

BOTANY.—*Two zoophagous species of Acrostalagmus with multicellular Desmidi-
ospora-like chlamydospores.*¹ CHARLES DRECHSLER, Bureau of Plant In-
dustry.

Considered collectively, the fungi that under terrestrial conditions attack actively motile eelworms after the usual manner of parasites, by invading them with germ tubes from affixed or ingested conidia, show more than an ordinary degree of morphological distinctiveness. The zoopagaceous form I described earlier (2) as *Euryancale sacciospora* bears curiously appendaged conidia on lateral branches of bizarre outward shape. In the helicoid modification of their distal portions, as also in the close septation of these portions, and in the production on them, mostly laterally, of plural sessile conidia, the conidiophores of my *Meristacrum asterospermum* (3) embody features thoroughly alien to the more familiar insectivorous members of the Entomophthoraceae. The somewhat similar conidiophores of the hyphomycetous parasite I named *Meria coniospora* (4) which in their transverse septation and in their production of

conidia on slender sterigmata arising singly from the delimited segments show curious analogy with promycelia of the rusts as well as with the basidia of *Auricularia*, appear to have no parallel among the Mucedinaceae except in *Meria Laricis* Vuillemin [= *Hartiella Laricis* (Hartig) Lindau]; a fungus whose sporulation was held very unusual both by Vuillemin (8) and by Lindau (5). *Harposporium anguillulae* Lohde (6) as set forth by Zopf (9) offers marked individuality in its globose conidiiferous branches and curious sickle-shaped conidia. Globose conidiiferous branches and conidia of peculiar design likewise give distinctive character to the three congeneric parasites which I presented as new species under the binomials *H. helicoides*, *H. oxycoracum*, and *H. diceraeum* (4).

On the other hand no exceptional distinctiveness attaches to the four nematode-destroying parasites I described as *Acrostalagmus bactrosporus*, *A. obovatus*,

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Cephalosporium balanoides, and *Spicaria coccospora* (4). With respect to the morphology of their conidial apparatus these species show close correspondence with the rather numerous group of entomogenous fungi that in large part have been subsumed under the same genera; the correspondence, indeed, appearing rather clearly presumptive of an intimate taxonomic relationship. Further evidence in favor of such a relationship is supplied by two similar hyphomycetous parasites that have come under my observation, one attacking eelworms, the other attacking rotifers.

The former parasite made its appearance in a maize-meal-agar plate culture that after being occupied by a species of *Pythium* had been further planted with a few pinches of leaf mold gathered in Arlington, Va., on January 7, 1941. A species of *Bunonema* introduced with the forest refuse, and like other representatives of the genus feeding only on the surface of agar plates, had multiplied steadily during the first four weeks to attain a population of approximately 2000 individuals. Scattered specimens were then observed succumbing to fungus infection. Additional animals were found dead on successive days, until by the end of another week all active individuals of the species were exterminated.

Owing to optical difficulties it was not possible to observe the entrance of the fungus into the animal host, or to follow the progress of mycelial invasion. After an infected eelworm had died, however, and been largely expropriated of its globulose degenerating contents, the fully developed assimilative mycelium became plainly visible. In many instances, a single filament, rather closely septate and bearing some few lateral branches, extended the entire length of the animal's body (Fig. 1, A, B), while in other instances two main filaments could be recognized (Fig. 1, C). From this decidedly meager mycelium two or three branches were soon pushed through the host integument to develop externally as colorless fertile hyphae (Fig. 1, A, a; B, a, b). The fertile hyphae that came to project into the air by virtue of an erect or ascend-

ing posture, as also the aerial terminations of similar hyphae procumbent in their proximal portions, often bore two, three, or four flask-shaped conidiiferous branches in verticillate arrangement at the distal end of one or more of their constituent segments (Fig. 1, A, b; C, a; D; E; F). Somewhat less often conidiiferous branches were borne singly on aerial portions of fertile hyphae (Fig. 1, C, a; D), while in procumbent portions they almost invariably arose singly and erect to present more nearly the appearance of autonomous conidiophores (Fig. 1, G). Regardless of posture and position, each flask-shaped branch produced at its tip usually from 5 to 15 small, hyaline, irregularly angular conidia (Fig. 1, H), which remained attached in a cohering cluster.

In addition to the conidial apparatus just described the fungus was occasionally found producing knots of yellowish-brown thick-walled cells within the agar culture medium underlying the body of a parasitized nematode. Some of these knots, or chlamydospores, if such they may be called, consisted of only three or four enlarged globose cells, which from their linear arrangement obviously represented distal segments of rather short hyphae that after emerging from the animal's body had directed their growth downward into the subjacent culture medium (Fig. 1, C, b). In the larger specimens three or four cells were likewise often present in a single row, but here they merely formed a stalk on which was borne distally an expanded part composed of 10 to 15 cells in sarciniform arrangement—the whole structure usually having a flattened clavate shape (Fig. 1, B, e). The colored cells of the chlamydospores, unlike the colorless cells of the fertile hyphae, contained numerous small globules of apparently somewhat oily character.

Development of submerged multicellular resting bodies supplementary to the production of hyaline aerial conidia on flask-shaped terminal or lateral branches has not been seen in any material of *Acrostalagmus bactrosporus*, *A. obovatus*, *Cephalosporium balanoides*, or *Spicaria coccospora*. Among the other hyphomycetes that I have observed attacking nematodes after the

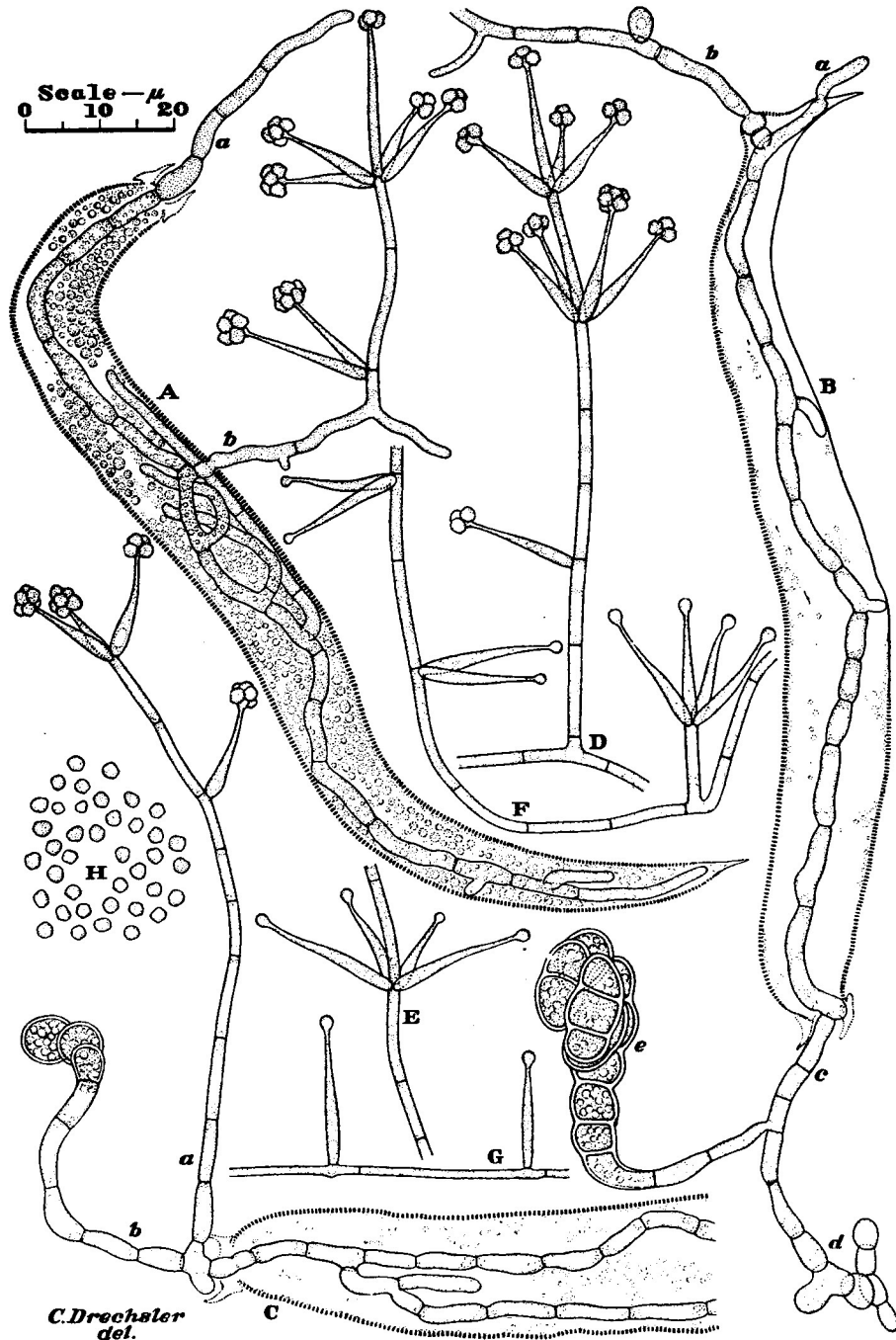


Fig. 1.—*Acrostalagmus goniodes*, drawn to a uniform magnification with the aid of a camera lucida; $\times 1,000$ throughout. A, Specimen of *Bunonema* sp. killed by the parasite; from the assimilative mycelium two branches, *a* and *b*, have been put forth externally; *b* has given rise to an erect conidiophore. B, Specimen of *Bunonema* sp. killed by fungus and almost depleted of its contents; the assimilative mycelium has put forth three external hyphae, *a*, *b*, *c*; the hypha *c* has given rise to an abortive chlamydospore, *d*, and to a well developed chlamydospore, *e*. C, Anterior portion of parasitized *Bunonema* host; from the assimilative mycelium an erect conidiophore, *a*, has grown out, together with a submerged branch, *b*, on which a small chlamydospore has been formed. D, An erect conidiophore. E, F, Portions of ascending conidiophores. G, Prostrate hypha bearing two erect conidiiferous branches. H, Conidia, showing variations in size and shape.

usual manner of parasites only *Harposporium anguillulae* has been found producing resting bodies to supplement its hyaline conidia, the resting bodies in this species being formed, however, within the animal host through modification mostly of intercalary cells in the assimilative mycelium. Apart from the development of chlamydo-spores by the *Bunonema* parasite, production of submerged multicellular resting bodies was noted in a culture prepared early in December, 1932, for the purpose of obtaining chytridiaceous fungi destructive to root-rotting species of *Pythium*. The culture in question was started by planting *P. ultimum* Trow on maize-meal-agar in a Petri dish. Several days later it was further planted by adding a small quantity of potting soil from a greenhouse in Washington, D. C., and, moreover, was flooded with about 1 cc of sterile water. A small species of rotifer, evidently introduced with the soil, soon began to multiply in the thin layer of free water. At first its population increased without hindrance, but after some weeks had elapsed periodic examinations never failed to show many specimens newly killed by a parasitic fungus. The same fungus later came to light as a parasite of small rotifers in a maize-meal-agar plate culture that had been planted with a decaying watercress (*Rorippa nasturtium* Rusby) leaf taken from a commercial watercress bed near Woodstock, Va., on May 13, 1938.

Individual rotifers killed by the fungus were usually found each with its head and tail strongly retracted; its rounded body, often less than 75μ in diameter, then showing little of the shape distinctive of living specimens (Fig. 2, A). The fleshy interior was permeated with a hyaline branching mycelium, composed of hyphae which at intervals were constricted in a manner somewhat suggestive of the haustorial filaments ascribed by Couch (1) to various species of *Septobasidium*, including, for example, his *S. purpureum*. The upper surface of the dead animal was usually overgrown abundantly with erect or ascending hyaline conidiophores whose axial filaments bore flask-shaped conidiiferous branches, mostly in whorls of three, immediately be-

low the several septa dividing them transversely (Fig. 2, A, a, b, c). The oblong colorless conidia (Fig. 2, B) formed at the tip of each flask-shaped branch, as well as at the tip of the tapering cell terminating each axial filament, remained attached in a cohering cluster. On the under side of the dead animal the assimilative mycelium would put forth into the agar substratum short filaments (Fig. 2, A, d) that sometimes concluded their development by giving rise terminally to a yellowish, thick-walled, globose structure either continuous (Fig. 2, A, e) or uniseptate (Fig. 2, A, f). Usually, however, the short filaments produced a much more distinctive structure consisting of 8 to 15 thick-walled, yellowish or brownish cells, filled with globuliferous contents and arranged, for the most part, in a single layer (Fig. 2, A, g-n). When viewed flatwise these structures in some instances presented a rather smoothly circular or smoothly elliptical peripheral outline, while in other instances the marginal outline was characteristically lobate.

Despite their more pronounced differentiation it is believed that the submerged multicellular bodies produced abundantly by the rotifer parasite are truly homologous with the submerged multicellular chlamydo-spores of the *Bunonema* parasite. A convincing homology is likewise evident with respect to the more commonplace aerial conidial apparatus whereby the two fungi are readily recognized as species of *Acrostalagmus* presumably related closely to the congeneric nematode-destroying forms, *A. bactrosporus* and *A. obovatus*, even though in the latter forms no accessory type of reproduction has been observed. An association of two types of asexual reproduction corresponding at least approximately to those here concerned was made known more than half a century ago by Thaxter (7) in the original descriptive account of his *Desmidiospora myrmecophila*, a remarkable fungus he found growing out of a large ant on the under side of a rotting log in Connecticut. The hyaline septate mycelium of this entomogenous form was set forth as giving rise at the apex of subulate basally inflated basidia to hyaline subfusiform microconidia

12 μ long and 2 to 2.5 μ wide. Since the branches that Thaxter designated as basidia in accordance with an older usage are clearly equivalent to the phialides of more recent authors, the conidia produced on them offer obvious homology with the aerial conidia of both the *Bunonema* parasite and the rotifer parasite. Aside from the hyaline microconidia, Thaxter attributed to *D. myrmecophila* the production of curious macroconidia—terminal, flat, short-stalked, multicellular, thick-walled, reddish-brown or fawn-colored bodies, dichotomously lobed several times in succession, 12 to 14 μ thick, and measuring 68 μ (maximum 90 μ) presumably along the median axis and 80 μ (maximum 100 μ) in the greater dimension transverse to this axis. From Thaxter's description and illustration it is evident that these macroconidia strikingly resemble the resting spores of the rotifer parasite in many respects, as, for example, in their terminal origin on rather short hyphal branches, in their brown coloration, in their unusual dimensional proportions, and in the flat, mostly uniplanar arrangement of their numerous thick-walled component cells. Differences of detail are, to be sure, present in the much greater size and much more pronounced lobation of the macroconidia ascribed to *D. myrmecophila*.

In considering the essential nature of the multicellular resting spores produced by the rotifer parasite it seems significant that although the animal host of this fungus has nearly always been found succumbing on the surface of agar plate cultures, the spores in question were always formed under the surface of the agar medium, while the associated reproductive apparatus referable to *Acrostalagmus* was always extended into the air. In view of these circumstances the multicellular spores must be regarded as having developed in submerged positions from normal preference rather than from constraint. Despite their distinctive morphology they would appear, therefore, to represent chlamydo-spores rather than conidia, and may appropriately be reckoned in the same category with the similarly yellowish or brownish, thick-walled, globuliferous chlamydo-spores of *Harposporium anguillu-*

lae and *Arthrotrichum oligospora* Fres. If analogy is not misleading, the remarkable macroconidia of *Desmidiospora myrmecophila* may likewise be more nearly equivalent to chlamydo-spores than to true conidia. Since much porous absorbent material is often found on the under side of rotting logs, a habitat like that of Thaxter's fungus might during dry periods permit aerial conidia to be formed in positions where during wet spells opportunity is afforded for the production of submerged reproductive bodies.

It is not evident at present that in the group of zoophagous fungi here concerned the production of chlamydo-spores, even of very distinctive chlamydo-spores, can be interpreted as an indication of taxonomic separateness. Accordingly the *Bunonema* parasite and the rotifer parasite are described as new members of the genus *Acrostalagmus*.

Acrostalagmus goniodes,² sp. nov.

Mycelium nutritum hyalinum, parve ramosum, septatum, intra vermiculos nematoideos viventes evolutum, ex hyphis filiformibus 1.5-3 μ crassis constans. Hyphae fertiles extra animal emortuum evolutae, incoloratae, repentes vel ascendentes vel erectae, axe simplicibus vel parvulum ramosae, vulgo 50-500 μ longae, 1.2-2.5 μ crassae, in cellulis 7-18 μ longis consistentes, quarum quaedam 1-4 ramulos conidiferos (phialas) ferunt; ramulis conidiferis saepe 2-4 verticellatis, lageniformibus, 10-20 μ longis, basi 1.2-2.3 μ crassis, quoque sursum in sterigma .5 μ crassum abeunte et ex apice ejusdem 5-15 conidia deinceps gerente; conidiis cohaerentibus, hyalinis, rotunde polygoniis, plerumque 1.3-2.1 μ diam. Chlamydo-spores in materia subjacenti oriundae, ex hyphis immersis leniter latescentes, flavidae vel fulvae, parte posteriore sarciniformes, omnino 12-30 μ longae, 6-15 μ latae, 3-18 cellulis constantes.

Vermiculos nematoideos speciei *Bunonematis enecans* habitat in humo silvestri in Arlington, Virginia.

Assimilative mycelium hyaline, somewhat branched, septate, growing within living

² γωνιώδης, angular, having reference to the shape of the conidia.

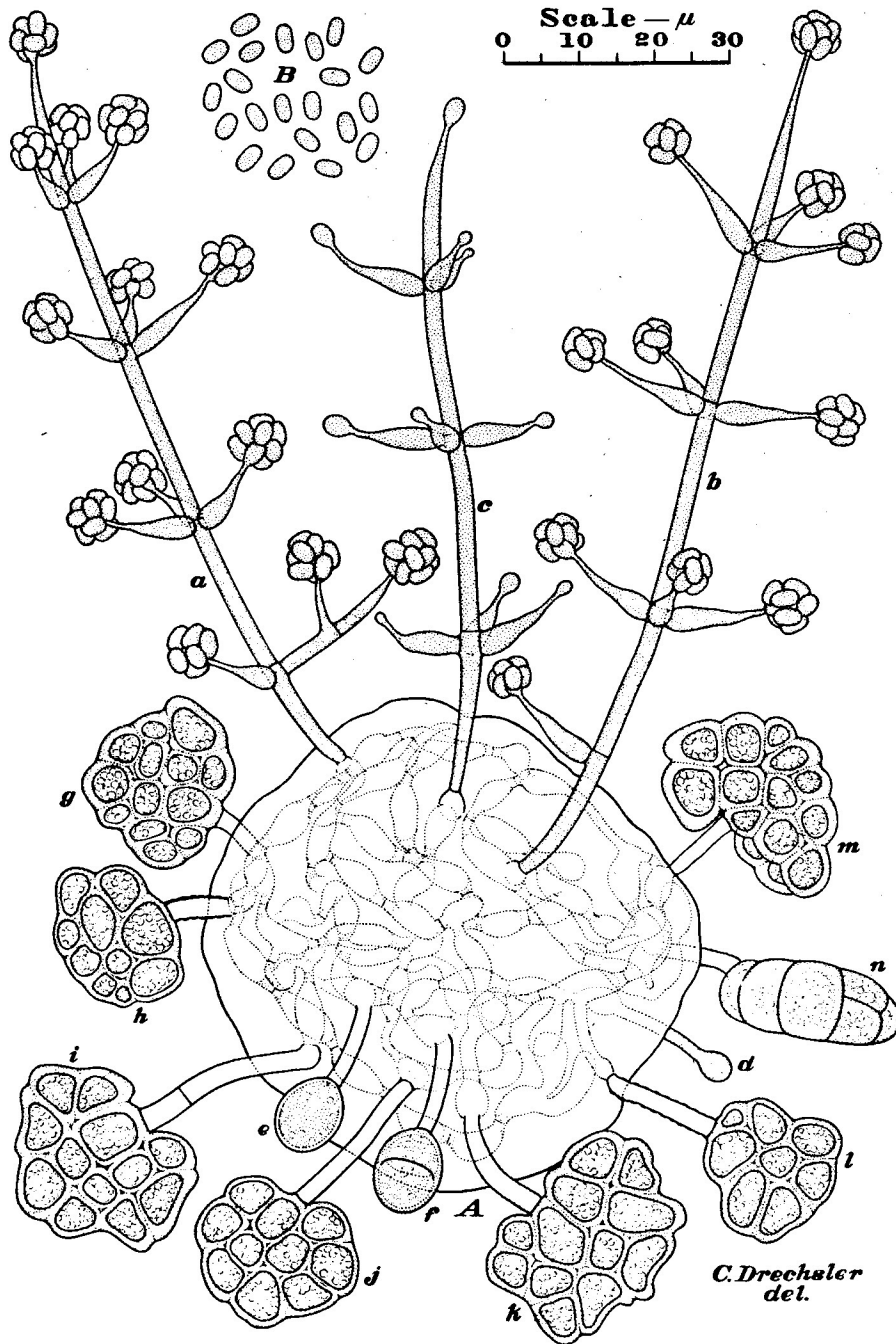


Fig. 2.—*Acrostalagmus tagenophorus*, drawn to a uniform magnification with the aid of a camera lucida; $\times 1,000$ throughout. A, Specimen of rotifer killed by the fungus. Three conidiophores, *a*, *b*, *c*, have been extended into the air; *a* and *b* are shown with conidial clusters attached, whereas *c* is shown in denuded condition. Into the underlying material have been extended eleven outgrowths, namely: a young hypha, *d*; two hyphae bearing poorly developed chlamydospores, *e*, *f*; eight hyphae bearing well developed chlamydospores, *g-n*, of which seven, *g-m*, are shown flatwise, whereas one, *n*, is shown edgewise. B, Conidia, showing variations in size and shape.

nematodes, and consisting of filamentous hyphae 1.5 to 3 μ wide. Conidiophorous hyphae formed outside of the dead animal host, creeping or ascending or erect, colorless, their axial filaments simple or sparingly ramified, commonly 50 to 500 μ long, 1.2 to 2.5 μ wide, and consisting of segments 7 to 18 μ long, of which some bear 1 to 4 conidiiferous branches (phialides); conidiiferous branches often arranged verticillately, flask-shaped, 10 to 20 μ long, 1.2 to 2.3 μ wide at the base, each tapering distally into a sterigma .5 μ wide whereon 5 to 15 conidia are formed one after another to cohere in a head; conidia colorless, rounded polyhedral, mostly 1.3 to 2.1 μ in diameter. Chlamydo-spores formed in the material underlying animal host, each borne terminally on a submerged hypha, its stalk-like proximal part widening gradually into the sarciniform distal part, yellowish or yellowish brown, altogether usually 12 to 30 μ long, 6 to 15 μ wide, and composed of 3 to 18 thick-walled cells.

Destroying nematodes belonging to a species of *Bunonema* it occurs in leaf mold in Arlington, Va.

Acrostalagmus tagenophorus,³ sp. nov.

Mycelium nutritum hyalinum, ramosum, septatum, intra viventia animalcula rotifera evolutum; hyphis hic illic constrictis, 1-4 μ crassis. Hyphae fertiles extra animal emortuum evolutae, erectae vel ascendentes, incoloratae, axe simplices vel parce ramosae, vulgo 50-250 μ longae, magnam partem 1.8-2.5 μ crassae, in cellulis plerumque 15-30 μ longis constantes quae vulgo 3 (rarius 1 vel 2) ramulos conidiferos (phialas) verticellatos sursum ferunt; ramulis conidiferis lageniformibus, plerumque 10-15 μ longis, basi 2.5-3.5 μ crassis, sursum in sterigma .5 μ crassum abeuntibus, 5-15 conidia deinceps gerentibus; conidiis hyalinis, ellipsoideis vel rotunde oblongis, plerumque 3.5-4 μ longis, 2-2.5 μ crassis. Chlamydo-spores in materia ambientis vel subjacenti immersae, ex hyphis fumadis 5-25 μ longis 2-3 μ crassis ortae, terminales, fulvae vel olivaceae, applanatae, subdisciformes vel margine aliquid lobosae, vulgo ex 8-15 cellulis constantes, plerumque medio 15-20 μ longae, 18-30 μ latae, 8-10 μ crassae.

Animalia rotifera necans habitat in humo

³ τάγγρον, pan for frying, having reference to the shape and attachment of the chlamydo-spores; and φορέω, to bear.

pingui in Washington, D. C., et in foliis *Rorippae nasturtii* putrescentibus prope Woodstock, Va.

Vegetative mycelium colorless, branched, septate, developing within living rotifers, consisting of hyphae 1 to 4 μ wide, which here and there are rather markedly constricted. Conidiophores rising erect or ascending from the dead animal host, colorless, their axial filaments simple or sparingly branched, commonly 50 to 250 μ long, mostly 1.8 to 2.5 μ wide, composed of segments usually 15 to 30 μ long which at the distal end commonly bear 3 (less often 1 or 2) conidiiferous branches (phialides) in verticillate arrangement; conidiiferous branches flask-shaped, mostly 10 to 15 μ long, 2.5 to 3.5 μ wide at the base, terminating in a sterigma .5 μ wide, on which 5 to 15 conidia are formed one after another to collect in a cohering head; conidia colorless, prolate ellipsoidal or rounded oblong, mostly 3.5 to 4 μ long and 2 to 2.5 μ wide. Chlamydo-spores formed terminally on smoky hyphae often 5 to 25 μ long and 2 to 3 μ wide, in positions under the surface of the material surrounding or underlying the dead animal host, flat disc-shaped or often with somewhat lobate margin, commonly consisting of 8 to 15 thick-walled cells, along the median axis measuring 15 to 20 μ , in the greater dimension transverse to this axis measuring 18 to 30 μ , in thickness measuring 8 to 10 μ .

Destroying rotifers in rich soil in Washington, D. C., and in decaying leaves of *Rorippa nasturtium* near Woodstock, Va.

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