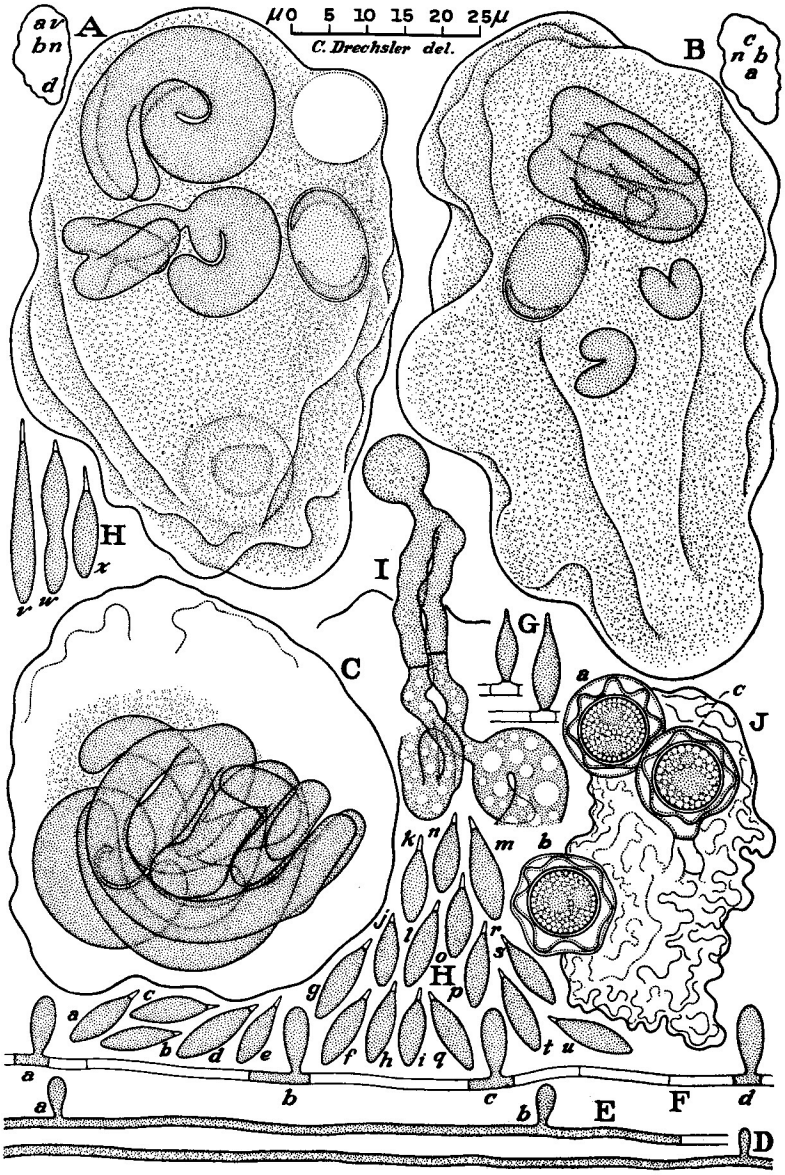

FIG. 1. *Endocochlus brachysporus.*

those attacked by *E. asteroides,* the larger specimens measuring about 60 μ in diameter when drawn up into a moderately rounded shape; they showed likewise a fairly substantial pellicle, a relatively transparent, dispersedly granular protoplasm, and a prolate ellipsoidal nucleus frequently about 15 μ long and 10 μ wide. The identity of the host animal with the form previously referred to in a broad sense as *Amoeba terricola* Greeff (and in a narrower sense as *A. terricola* I) was indicated with much certainty through the nucleus consistently revealing a slightly darker, somewhat irregularly concavo-convex body appressed closely to the peripheral membrane at each of its poles (FIG. 1, *A, n; B, n*).

Apart from the evident conspecific identity of the animals attacked, similarity to *Endocochlus asteroides* was apparent in the dimensions and involute arrangement of the vegetative thallus of the fungus itself (FIG. 1, *A, a, b; B, a-c; C*). The similarity appeared, however, to be somewhat less than complete, as in the Iowa parasite the thallus instead of always branching dichotomously sometimes gave rise to a monopodial branch (FIG. 1, *A, b*), which then developed geometrically independent of the parent axis as a subsidiary cochleate structure. That such monopodial branching may take place also in *E. asteroides* and *E. gigas* is, to be sure, not impossible; but, if so, it would seem to occur so rarely as ordinarily to escape notice.

Sexual reproduction in the Iowa parasite follows the same course as in *Endocochlus asteroides* (FIG. 1, *I*); the resulting zygosporangium and zygospore (FIG. 1, *J, a-c*) being apparently slightly larger than the homologous structures in the latter species, which, nevertheless, they closely resemble. As in the other known members of the genus, the zygosporangial wall usually collapses perceptibly when the maturing zygospore contracts—this contraction gradually bringing about the stellate contour of the outer zygospore membrane, which ultimately appears to become well separated from the smoothly spherical inner membrane immediately surrounding the protoplast.

The aerial conidiiferous hyphae growing out from the thallus of the Iowa fungus (FIG. 1, *D, E, G*) give rise to conidia through lateral budding in much the same manner as those of *Endocochlus asteroides.* A fairly conspicuous difference soon appears, how-

ever, in the consistently closer spacing of the conidia on the parent hyphae (FIG. 1, *F*). Correlated with this closer arrangement, the conidia on maturity are noticeably smaller, the lesser bulk being accounted for through a marked inferiority in length (FIG. 1, *H, a-u*). The elongate ovoid shape thus brought about is easily distinguished from the more slender fusiform conidial shape characteristic of *E. asteroides*. Even though on examining a large number of conidia, a few specimens (FIG. 1, *H, v-x*) can be found comparable to those of the species described earlier, the general run of these bodies maintain their distinctive dimensions and shape with much constancy. The parasite is therefore described under a specific name having reference to its relatively short spore.

Endocochlus brachysporus sp. nov.

Hyphae nutritae 4–8.5 μ, semel vel bis spiraliter convolutae. Conidia fusoidea vel elongato-ovoidea, 7–15 μ (raro usque 21 μ) saepius 8–12 μ longa, 3–4.2 μ lata, in apice appendicula vacua 1–3.5 μ longa praedita, ex hyphis arachnoideis 1.3–1.6 μ crassis 1–4 mm. longis ad intervalla 25–45 μ longa enata. Zygosporae hyalinae vel luteolae, echinatae, intra zygosporangium sphaeroideum 12–15 μ diam. formatae, loculo 6.5–9 μ diam. Hyphae zygosporiferae 2.5–4 μ crassae, 25–50 μ longae.

Amoebam terricolam (sensu latiore) enecans habitat in humo silvarum, Ames, Iowa.

Vegetative hyphae 4 to 8.5 μ in diameter, simple or often when well developed sparingly branched dichotomously or monopodially, and compactly convoluted in 1 to 2 turns. Conidia rather broadly spindle-shaped or elongate ovoid, measuring 7 to 15 μ (rarely up to 21 μ), mostly 8 to 12 μ (average 10.2 μ) in length by 3 to 4.2 μ (average 3.5 μ) in diameter, exclusive of an empty apical appendage 1 to 3.5 μ (average 1.6 μ) long and .5 to 1 μ wide at the base; produced erect and sessile or nearly sessile at intervals of 25 to 45 μ on aerial hyphae often 1 to 4 mm. long and 1.3 to 1.6 μ wide. Zygospore colorless or slightly yellowish; at maturity bullate, the outer membrane being disposed in 15 to 20 protuberances of which about 6 are visible in the stellate profile; containing a locule 6.5 to 9 μ in diameter, surrounded by the smooth inner membrane; produced within a spherical zygosporangium mostly 12 to 15 μ in diameter arising from a short hyphal extension from the junction of paired zygophoric hyphae that measure usually 25 to 50 μ in length and 2.5 to 4 μ in width.

Destructive to *Amoeba terricola* (in the broad sense more particularly of Penard) in leaf mold from Ames, Iowa.

ENDOCOCHLUS GIGAS

The same sample of leaf mold from which was obtained the fungus just described yielded also a congeneric form much more impressive in its generous dimensions. This larger species was found to confine its attack exclusively to an *Amoeba* measuring mostly 60 to 110 μ in diameter. In its firm substantial pellicle and its transparent, dispersedly granular protoplasm the animal showed similarities to the one habitually parasitized by *Endocochlus asteroides* and *E. brachysporus,* as well as to the *Amoeba* serving as host to *Bdellospora helicoides* Drechsl. In its nucleus, however, it was markedly different from both. Viewed in optical section, this prolate ellipsoidal structure, which measured often about 20 μ in length by 13 μ in diameter, revealed the darker material as rod-like parts arranged in an interrupted ring close to the periphery (FIG. 2, *A, n; B, n; C, n*) ; although on focusing on the upper and lower surfaces the darker parts appeared more nearly as if connected in a continuous reticulum. Because of the close correspondence in shape and composition with the nucleus set forth as characteristic of *A. terricola* (**6**), it would seem that Greeff's binomial is applicable here in a narrower sense.

Infection is accomplished in the same manner as has been described for *Endocochlus asteroides.* Germination of an adhering conidium here likewise first results in a somewhat swollen protuberance that clearly betrays its character as an appressorium by its easily visible coating of yellowish adhesive material (FIG. 2, *A, a*). In spite of this adhesive material, the animal sometimes must manage to disengage itself successfully, as a living detached conidium is occasionally to be found bearing an empty appressorium with an empty incipient germ tube (FIG. 2, *K*). When no mishap intervenes the germ tube penetrates well towards the center of the animal, often taking a somewhat irregular course (FIG. 2, *A*). With the disarticulation of the swollen body resulting from the migration of the conidial contents to the tip of the germ tube (FIG. 2, *B, a, b*), appropriation of the substance of the host begins. The animal endures the continuing depletion of its protoplasm with remarkable fortitude (FIG. 2, *C*), but finally succumbs when the small residue of cytoplasm together with the visibly degenerating

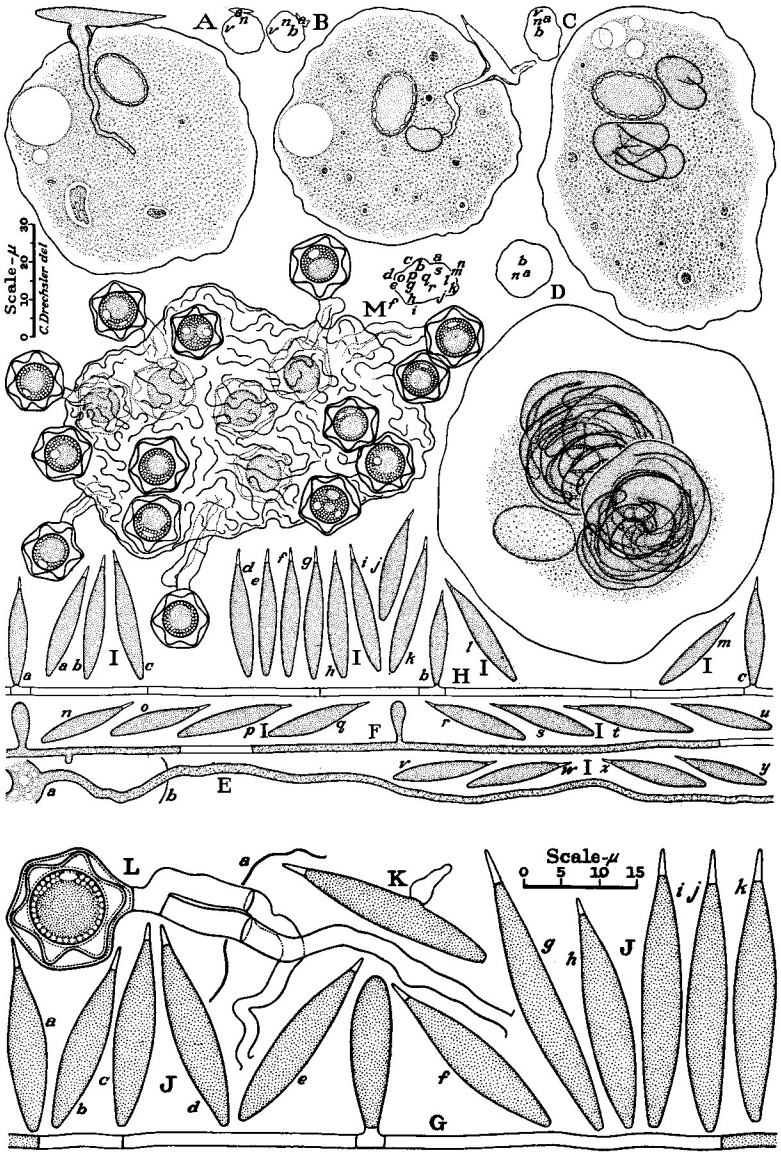

FIG. 2. *Endocochlus gigas.*

nucleus (FIG. 2, *D, n*) is no longer able to actuate the relatively little diminished pellicle.

Owing no doubt to the large supply of food material in the massive sarcode of the host animal, the thallus of the present fungus often attains a size never observed to be equalled in *Endocochlus asteroides* and *E. brachysporus*. The two impressive thalli shown in figure 2, *D, a, b,* each consisting of a stout filament bifurcating three times in succession and coiled in three turns, are yet individually of smaller bulk than a thallus developing alone in a host animal of comparable or, perhaps, even larger dimensions. Just as in the two congeneric forms, the contents of the thallus must be of extraordinary concentration; for the output of reproductive apparatus, whether sexual or asexual, is always far in excess of what might reasonably be expected from the volume of the vegetative structure from which it arises.

The hyphae associated with asexual reproduction, including the usually submerged and sterile proximal portions (FIG. 2, *E*) as well as the aerial or somewhat prostrate conidiiferous prolongations that radiate for several millimeters above the dead host animal, are noticeably stouter than the corresponding elements of *Endocochlus asteroides* and *E. brachysporus*. The conidia, half again as wide and nearly three times as long as those of *E. brachysporus,* arise at intervals approximately three times as long as the intervals in that species (FIG. 2, *F–H*). As in the two congeneric species the apex of the conidium is evacuated toward maturity and persists as an empty conical appendage (FIG. 2, *H, a-c; I, a-y; J, a-k*). Considered by itself the spindle-shaped living cell is rather similar in size and shape to the living cell in the conidium of *Acaulopage ceratospora* Drechsl.

Sexual reproduction would seem, in general, more abundant than in *Endrochlus brachysporus*. As many as 24 zygospores have been found clustered about the collapsed pellicle of what before must have been an unusually large animal; therefore the output represented in figure 2, *M, a-s,* consisting of 19 such spores cannot be considered extreme. The zygosporangia and zygospores are noticeably larger than those of the two known congeneric species; so that the separation of the stellate outer zygospore membrane from both the enveloping zygosporangial wall and the spher-

ical membrane surrounding the locule is more clearly evident (FIG. 2, *L*). Within the locule the arrangement of contents widely prevalent in oospores is recognizable: an elliptical refringent body, or sometimes two such bodies, being imbedded in the parietal layer of uniformly coarse granules that surrounds the relatively large, vacuole-like reserve globule.

A term having reference to the large dimensions of the fungus is deemed appropriate as a specific name.

Endocochlus gigas sp. nov.

Hyphae nutritae 3.5–9.5 μ diam., bis vel ter spiraliter convolutae. Conidia fusoidea, 21–36 × 4.4–6.2 μ, in apice appendicula 2.2–5 μ longa praedita, ex hyphis arachnoideis 1–5 mm. longis 1.8–2.3 μ crassis ad intervalla 80–130 μ longa enata. Zygosporae hyalinae vel luteolae, echinatae, intra zygosporangium sphaeroideum 13–17 μ diam. formatae, loculo 8–10 μ diam. Hyphae zygosporiferae 1.5–4 μ crassae, 25–60 μ longae.

Amoebam terricolam (sensu strictiore) enecans habitat in humo silvarum, Ames, Iowa.

Vegetative hyphae 3.5 to 9.5 μ in diameter, when well developed often bifurcating 3 times in succession and convoluted compactly in 2 to 3 or even 3½ turns. Conidia spindle-shaped, measuring 21 to 36 μ (average 28 μ) in length by 4.4 to 6.2 μ (average 5.1 μ) in diameter, exclusive individually of an empty pointed apical appendage 2.2 to 5 μ (average 3.6 μ) long and .8 to 1.2 μ wide at its base; produced erect and sessile or nearly sessile at intervals of 80 to 130 μ on aerial hyphae 1 to 5 mm. long and 1.8 to 2.3 μ wide, that ramify more or less to extend over the substratum in a somewhat arachnoid pattern. Zygospore colorless or slightly yellowish, its outer membrane disposed in 15 to 20 bullate protuberances of which usually 6 or 7 are visible in the stellate profile, its smooth inner membrane surrounding a subspherical locule 8 to 10.5 μ in diameter; produced within an originally subspherical zygosporangium measuring 13 to 17 μ in diameter and borne on a short hyphal extension from the junction of zygophoric hyphae 1.5 to 4 μ wide and 25 to 60 μ long,—the zygosporangial wall at maturity collapsing loosely about the bullate zygospore membrane.

Destructive to *Amoeba terricola* (in a stricter sense) in leaf mold from Ames, Iowa.

ACAULOPAGE CERCOSPORA

A fungus readily referable to the genus *Acaulopage* made its appearance several times on old agar plate cultures to which had

been added pinches of muck originating from near South Bend, Indiana. Like the other members of the genus it subsists on *Amoebae,* the animals captured by it, mostly 10 to 20 μ in diameter, belonging evidently to a single species. As no nucleus could be distinguished in the peculiarly turbid and mostly homogeneous protoplasm bounded by the very delicate, scarcely visible pellicle, the identity of the prey could not be determined. The materials composing the smaller animals are usually assimilated by means of a single haustorium, consisting of a stalk together with several wider elements branching from it (FIG. 3, *A, a; B; C; E*). Larger animals, however, often occasion the production of two (FIG. 3, *D*) and sometimes three or four haustoria, especially when capture takes place at the junction of two branches (FIG. 3, *A, b*), or where two filaments happen to lie near one another.

Closely resembling the haustorial stalks in dimensions, the sterigmata on which the conidia are borne singly arise erect from the prostrate superficial hyphae (FIG. 3, *C–I*) at rather close intervals. Though the sterigmata and the fertile hyphae together have an appearance suggestive of the homologous structure in *Acaulopage macrospora* Drechsl., the simility is not extended to the conidia, which consist here individually of a rather small elongated ellipsoidal living cell bearing distally a relatively long, narrow, empty appendage (FIG. 3, *E–I*). Conspicuous differences from the conidium of *A. ceratospora* are evident in the much smaller dimensions throughout and in the absence of a basal appendage. When viewed under a dry objective, the conidia, bristling in close linear arrangement in an open arachnoid pattern corresponding to the disposition of the prostate hyphae, present a most distinctive appearance.

Sexual reproduction has never been observed. A term having reference to the tail-like conidial appendage would seem appropriate as specific name for the fungus.

Acaulopage cercospora sp. nov.

Paulo sparsa; hyphis incoloratis, 1–1.7 μ crassis; haustoriis ex stipe et 4–6 lobulis vel ramulis divaricatis 1.2–2 μ crassis compositis. Conidia solitaria, ex sterigmatibus erectis 2–5.5 μ altis orta, hyalina, appendiculata: Cellula viventi protoplasmatis repleta, fusoidea vel elongato-ellipsoidea, 7–15 μ

longa, 2.2–3.6 μ crassa, appendicem apice ferente; appendice vacua, angustata, 6–20 μ longa, .4–.8 μ crassa, in aere saepe marcida. Zygosporae ignotae.

Habitat in humo palustri, *Amoebas* 10–20 μ latas capiens et consumens, prope South Bend, Indiana.

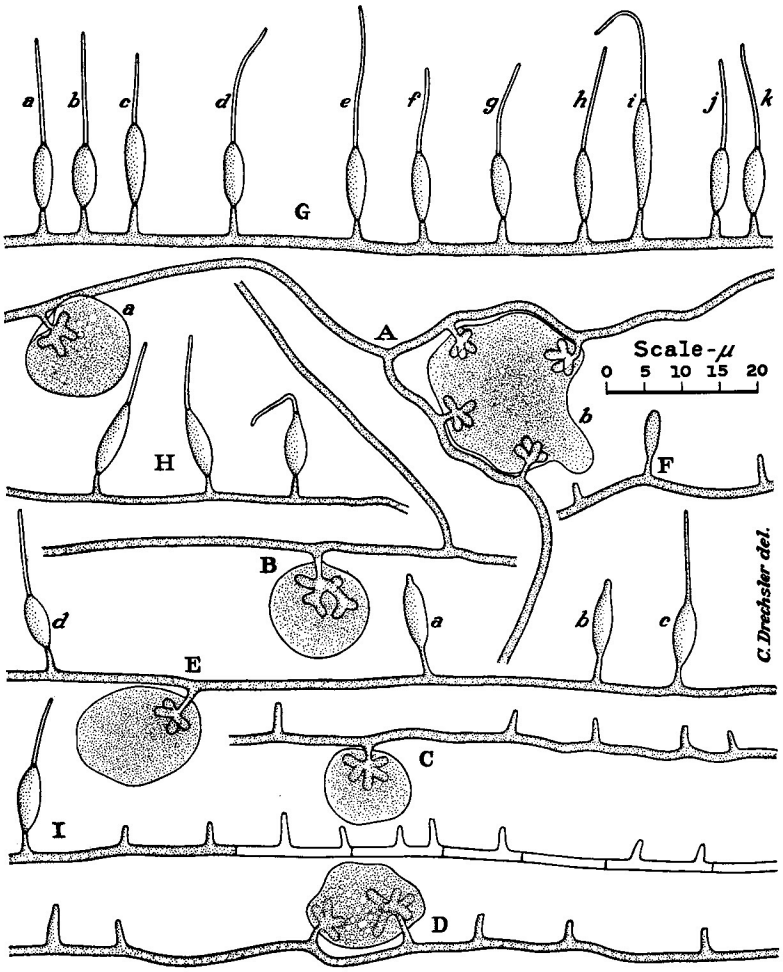

FIG. 3. *Acaulopage cercospora.*

Somewhat sparse; hyphae colorless, 1 to 1.7 μ wide, producing stalked haustoria with 4 to 6 spreading lobate or digitate elements mostly 1.2 to 2 μ wide. Conidia hyaline, solitary; borne on erect, somewhat tapering sterigmata, 2 to 5.5 μ high, that arise at intervals of 5 to 30 μ from superficial prostrate filaments; consisting

individually of a living fusoid or elongated ellipsoid cell 7 to 15 μ (average 9.1 μ) long and 2.2 to 3.6 μ (average 2.8 μ) wide, together with an empty narrow distal appendage, often withered on exposure to air and measuring 6 to 20 μ (average 12.2 μ) in length by .4 to .8 μ in width.

Occurring in muck soil near South Bend, Indiana; capturing and destroying *Amoebae* mostly 10 to 20 μ in diameter.

STYLOPAGE RHABDOSPORA

A species of *Stylopage* different from any of the four forms hitherto assigned to that genus appeared in a few old agar plate cultures on which had been planted pinches of leaf mold collected in a wooded tract in Clarendon, Virginia. In all instances it subsisted apparently altogether by the capture of *Amoebae* undoubtedly referable to a single species. The animal taken measured mostly from 30 to 40 μ in diameter when drawn into an approximately round shape. Except for a sappy homogeneous layer immediately under the delicate pellicle, the protoplasm consisted of rather densely and coarsely granular material, which was nevertheless sufficiently transparent to reveal very clearly a single prolate ellipsoidal nucleus mostly 9 to 10 μ in length and 7 to 8 μ in diameter (FIG. 4, *A, a, b; C*). In optical section this nucleus revealed close under its own membrane about a dozen subspherical masses of slightly darker material. The nuclear structure represented here thus corresponds to that which Penard (**6**) once figured as being characteristic of an *Amoeba* he considered probably identical with *Amoeba similis* Greeff. Adoption of the binomial mentioned has at least the advantage of setting the animal in question apart from any of the four forms to which I have referred as *A. terricola.*

The mycelium of the fungus is rather sparse, being composed of filaments that often traverse relatively long distances in a nearly straight line without giving off any branches. When contact with a susceptible *Amoeba* has been effected, a delicate process is thrust through the pellicle some distance into the protoplasm, there widening abruptly and branching dichotomously with a variable degree of regularity, and thus giving rise to a haustorium comparable, for example, to that of *Acaulopage macrospora* (FIG. 4, *A, a, b*). De-

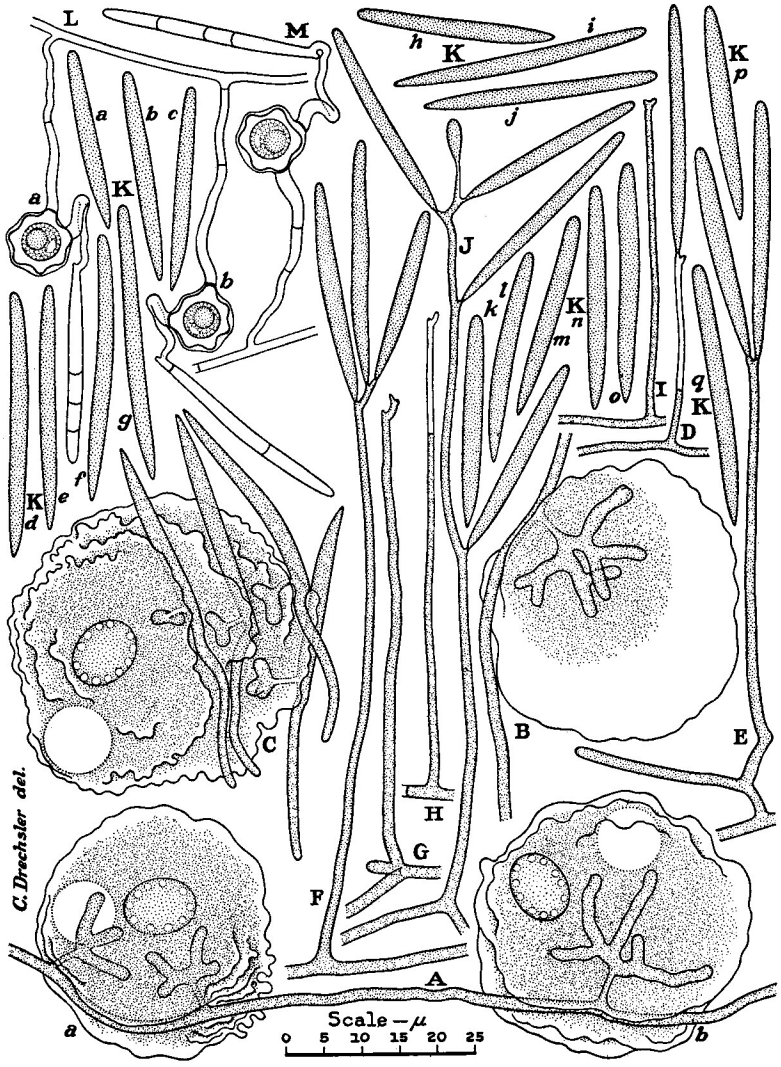

FIG. 4. *Stylopage rhabdospora.*

pletion of the protoplasmic materials of the rhizopod continues until little remains but the pellicle (FIG. 4, *B*).

Haustoria are often produced also by adhering conidia when an animal has had the ill fortune to encounter one or often several of these bodies in moving over the surface of a substratum strewn with them (FIG. 4, *C*). In performance, therefore, and, indeed, in general appearance as well, the conidia (FIG. *K, a-g*) recall those of *Acaulopage macrospora;* differing from them, however, in their smaller dimensions and in being borne on hyphae of sufficient height to deserve to be regarded as conidiophores (FIG. 4, *E–J*). After giving rise to one conidium, these conidiophores, like the homologous structures of *Stylopage lepte* and *S. hadra,* often produce others following repeated prolongation below successive spores in the manner of development made familiar in *Phytophthora infestans* (Mont.) de Bary.

The production of a haustorium directly from a conidium does not preclude simultaneous production of a vegetative germ hypha (FIG. 4, *C*). In instances where a conidium germinates by giving rise directly to a zygophore (FIG. 4, *L, M*), the protoplasmic contents are usually contributed in their entirety to the resulting sexual apparatus. Just as in similar sexual development already noted in some related forms, the progressive evacuation of the conidium is generally accompanied by the laying down of a number of successive cross-walls.

Sexual apparatus is formed in moderate quantity wherever the fungus attains any considerable growth, pairs of zygophoric branches arising either from separate hyphae having no close mycelial connection with each other, or from a hypha and a conidium, or from two conidia. Fusion of the sexual branches at their tips, development of a spherical zygosporangium at the junction, delimitation of the fusion cell by septa, and transformation of its contents into a yellowish zygospore with a relatively thick bullate wall, show unmistakable parallelism with sexual development in related species such as *Zoopage phanera* Drechsl. and *S. lepte.* Indeed, as the latter congeneric form was present in quantity in all cultures wherein the fungus under discussion was found, the structural parallelism between the intermingled sexual reproductive

bodies was evident to a troublesome degree. The dimensional differences, to be sure, were in nearly all cases, sufficient to distinguish the product of the one species from that of the other; though in choosing specimens for illustration it was thought advisable to obviate the possibility of error by selecting only unambiguous apparatus originating at least partly from conidia.

A term having reference to the rodlike shape of the conidium is deemed tolerably appropriate as specific name for the fungus.

Stylopage rhabdospora sp. nov.

Sparsa; hyphis sterilibus incoloratis, 1–1.8 μ crassis, haustoria pedicellata evolventibus; pedicello saepius .6–.8 μ crasso, 2–4 μ longo, ramulis dichotomis, divaricatis, 1.2–2 μ crassis, usque 15 μ longis; hyphis fertilibus incoloratis, 20–100 μ altis, basi .8–1.5 μ crassis, sursum saepe paulatim attenuatis, apice .6–1.2 μ crassis, usque 4 conidia post incrementa brevia repetita ferentibus. Conidia elongato-cylindracea, sursum leniter attenuata et abrupte rotundata, deorsum plerumque attenuata, itaque basi acutiuscula, 22–38 μ longa, 2.2–2.8 μ lata. Zygosporangia primo levia, sphaeroidea, 7.5–9.5 μ diam., in maturitate membrana circa zygosporam collabente; zygospora flavida, sphaeroidea, 6.5–8.5 μ diam., membrana .7–1.7 crassa, 10–20 verrucis ornata.

Habitat in materiis plantarum putrescentibus, praecipuo in humo silvarum, *Amoebam similem* capiens et consumens, Clarendon, Virginia.

Sparse; vegetative hyphae colorless, 1 to 1.8 μ wide, producing haustoria composed individually of a stalk mostly .6 to .8 μ wide and 2 to 4 μ long, together with spreading, irregularly dichotomous branching elements 1.2 to 2 μ wide and up to 15 μ long; fertile hyphae colorless, 20 to 100 μ high, .8 to 1.5 μ wide at the base, usually tapering gradually to an apical width of .6 to 1.2 μ, bearing mostly from 1 to 4 conidia, of which those following the first are formed after repeated, usually rather slight elongation. Conidium elongated cylindrical, generally tapering rather slightly toward the abruptly rounded apex, and more markedly toward the somewhat acute base, 22 to 38 μ, mostly 25 to 35 μ (average 30 μ) long, and 2.2 to 2.8 μ (average 2.5 μ) wide. Zygosporangium at first smooth, spherical, 7.5 to 9.5 μ in diameter, its wall at maturity collapsing loosely about the zygospore; zygospore yellowish, subspherical, 6.5 to 8.5 μ in diameter, with a wall, .7 to 1.7 μ thick, ornamented with 10 to 20 wartlike protuberances, of which 6 to 8 are visible in the sigillate profile.

Occurring in decaying plant materials, especially in leaf mold, capturing and consuming *Amoeba similis,* Clarendon, Virginia.

ZOOPAGE ATRACTOSPORA

The leaf mold from Ames, Iowa, that gave rise to *Endocochlus brachysporus* and *E. gigas,* yielded in nearly all of the old agar plate cultures to which it was added, flourishing growths of a fungus immediately recognizable as a species of *Zoopage*. The plate cultures used were infested very abundantly with a species of *Amoeba* measuring mostly 12 to 25 μ in diameter when drawn into a fairly rounded shape. In the normal animal a pellicle could hardly be recognized, though an individual depleted largely of its protoplasmic material generally revealed a very delicate envelope (FIG. 5, *B*). Very probably because of the characteristic turbidity of the protoplasmic body, no nucleus, nor, indeed, any normal structure except a relatively small contractile vacuole could be definitely made out (FIG. 5, *A; C; D; G, a*) ; the animal thus showing a general similarity to the one captured by *Acaulopage cercospora*. On this protozoan the fungus subsisted evidently to the exclusion of other sources of nourishment, capture being effected by adhesion to submerged as well as superficial hyphae, and assimilation being accomplished by means of haustoria bearing individually a half dozen divergent elements on a slender stalk (FIG. 5, *A–D; G, a*).

Nourished from an extraordinarily abundant supply of *Amoebae* the fungus gave rise to a tangled profusion of conidial chains that often extended over large areas of the plate cultures and became visible to the naked eye as a delicate efflorescence. Perhaps most of the chains consisted of approximately 10 spores, though many were found containing more than twice that number. As in *Zoopage phanera* the young chains are represented by continuous, somewhat moniliform filaments constricted at fairly regular intervals. The presence frequently of a minute swollen bud at the tip of an elongating moniliform filament (FIG. 5, *E, F*) supplies good evidence that increase of swollen components ensues through successive proliferation from the constricted apex of the component last completed. After the filament has attained its definitive length, the insertion of two crosswalls a short distance from one another in the narrowest part of each isthmus, preceded presumably by evacuation of the very minute constricted section, brings about the conversion of the swollen components into separate conidia (FIG. 5, *C, b; E, b*). Though most of the conidia

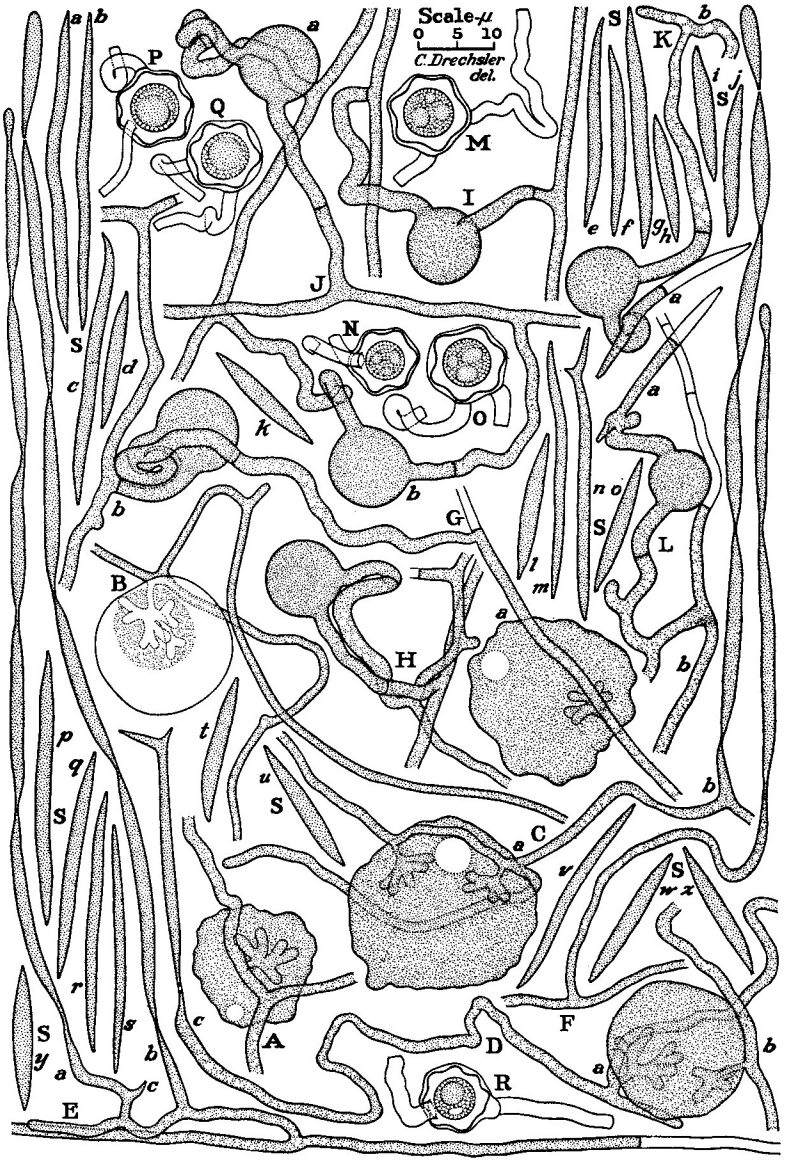

FIG. 5. *Zoopage atractospora.*

(FIG. 5, *S a-y*) are rather acute at both ends the terminal conidium of each chain (FIG. 5, *C, b; E, b*) is recognizable even after disarticulation by its broadly rounded apical extremity. Branching of a chain especially near its base occurs with some frequency, resulting in occasional bifurcate conidia (FIG. 5, *C, c; S, n*). Somewhat analogous branching of the relatively short, erect sterigmata, or of the parent hyphal branches in close proximity to them, is equally frequent (FIG. 5, *E, a-c*), but is reflected merely in the spore chains arising in small groups, rather than in the shape of the spore itself.

In spite of the general resemblance of the conidial apparatus to that of *Zoopage phanera,* specific differences are easily recognized. The conidia of the present species are conspicuously shorter, and as might be expected from the smaller diameter of the mycelial hyphae, also narrower than those of the form described earlier. In *Zoopage phanera* the variation in width of conidium is relatively small; and in any particular spore, width seems little influenced by length, so that the longer specimens are also very generally proportionately bulkier. Whereas in the fungus under consideration the longer conidia (FIG. 5, *S, b, m, n, r, s, v*) are often noticeably narrower than the shorter ones (FIG. 5, *S, d, i, j, l, o, u, w, y*), variation in one dimension being, therefore, in some measure compensated by opposite variation in the other. Moreover, the verrucose sculpturing of the conidial membrane, though visible in dry preparations, is much less prominent than in *Z. phanera,* being mostly so minute that at the magnification of the accompanying figure, it could hardly be shown without considerable exaggeration.

On the other hand, the sexual reproductive structures of the fungus closely resemble those of *Zoopage phanera:* similarities being evident, for example, in the origin of zygospores from conidia (FIG. 5, *K, a; L, a*) as well as from mycelial filaments (FIG. 5, *G, b; H; I; J, a, b; K, b; L, b*); in the size of the zygosporangium and the noticeable collapse of its wall at maturity (FIG. 5, *M–R*); and in the size, coloration and bullate sculpturing of the zygospore itself (FIG. 5, *M–R*).

A term having reference to the spindle-like shape characteristic more particularly of its shorter conidia, may perhaps serve acceptably as specific name for the fungus.

Zoopage actractospora sp. nov.

Mycelium ramosum; hyphis hyalinis, saepe irregulariter flexuosis, 1–2 μ crassis; haustoriis pedicellatis, pedicello 1.5–4 μ longo, .5–1 μ crasso, 4–8 ramulos digitatos circa 1.2–1.5 μ crassos ferente. Conidia minute et imperspicue verrucosa, fusoidea vel elongato-fusoidea, interdum bifurcata, 10–45 μ longa, 1.4–2.7 μ crassa in calenulis ex apice attenuato sterigmatum brevium et interdum ramosorum oriunda, in quaque catenula quina usque vicena quina. Zygosporangia 8–11.5 μ diam., primum levia, mox paulo collabentia. Zygosporae flavida, 6.5–10 μ diam., membrana .6–1.8 μ crassa, loculo 5–6.7 μ diam.; 15–25 verrucis ornata.

Amoebas 12–25 μ latas capiens et consumens habitat in humo silvarum, Ames, Iowa.

Mycelium branched; hyphae hyaline, often following irregular haphazard courses, 1 to 2 μ wide; haustoria pedicellate, the pedicels 1.5 to 4 μ long, .5 to 1 μ wide, and bearing 4 to 8 digitate branches 1.2 to 1.5 μ wide. Conidia minutely and very inconspicuously warted, fusiform or elongated fusiform, sometimes distally forked; measuring 10 to 45 μ, mostly 17 to 37 μ (average 25 μ) in length, and 1.4 to 2.7 μ (average 2.1 μ) in width; produced in chains of 5 to 25 on tapering, short, yet sometimes branched sterigmata. Zygosporangium 8 to 11.5 μ in diameter, at first smooth, at maturity collapsing loosely about the sculptured zygospore. Zygospore yellowish, 6.5 to 10 μ in diameter, with a locule 5 to 6.7 μ in diameter and a wall .6 to 1.8 μ thick; the wall provided with 15 to 25 warty protuberances of which 6 to 8 are usually visible in the sigillate contour.

Occurring in leaf mold, capturing and consuming *Amoebae* mostly 12 to 25 μ in diameter, Ames, Iowa.

ZOOPAGE NEMATOSPORA

A species of *Zoopage* markedly different from *Z. phanera* and *Z. atractospora* developed luxuriantly in a series of old agar plate cultures to which had been added pinches of decaying vegetable matter collected by S. P. Doolittle and F. L. Wellman in a ditch at the Subtropical Experiment Station near Homestead, Florida, early in March, 1935. In these cultures it lived from all appearances exclusively on the numerous *Amoebae* that it held fast on its mycelium and depleted of substance by means of stalked haustoria whose longish digitate absorptive elements were displayed in a characteristically graceful broom-like arrangement (FIG. 6, *A*). The *Amoebae* captured measured mostly from 40 to 50 μ in diam-

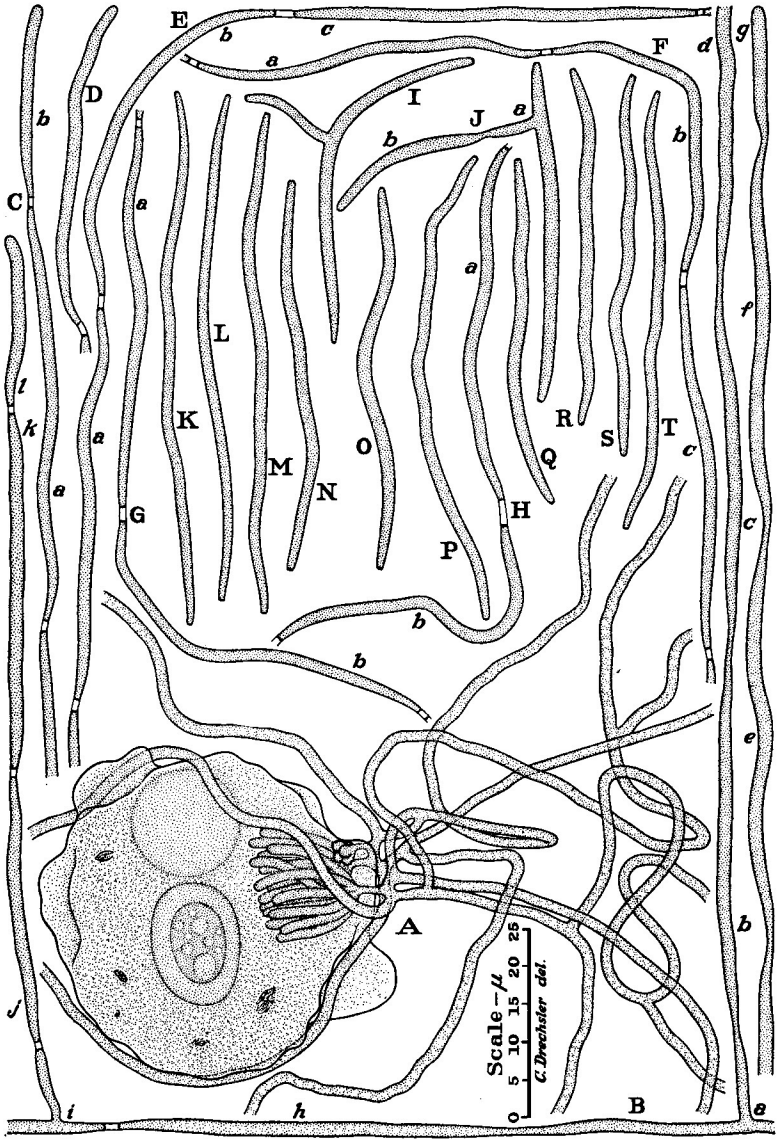

FIG. 6. *Zoopage atractospora.*

eter, and were surrounded individually by a moderately substantial pellicle. A single roughly ellipsoid nucleus, composed of an outer clearer layer and a darker ellipsoid body interspersed with a number of clearer lacunae, was visible in the flocculently granular protoplasm of the rhizopod. The dimensions of the animal, together with the shape and composition of its nucleus, would seem indicative of identity with the form discussed by Penard (**6**) under the binomial *Amoeba striata* Pen.

Aside from the distinctive design of its haustorium, the fungus shows little in its vegetative stage to set it apart from the several other known members of the genus. At times the individual hyphae pursue fairly sraightforward courses; but again, for no evident reason, they follow capricious bends. The tendency toward haphazard arrangement is expressed also in the aerial filaments devoted to asexual reproduction. These filaments reveal less differentiation from the vegetative hyphae than in other species, the narrowed parts being not only spaced at longer intervals but also constricted less, ordinarily, indeed, measuring about one-half as much in width as the intervening parts (FIG. 6, *B, a-h*). When the isthmi are evacuated of protoplasm for lengths often equivalent to twice their widths, and the protoplasts thus separated deposit a delimiting septum at each of their respective ends, the filament becomes converted into a chain of spores (FIG. 6, *B, i-l; C–H*). Ramification of the sporiferous hyphae (FIG. 6, *B, a, i*), which would seem fully as frequent as in *Zoopage atractospora,* here likewise results in occasional branched spores (FIG. 6, *I, J*). Of evident flexibility when subjected to mechanical disturbances, as, for example, in being mounted for microscopic examination, and of a relatively small diameter little given to variation except for the rather slight tapering toward the two ends, the longish conidia present a threadlike appearance that has suggested the specific name proposed for the fungus.

Zoopage nematospora sp. nov.

Mycelium ramosum; hyphis hyalinis, saepe irregulariter flexuosis, 1.1–1.9 μ crassis; haustoriis pedicellatis, pedicello 1.5–4 μ longo, .7–1 μ crasso, 5–12 ramulos digitatos, 5–13 μ longos, 1.2–1.5 μ crassos, scopis paulo similiter digestos ferente. Conidia interdum bifurcata sed saepius filiformia, utrimque paulo attenuata, flexilia, saepius 35–65 μ longa, 1.5–2.1 μ crassa, in catenulas

saepe longas simplices vel furcatas digesta, in quaque catenula usque vicena. Zygosporae ignotae.

Habitat in materiis plantarum putrescentibus, *Amoebam striatam* capiens et consumens, prope Homestead, Florida.

Mycelium branched; hyphae hyaline, often following irregular haphazard courses, 1.1 to 1.9 μ wide; haustoria pedicellate, the pedicel 1.5 to 4 μ long, .7 to 1 μ wide, and bearing in somewhat scopulate arrangement usually 5 to 12 digitate branches mostly 5 to 13 μ long and 1.2 to 1.5 μ wide. Conidia occasionally branched but more regularly filiform, rather slightly tapering at the ends, flexible, measuring 23 to 71 μ, mostly 35 to 65 μ (average 50 μ) in length, and 1.5 to 2.1 μ (average 1.7 μ) in width; produced in numbers up to 20 in usually long, simple or branched chains, wherein they are separated from one another by evacuated narrow portions of filament mostly 1 to 2 μ long and .7 to 1 μ wide. Zygospores unknown.

Occurring in decaying plant materials, capturing and consuming *Amoeba striata,* near Homestead, Florida.

ZOOPAGE CLADOSPERMA

A species of *Zoopage* somewhat smaller than any of the three congeneric forms so far described, appeared in an old agar plate culture to which had been added a few pinches of leaf mold gathered in Clarendon, Virginia. The meager development of the fungus was probably due in part to the relative scarcity of the animal on which it preyed,—an *Amoeba* measuring usually about 15 or 20 μ in diameter, with a very delicate, inconspicuous pellicle and rather turbid, slightly granular protoplasm. Capture was effected by adhesion to submerged as well as to superficial hyphae; after which the substance of the protozoan was appropriated by means of a haustorium consisting of a slender stalk and thickened dichotomous absorptive branches (FIG. 7, *A, a*).

The conidia of the fungus, though much smaller, resembled those of *Zoopage phanera* in their elongate fusiform shape and readily noticeable verrucose sculpturing (FIG. 7, *B; C, a-o*). Branching of the conidial chains, or of the erect tapering sterigmata on which they were borne, was not observed. It is possible that the absence of such branching, and also the moderate development of the simple chains (FIG. 7, *B*), may have been an expression of restricted luxuriance rather than of a definite morphological tendency.

In its sexual apparatus the species reveals a departure from the relationship prevalent not only in the genus, but throughout the family to which it belongs. A fusion of separate branches ap-

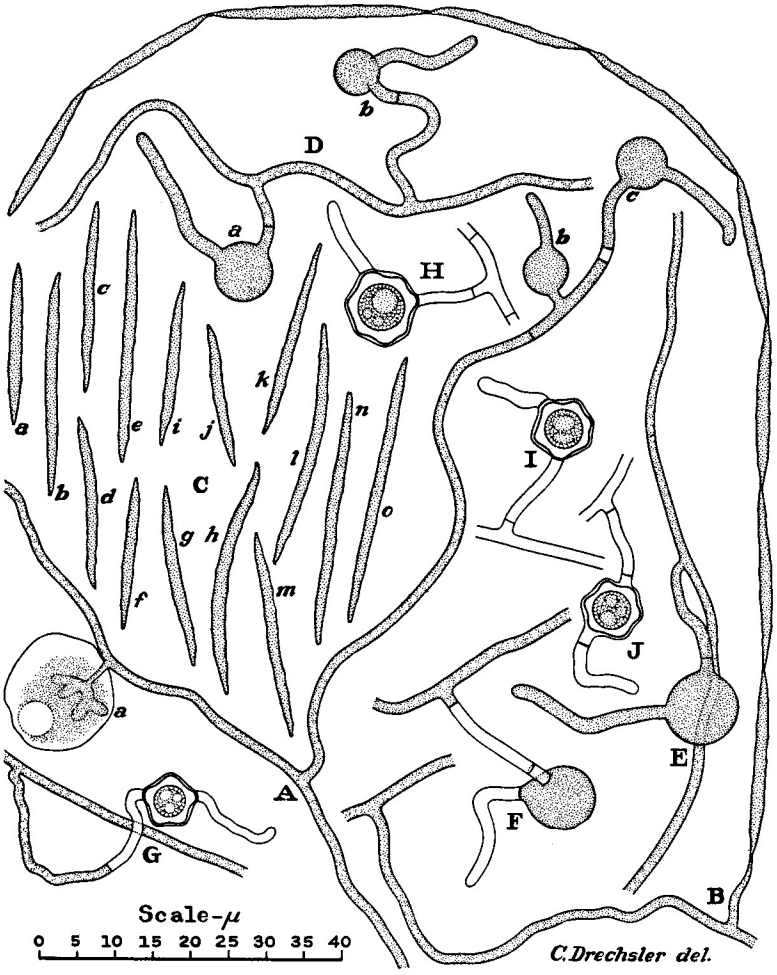

FIG. 7. *Zoopage cladosperma.*

parently never occurs. The zygosporangium makes its appearance first as a globose swelling some distance below the tip of a slightly thickened branch of limited length arising laterally from an ordinary mycelial filament. After the swelling has attained a certain

size, a septum is inserted a short distance below it, leaving the globose part still continuous distally with the apical portion of filament above it, and proximally with the portion of filament extending to the septum (FIG. 7, *A, c; D, a, b; E*). The contents of both portions of filament now pass into the globose part, which then becomes more closely delimited as a fully grown zygosporangium by the insertion of an approximately tangential septum at both of its poles (FIG. 7, *F*). Internal development ensues much as in *Zoopage phanera* and *Z. atractospora,* and yields here likewise a zygospore with bullate sculpturing and sigillate profile (FIG. 7, *G–J*).

Variations occur in the mycelial relationships of the sexual apparatus, as in instances, for example, where the proximal filamentous element consists of an intercalary segment of the axial hypha (FIG. 7, *A, b*). In any case the make-up of the very simple apparatus is such that were it found in the Mucoraceae the resultant reproductive body would almost certainly be regarded as an azygospore. In the series of predacious Phycomycetes under consideration, however, owing to the absence in declinous forms, of septa delimiting anything definitely recognizable as gametangia previous to fusion of separate hyphal tips, any distinction between an azygospore on the one hand, and, on the other, a zygospore formed presumptively through integration of portions of hypha continuous with one another from the beginning, would be much more difficult. The general analogy in development, and more particularly the passage of the protoplasmic contents of the two portions of filament into the young zygosporangium, seems to betoken a close parallelism in essential sexual processes, even though an outwardly manifest fusion entailing a breakdown of hyphal membranes is obviated.

A term having reference to the usual production of the zygospore in a special branch is deemed appropriate as specific name for the fungus.

Zoopage cladosperma sp. nov.

Mycelium ramosum, sparsum; hyphis hyalinis, 1–1.6 μ crassis; haustoriis pedicellatis, pedicello 1.5–3 μ longo, circa .7 μ crasso, aliquot ramulos dichotomos divaricatos digitatos circa 1.5 μ crassos ferente. Conidia minute sed distincte verrucosa, elongato-fusoidea, 18–36 μ longa, 1.3–1.8 μ crasso ex

apice hypharum brevium oriunda, in quaque catenula quina usque quina dena. Zygosporangia non ex copulatione hypharum separatarum sed in ramo saepius breviusculo usque 2 μ crasso sub apice ejusdem sine copulatione manifeste orta, 7–10 μ diam., primum levia, in maturitate paulo collabentia. Zygosporae flavidae, 6–8.5 μ diam., loculo 4.2–6.5 diam., membrana .6–1.5 μ crassa, 12–20 verrucis ornata.

Amoebas 15–20 μ latas capiens et consumens, habitat in humo silvarum, Clarendon, Virginia.

Myceilum branched, sparse; hyphae hyaline, 1 to 1.6 μ wide; haustoria pedicellate, the pedicel mostly 1.5 to 3 μ long and .7 μ wide bearing several bifurcating divergent digitate branches up to 1.5 μ in thickness. Conidia minutely but distinctly verrucose, elongated fusiform, 18 to 36 μ (average 26 μ) long, 1.3 to 1.8 μ (average 1.5 μ) wide, and produced in chains mostly of 5 to 15 on distally attenuated, rather short, erect branches. Zygosporangium not arising from the union of separate hyphae but developing without cellular fusion some distance below the apex of a usually rather short branch up to 2 μ wide; when fully grown 7 to 10 μ in diameter, at first smooth, later collapsing somewhat about the sculptured zygospore. Zygospore yellowish, 6 to 8.5 μ in diameter, with a locule 4.2 to 6.5 μ in diameter and a wall .6 to 1.5 μ thick; the wall provided at maturity with 12 to 20 bullate protuberances, of which 5 to 7 are usually visible in the sigillate profile.

Occurring in leaf mold, capturing and consuming a species of *Amoeba* mostly 15 to 20 μ in diameter; Clarendon, Virginia.

BUREAU OF PLANT INDUSTRY,
U. S. HORTICULTURAL FIELD STATION,
BELTSVILLE, MARYLAND.

LITERATURE CITED

1. **Drechsler, C.** Morphological features of some fungi capturing and killing *Amoebae*. Jour. Wash. Acad. Sci. **23**: 200–202. 1933.
2. ——. Some conidial Phycomycetes destructive to terricolous *Amoebae*. Mycologia **27**: 6–40. 1935.
3. ——. Some non-catenulate conidial Phycomycetes preying on terricolous *Amoebae*. Mycologia **27**: 176–205. 1935.
4. ——. A new species of conidial Phycomycete preying on nematodes. Mycologia **27**: 206–215. 1935.
5. **Lieske, R.** Morphologie und Biologie der Strahlenpilze (Actinomyceten). 1912.
6. **Penard, E.** Observations sur les amibes à pellicule. Arch. Protistenk. **6**: 175–206. 1905.

EXPLANATION OF FIGURES

Fig. 1. *Endocochlus brachysporus*; drawn with the aid of the camera lucida at a uniform magnification; × 1000 throughout. *A*, *Amoeba terricola* I infected with two thalli, *a* and *b*; *d*, digestive vacuole; *n*, nucleus; *v*, contractile vacuole. *B*, *A. terricola* I infected with two small thalli, *a* and *b*, as well as with a larger thallus *c*; *n*, nucleus. *C*, *A. terricola* I depleted of protoplasm by the three compacted thalli within the pellicle. *D*, *E*, *F*, Portions of conidiiferous hyphae, showing successively later stages in the formation of conidia. *G*, Conidia previous to evacuation of their respective tips. *H*, Mature conidia: *a–u* representing a random assortment; *v*, *w*, *x*, specimens unusual in length, shape and length of appendage respectively. *I*, Zygophores and developing zygosporangium. *J*, Collapsed pellicle of host animal and three mature zygospores, *a–c*.

Fig. 2. *Endocochlus gigas;* drawn with the aid of the camera lucida at a uniform magnification. *A*, *Amoeba terricola* being penetrated by a germ tube from the adhering conidium *a*; *n*, nucleus; *v*, contractile vacuole; × 500. *B*, An infected specimen of *A. terricola*, the adhering conidium *a* having become emptied in giving rise to the young thallus *b*; *n*, nucleus; *v*, contractile vacuole; × 500. *C*, A specimen of *A. terricola* containing two thalli of the parasite, *a* and *b*; *n*, nucleus; *v*, group of vacuoles about to merge into a single contractile vacuole; × 500. *D*, Dead or dying specimen of *A. terricola* with two well developed thalli, *a* and *b*; *n*, degenerating nucleus; × 500. *E*, Submerged portion of asexual reproductive filament; × 500. *F*, Aerial hypha with two conidia in early stages of development; × 500. *G*, Aerial hypha with a conidium at a somewhat later stage; × 1000. *H*, Aerial hypha with three mature conidia, *a*, *b* and *c*; × 500. *I*, Detached mature conidia, *a–y*; × 500. *J*, Detached mature conidia, *a–k*; × 1000. *K*, Conidium with an unsuccessful germ tube from which the protoplasm has been retracted; × 1000. *L*, Mature zygosporangium with attached zygophores; *a*, pellicle of host; × 1000. *M*, Collapsed pellicle of host animal surrounded with 19 mature zygospores, *a–s*; × 500.

Fig. 3. *Acaulopage cercospora;* drawn with the aid of the camera lucida at a uniform magnification; × 1000 throughout. *A*, Portion of mycelium on which have been captured two *Amoebae*, *a* and *b*. *B*, Portion of mycelium with a captured *Amoeba*. *C*, *D*, Portions of hypha, each with a captured *Amoeba* and five denuded sterigmata. *E*, Portion of hypha with a captured *Amoeba*, three developing conidia, *a–c*, and a mature conidium *d*. *F*, Portion of hypha with a young conidium and two denuded sterigmata. *G*, Portion of prostrate hypha with 11 conidia, *a–k*, in place. *H*, Portion of prostrate hypha with three conidia in place. *I*, Portion of prostrate hypha consisting of an evacuated septate part with 7 denuded and evacuated sterigmata, and a living part with three sterigmata, one bearing a conidium in place.

Fig. 4. *Stylopage rhabdospora*; drawn with the aid of the camera lucida at a uniform magnification; × 1000 throughout. *A*, Portion of hypha whereon have been captured two animals, *a* and *b*, referred to *Amoeba similis*. *B*, Portion of hypha with a captured animal largely depleted of protoplasm. *C*, A specimen of *A. similis* attacked by four adhering conidia. *D–J*, Conidiophores: *E*, *F*, *J*, with all spores attached; *D*, partly denuded; *G*, *H*, *I*,

wholly denuded. *K*, *a–q*, Detached conidia. *L*, Two mature zygospores, *a* and *b*, each formed from union of a zygophore arising from a mycelial filament with a zygophore arising from a conidium. *M*, Another zygospore of like origin.

Fig. 5. *Zoopage atractospora;* drawn with the aid of the camera lucida at a uniform magnification; × 1000 throughout. *A*, *B*, Portions of mycelium, each with a captured *Amoeba*. *C*, Portion of mycelium with a captured *Amoeba*, *a*, and a mature chain of conidia, *b*. *D*, Portions of mycelium with a captured animal penetrated by two haustoria, *a* and *b*, and with a sterigma, *c*, bearing a bifurcate basal conidium. *E*, Portion of mycelium with one sterigma, *a*, bearing a growing aerial filament, and another, *b*, bearing a mature chain of conidia. *F*, Portion of hypha with a growing conidiiferous filament. *G*, Portion of mycelium with a captured animal, *a*, and an immature sexual apparatus, *b*. *H–J*, Immature sexual apparatus, all zygophores arising from mycelial filaments. *K*, *L*, Immature sexual apparatus, one of each pair of zygophores arising from a conidium. *M–R*, Mature sexual apparatus. *S*, *a–y*, Detached conidia.

Fig. 6. *Zoopage atractospora;* drawn with the aid of the camera lucida at a uniform magnification; × 1000 throughout. *A*, Portion of submerged mycelium and a specimen of *Amoeba striata* captured thereon. *B*, Portion of aerial filament consisting of three axial components *a*, *h* and *i*, together with a young branch made up of the components, *b-g*, and a short chain of separated mature conidia, *j-l*. *C–H*, Portions of mature conidial chains. *I*, a branched conidium. *J*, A branched conidium, the part *a* perhaps still to be separated from the part *b*. *K–T*, Detached conidia.

Fig. 7. *Zoopage cladosperma;* drawn with the aid of the camera lucida at a uniform magnification; × 1000 throughout. *A*, Portion of a vegetative hypha with a captured *Amoeba*, *a*; together with a sexual branch on which two immature zygosporangia, *b* and *c*, are in process of development. *B*, Portion of hypha with a chain of mature conidia. *C*, *a-o*, Detached mature conidia. *D*, Portion of hypha with zygosporangia developing on the sexual branches, *a* and *b*. *E*, Portion of hypha with a zygosporangium developing on a sexual branch. *F*, A fully grown but immature zygosporangium. *G–J*, mature sexual apparatus with portions of mycelium showing attachments.