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A NEMATODE-DESTROYING PHYCOMYCETE FORMING IMMOTILE SPORES IN AERIAL EVACUATION TUBES

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A new nematode-destroying fungus which offers unusual features both in its parasitic development and in its asexual reproduction was obtained from partly decomposed leaves of the red maple (*Acer rubrum* L.) that were taken, on August 27, 1944, from a thick mat of decaying foliage bordering a pond several miles north of Georgetown, Delaware. At the time the collection was made, the mat, about 20 cm. in depth, held only such moisture as had been absorbed from the ground, but its low position must have exposed it to flooding whenever the pond was swollen by rain. In accordance with routine procedure small quantities of the friable detritus were added to maize-meal-agar plate cultures already thoroughly overgrown with either *Pythium ultimum* Trow or *P. undulatum* Petersen sensu Dissmann. During the ensuing two weeks various forms of animal life, including nematodes in large part referable to the genera *Acrobeloides, Aphelenchoides, Plectus,* and *Rhabditis,* multiplied freely in the cultures. The abundant eelworms soon were attacked by several widely distributed parasitic and predaceous hyphomycetes such as *Arthrobotrys oligospora* Fres. and *Harposporium anguillulae* Lohde. Somewhat later, 19 days after the plantings had been made, the new parasitic fungus was first observed in small quantity in one of the plate cultures. Afterward it came to light also in more than a dozen other cultures of the same series. In all the cultures it attacked only a single species of eelworm which Dr. G. Steiner has kindly identified as a species of *Acrobeloides* clearly distinct though not widely different from *A. bütschlii* (De Man) Thorne so prevalent in the vicinity of Washington, D. C.

The attack of the fungus begins with the adhesion of one or more of its conidia to the integument of a susceptible animal (fig. 1, a). Each of the adhering conidia puts forth a germ tube which maintains a width of approximately 1 μ in penetrating the host cuticle and in passing through the muscular body wall. When the body cavity is reached the germ tube immediately widens out in the manner of a pestle (fig. 1, b). The entire protoplasmic contents of the conidium then migrate into the expanded tip (fig. 3, a, b) to form a globose bud which soon detaches itself as a young thallus ready for para-

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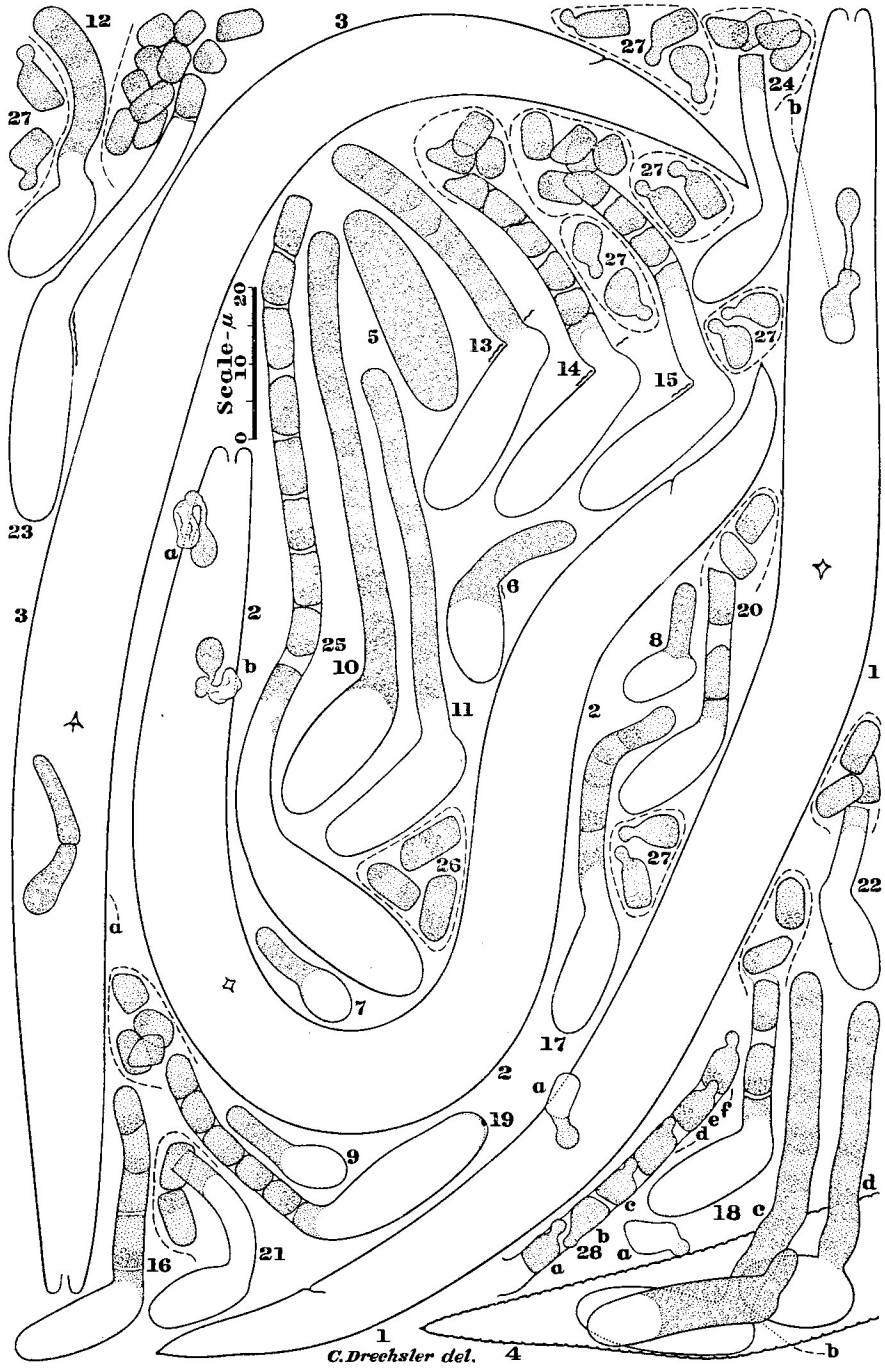
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sitic growth; the empty infection tube thereupon being nearly always lost to view, though the empty conidial envelope may often be seen affixed in much later stages (figs. 4, a; 33, a, b, c).

The young thallus, loose within the body cavity of the host, gradually elongates despite the frequently rather active bustling to which it is subjected by the animal's undiminished locomotion. When its length has come to exceed its width 3 or 4 or 5 times a cross wall appears in the middle, dividing it into 2 subequal cells (fig. 29) only slightly larger than the parent cell was originally. The 2 daughter cells grow somewhat in size as they become rounded off at the median septum in preparing for disjunction (figs. 2, a; 30), an event apparently hastened a little by the repeated flexural strains resulting from active movements of the eelworm. The separated unicellular bodies then gradually elongate and in due course, like their parent, undergo median partitioning and disjunction (fig. 31). Before long, on continued repetition of the same developmental sequence, a dozen thallodic cells are to be seen jostled about in loose disorder (fig. 32). Far from affecting these cells unfavorably, the jostling seems actually to help them in extending their distribution lengthwise within the animal, and more particularly in pushing them slowly through the narrowed portion of the body cavity where the

Explanation of figures 1–28

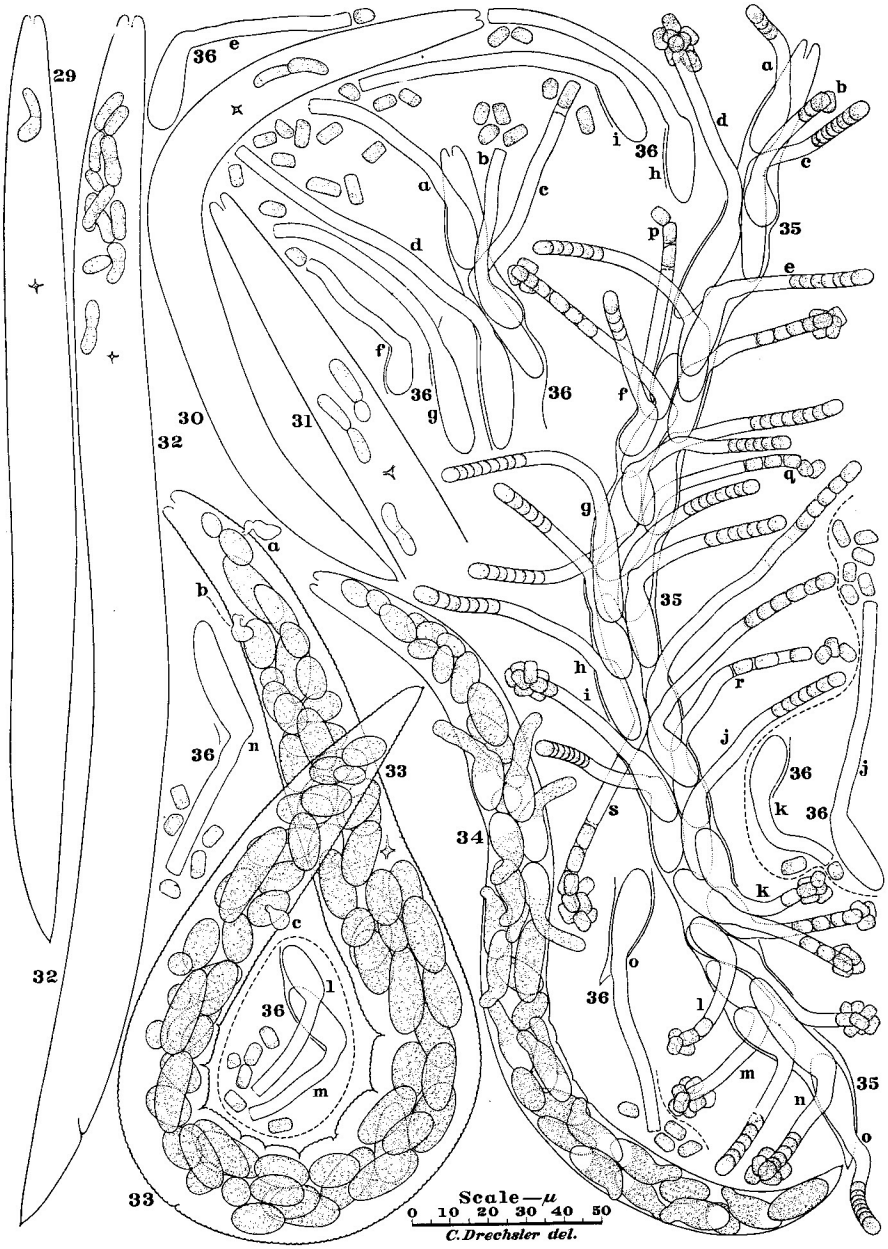
Gonimochaete horridula, drawn to a uniform magnification with the aid of a camera lucida; ×1000. FIG. 1. Small specimen of *Acrobeloides* sp. in early stage of infection from 2 adhering conidia, a and b; the infection tube from b is extended at an angle affording a good view. FIG. 2. Small specimen of *Acrobeloides* sp. with 2 adhering conidia, a and b, that have yielded their protoplasmic contents to the terminal enlargements within the body cavity of the host. FIG. 3. Small specimen of *Acrobeloides* sp. containing in its body cavity a uniseptate thallus whose 2 cells are about to become disjointed. FIG. 4. Posterior portion of infected specimen of *Acrobeloides* sp. with an empty spore envelope, a, adhering to it externally, and with 3 thallodic cells contained inside of it; one of the cells, b, having just begun to put forth a hyphal outgrowth, the other 2 cells, c and d, having each completed production of a hyphal outgrowth. FIG. 5. Large thallodic cell. FIG. 6. Thallodic cell in course of extending a hyphal outgrowth. FIGS. 7–9. Thallodic cells with fully extended hyphal outgrowths. FIGS. 10–13. Thallodic cells with hyphal outgrowths whose contents are arranged in alternate granular and homogeneous layers, indicating cleavage into spores. FIG. 14. Same sporangium as in figure 13, but after 3 spores have been liberated in a first discharge. FIG. 15. Same sporangium, again, as in figure 13, but after 2 more spores have been liberated by a second discharge. FIGS. 16, 17. Thallodic cells with sporangial hyphae ready for discharge of spores. FIGS. 18–22. Thallodic cells with sporangial hyphae, after discharge of a few spores from each. FIG. 23. Large thallodic cell whose sporangial hypha has liberated 10 spores, 1 spore being still attached to the closed end of the persistent basal part of tubular membrane; the proximal end of each spore is distinguished internally by an accumulation of granules. FIG. 24. Rather small thallodic cell whose sporangial hypha retains some protoplasm, after it has discharged 4 spores. FIG. 25. Large thallodic cell whose sporangial hypha retains some protoplasm and 8 spores, following the liberation of one or more spores at the tip. FIG. 26. Liberated spores of more than average size. FIG. 27. Spores that after their liberation have each put forth an adhesive protuberance. FIG. 28. Spores *a–f*, each of which has put forth an adhesive protuberance while still inside the envelope of the sporangial hypha.

oesophageal bulb occupies nearly the entire lumen of the body wall. Owing to the greater frequency of anterior infections, the portion of body cavity forward of the bulb is usually occupied earlier than the posterior portion. However, development of the fungus around the yielding intestine would seem to proceed more rapidly than about the resistant oesophagus, for when the thallodic cells have attained their definitive number they are usually found distributed rather evenly from one end of the animal to the other. As might be expected from the manner of multiplication, the definitive number of thallodic cells—commonly between 15 and 80—is little influenced by the number of original infections, but is determined primarily by the size of the individual animal host.

After their multiplication has ceased the thallodic cells grow in size without undergoing any pronounced change in their elongate ellipsoidal or occasionally subspherical shape. They increasingly choke the body cavity, yet for a protracted period the animal continues to move about with little show of distress or physical weakness. In many instances its behavior remains seemingly normal even after the total volume of the fungus cells appears approximately equal to the combined volume of its musculature and organs. Somewhat later, however, its locomotion slows down gradually and stops, disablement here being accompanied by incipient evanescence of the peripheral musculature. Usually the body wall backward from the oesophageal bulb begins to fade from view somewhat earlier than the anterior portion of the wall. In all cases, certainly, the oesophagus and bulb resist dissolution far better than the intestine or, indeed, than any other fleshy part. Thus, in the specimen shown in figure 33 the oesophagus and bulb, though crowded from their normal position, could still be clearly distinguished at a stage when all other contents had been reduced to diaphanous vestiges. Eventually these durable muscular parts also suffer obliteration in some degree, even if in more than a few instances they remain discernible when the thallodic cells

Explanation of figures 29–36

Gonimochaete horridula, drawn to a uniform magnification with the aid of a camera lucida; ×500. FIGS. 29, 30. Specimens of *Acrobeloides* sp., each infected by a single uniseptate thallus. FIG. 31. Anterior portion of a specimen of *Acrobeloides* sp. infected with 3 uniseptate thallodic bodies. FIG. 32. Specimen of *Acrobeloides* sp. infected with 12 thallodic bodies, some continuous, others uniseptate. FIG. 33. Large specimen of *Acrobeloides* sp. killed by parasite, following infection from 3 conidia, a–c, and development of 76 thallodic cells in its body cavity. FIG. 34. Specimen of *Acrobeloides* sp. killed and expropriated of contents through development of 40 thallodic bodies of the parasite; many of the bodies have begun to extend sporangial hyphae. FIG. 35. Integument of a specimen of *Acrobeloides* sp. occupied by 34 empty thallodic cells whose contents have been utilized for production of spores; most of the sporangial hyphae, including the 15 designated by the letters from a to o are shown in ascending posture; 4 others, p, q, r, and s, being shown in submerged positions. FIG. 36. Fifteen aerial sporangial hyphae, a–o, flattened down in a moist preparation under a cover glass; these being the same hyphae as those designated by corresponding letters in the preceding figure.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have manifestly concluded their vegetative growth, to proceed with asexual reproduction.

Reproductive development is initiated by the extension of a single stout hyphal outgrowth from one end (figs. 4, b; 34) or from a position close to one end (fig. 4, c, d) of the individual thallodic cell. To provide material for this outgrowth, the thallodic cell, which during the vegetative stage remains filled throughout with dispersedly granular protoplasm (figs. 5, 33), is progressively cleared of visible contents at the opposite end as if by the enlargement of a vacuole (figs. 4, b; 6; 34). The movement of materials proceeds steadily as the outgrowth forces its way through the host integument to continue its elongation externally (fig. 4, c, d). In occasional instances the protoplasmic column in the hyphal outgrowth may temporarily keep a slight foothold inside the ellipsoidal envelope (figs. 7–10) but as a rule this envelope is evacuated forthwith of all living contents.

A conspicuous characteristic of the hyphal element is its strong preference for aerial development. Since in agar cultures the host animals habitually live and feed on rather than under the surface of the substratum, they ordinarily succumb on the surface. For the most part, consequently, the hyphal elements after emerging from the host integument are free to follow their natural bent in choosing between submerged, procumbent, and aerial development. Although some of the hyphae, especially those arising from thallodic cells covered or laterally hemmed in by their fellows, thrust their way into the agar or grow procumbently over it, virtually all hyphae from favorably situated thallodic cells grow ascendingly into the air, and thus collectively offer a bristling appearance (fig. 35) when viewed under a microscope with a dry objective.

Soon after a hyphal element has attained definitive length its contents show significant changes. The granular constituents of its protoplasm, which during the period of growth remained rather evenly distributed (figs. 6, 7) are now brought together at intervals in a series of transverse clumps numbering usually fom 2 to 11 (figs. 4, c, d; 10–12). Beginning near the tip, lines of demarcation, often curving downward somewhat obliquely (figs. 13, 16, 17), appear below the individual granular clumps, at first being only faintly visible, but gradually becoming more and more distinct. Suddenly, with an abrupt though hardly violent upward movement of the whole stratified column, the 2 or 3 or 4 parts delimited by the uppermost lines are pushed forward; and as at the same time both their linear arrangement and their connections with one another become disrupted through buckling, they are revealed as discrete spores (figs. 14, 18, 19–22, 24). Apparently the newly liberated spores are somewhat adhesive, for in instances of aerial development they flip backward and remain clinging to the shortened hypha in an irregular cluster. The portions of protoplasm still in the hypha then undergo

further gradual individualization, and after a period of perhaps 15 to 30 minutes 2 or 3 more spores are abruptly though gently pushed forward (fig. 15). Many of the shorter hyphal outgrowths discharge only once or twice, but the longer hyphae originating from the more voluminous thallodic cells (fig. 23) may give 3 or 4 puffs; each successive increment of spores, in the case of aerial hyphae, becoming agglutinated to those already clustered at the tip. Sometimes the lowermost spore remains in place, attached to the empty hyphal membrane (figs. 23; 36, c). The occasional instances where several spores or, at times, nearly all of the spores remain in alignment (fig. 25) until the enveloping hyphal membrane disintegrates must be held to have their explanation in partial or complete failure of the discharge mechanism.

Thus, in a general way, the hyphal outgrowth functions both as a sporangium and as an evacuation tube. Its operation in the latter capacity, however, shows marked peculiarity not merely in the gentle, intermittent propulsion of the spores, but also, and more especially, in a progressive wastage of the distal portion of the hyphal membrane, through which the original length of the membrane may be reduced by more than a half. It is not easily determined just how this wastage is accomplished. As the outgrowth before discharge reveals no conspicuous modification of its apex, there is reason to believe that the initial rupture of the membrane is not usually at the tip, but more often between the apical and the penultimate spore; wherefore it seems probable that in the very beginning the tubular envelope is shortened through removal of a distal portion adnate to the apical spore. If the first pufflike discharge leaves unoccupied a portion of hyphal envelope at the new apex, this ordinarily disintegrates quickly, thereby further shortening the tube. Similar loss of membrane takes place with each succeeding puff, until discharge is completed. Another peculiarity then becomes manifest in that the abbreviated hyphal membrane is usually not left open at the tip, like evacuation tubes generally, but is closed securely by a terminal wall (fig. 36, a–o). Where deposition of such a wall is omitted, as is frequently the case in specimens submerged in an agar mount prepared for study under the microscope, the hyphal membrane and the empty envelope of the thallodic cell promptly collapse and are soon lost to view. Where, however, the tip of an ascending aerial element has been closed, the entire membranous container, like an ancient skin bottle, retains its turgor and shape for a prolonged period, with the result that the shortened hyphal element continues to project upward, bearing aloft its cluster of spores. In fine, through closure of its tip the hyphal element that previously had served as sporangium and evacuation tube is enabled to operate as a sporophore. Occasionally hyphal outgrowths in submerged or procumbent positions likewise become sealed distally, though here it is not evident that any purpose could be fulfilled by the continuing turgor of the evacuated receptacle.

When newly liberated the spores (figs. 14, 15, 18–20, 22–24, 26; 36, a–o) are of a generally cylindrical shape. In the shorter specimens the length scarcely exceeds the width, while in the longer specimens it may slightly exceed twice the width. Most of the spores are somewhat unsymmetrically rounded or obliquely truncate at the ends; those formed terminally being, as a rule, quite readily distinguishable from their fellows since they regularly retain the symmetrically rounded apical contour of the parent hyphal outgrowth. All of them lack locomotor organs of any kind, and consequently are completely immotile. When brought into contact with a moist substratum they undergo incipient germination, each giving rise, often obliquely from one end, to a small excrescence (fig. 27) with a profile suggestive of the protruded head of a turtle. Judging from instances where frustration of the discharge mechanism has left the spores within the envelope of the parent hypha (fig. 28), the excrescence more often arises from the distal end (fig. 28, a, c–f) than from the proximal end (fig. 28, b). As might be surmised from analogy with similar development in other fungi parasitic on free-living terricolous nematodes, the germ protuberance is strongly adhesive and serves an important function in attaching the spore securely to the integument of a prospective host.

The vegetative development of the fungus can be followed no less clearly than its asexual reproduction, owing to the fortunate circumstance that animals infected by it suffer expropriation of their contents without showing the globuliferous degeneration through which the invasion of nematodes by nearly all parasitic and predaceous forms is often obscured to a troublesome degree. While the determination of its morphology and development in most particulars thus offers little difficulty, the taxonomic relationships of the fungus are not as obvious as might be desired. The general resemblance of its thallodic cells to the thalli of various zoospore-producing phycomycetes that have been made known as nematode parasites—*Chytridium endogenum* Braun (41), *Chytridium zooticum* Braun (2), *Catenaria anguillulae* Sorok. (7, 41), *Achlyogeton entophytum* Schenk (40), and *Myzocytium vermicolum* (Zopf) Fischer (11, p. 75; 44) may be cited as examples—immediately suggests that the immotile spores could well have been derived through evolutionary processes from some type of motile zoospore. Loss of motility in zoospores might, indeed, readily be associated with adaptation to parasitism on free-living nematodes, since the very active locomotion of these animals in itself provides adequate opportunity for encounter between host and parasite, thereby making independent movement of the parasite unnecessary, while at the same time encouraging strong adhesiveness as a feature of primary importance. The immotile spores of the fungus I have described (10) as *Haptoglossa heterospora* can be credibly interpreted as being homologous with zoospores not only by reason of their original subspherical shape

and their violent discharge from massive sporangia formed from endoparasitic thalli, but by reason further of the persuasive parallelism that is evident when their emission of individual glossoid infective bodies is compared with the emission of a second zoospore stage in diplanetic development of the type familiar in *Achlya* and *Aphanomyces*. However the immotile spores of the Delaware fungus are not typically subspherical at any time, and do not reveal anything suggestive of diplanetism or of any other developmental feature especially characteristic of zoospores. In respect to their ambiguous morphology they invite comparison with the acutely pointed tapering immotile spores of the nematode parasite *Protascus subuliformis* Dangeard (8), which in shape likewise differ very markedly from zoospores, and which in manner of germination betray no particular homologies of any kind. If Maire (29) was able, with some credibility, to interpret the tapering spores as aplanospores equivalent to zoospores, it was mainly because the morphology of the thallodic sporangium in which they were formed and the violent manner of their discharge, together with the morphology of the sexual apparatus ascribed by Maupas (30) to *P. subuliformis*, gave grounds for recognizing a possible relationship to the zoosporiferous genera *Achlyogeton* and *Myzocytium*. While such relationship might be held similarly indicated for the Delaware fungus by the multiplication and outward morphology of its thallodic cells, parallelism with zoosporiferous phycomycetes generally is not well sustained either in the behavior of its hyphal outgrowths or in the intermittent maturation and discharge of its immotile spores.

What would seem in some measure a departure from the usual course of development among zoosporiferous phycomycetes is shown by the Delaware fungus in the complete evacuation of undifferentiated materials from the thallodic cell into a hyphal outgrowth corresponding structurally to the evacuation tubes of various chytrids and oomycetes. Yet however alien such transfer of protoplasmic materials, followed by zoospore or aplanospore individualization within the filamentous element, may be to the genera *Achlyogeton, Myzocytium, Protascus,* and *Haptoglossa,* similar movement of contents occurs as a rather commonplace event in the germination of some oospores. Thus, for example, when the oospores of my *Aphanomyces camptostylus* germinate by the production of zoospores, individualization of the swarm spores often takes place wholly within the germ hypha (9, p. 340, fig. 11, J). But while the sporogenous germ hyphae produced by *Aphanomyces* oospores are habitually extended into any deposit of liquid water that may be available, the sporogenous hyphal outgrowths of the Delaware fungus reveal a strong preference for aerial development wherever their positional relationships are not too unfavorable. To this preference, which even by itself would need to be regarded as very exceptional in an evacuation tube, are added further anomalous features in the curious evanescence of the distal

portion of the hyphal membrane during spore discharge, and in the terminal closure of the empty proximal portion persisting after discharge is completed.

Most of the features that give difficulty in reckoning the Delaware fungus among the zoospore-producing phycomycetes find striking analogies in the entomophthoraceous nematode parasite I described earlier (10) as *Meristacrum asterospermum*. In one species as in the other the thallodic cells are completely evacuated of contents as the protoplasmic materials migrate into sporogenous hyphae that show a strong tendency toward aerial development. In both fungi, again, spore formation proceeds from the tip toward the base, and spore liberation is accompanied by rapid collapse and evanescence of a terminal portion of the hyphal membrane. The wall which in the Delaware fungus closes the empty portion of the sporogenous outgrowth offers good correspondence with the septum that in *M. asterospermum* proximally delimits the lowermost sporogenous hyphal segment. *M. asterospermum,* it is true, forms its immotile spores not endogenously, like the Delaware fungus, but in a typically exogenous manner by burgeoning them forth laterally from the several individual segments formed through deposition of cross-walls in the helicoid distal portion of the sporogenous hypha. Although these exogenous spores, or conidia, show unmistakable general resemblance to the much larger conidia familiar in the insectivorous Entomophthoraceae, they would seem more accurately homologous with the small secondary conidia whose production plurally from large primary conidia, following simultaneous emission of multiple sterigmata, was first made known by Costantin (5) as a distinctive feature of *Delacroixia coronata* (Cost.) Sacc. & Sydow (39, p. 457) and more recently was also observed by Couch (6) as an incidental phase in the development of his *Conidiobolus Brefeldianus*. In accordance with such homology the large conidium of *D. coronata,* and, by extension, the large conidia of the Entomophthoraceae generally, would be morphologically equivalent to the distal helicoid sporogenous portion of the hyphal element thrust into the air by the individual thallodic segment of *M. asterospermum*. Similar parallelism, but relating to endogenous immotile spores rather than to conidia, becomes evident when the Delaware fungus is compared with *Basidiobolus ranarum* Eidam: the distal sporogenous portion of the hyphal outgrowth in the former having its morphological equivalent in the large conidium of the latter; and the immotile spores of the former corresponding to the secondary bodies formed plurally, according to Levisohn's (28) account, within the large conidia of the latter after their ingestion by frogs, or often, too, on immersion in a glycerin-peptone-glucose culture solution. Levisohn discussed the endogenous bodies merely as products of multiplication, referring to them and to their development in language (Tochterzellen, Abkömmlinge, Darmform, Konidienzerfall, Hyphenzerfall, Teilung) even less connotative of homologies pertaining to reproduction

than the term "Palmellastadium" by which Raciborski (38) had earlier designated aggregations of similar bodies he found produced within mycelial segments when he grew *B. ranarum* in a culture solution containing ammonium sulphate and glucose. Nevertheless in subsequent text-books on mycology (13, p. 118, 119; 12, p. 285; 1, p. 115–117; 14, p. 147) the endogenous bodies have been interpreted as sporangiospores, and for the most part Levisohn's findings seem to be construed confidently as having established the sporangial nature of the large conidia common to nearly all known members of the Entomophthoraceae. It is not difficult to understand how an investigator dealing at first hand with *B. ranarum* might well be reluctant to use terminology distinguishing between asexual reproduction and vegetative segmentation, for in that fungus, under natural conditions, the development corresponding to the formation of endogenous spores in the hyphal outgrowths of the Delaware parasite takes place, apparently without much spatial separation, in the same milieu—the interior of the frog's alimentary tract—as the vegetative multiplication corresponding in the Delaware parasite to the repeated fission of young thallodic cells inside the body cavity of the nematode host. The circumstances making for confusion of the reproductive and vegetative stages in *B. ranarum* are wholly absent in the Delaware fungus; so that this fungus—unless the parallelisms it offers are misleading—displays advantageously what would appear to be the primal manner of asexual reproduction in the family. The difference between its method of spore formation and the method of spore formation in *M. asterospermum* seems approximately of the same sort as the difference between the types of asexual sporulation found, respectively, in *Mucor* and *Cunninghamella;* though the *Dictyuchus*-like partitioning of the sporogenous hyphal tip in *M. asterospermum* has no equivalent in *Cunninghamella* nor, for that matter, in *D. coronata* and *C. Brefeldianus.* It may be noted that the spores of *M. asterospermum* put forth no special adhesive protuberance, but become affixed to the animal host by means of adhesive material which they exude without undergoing any modification in outward shape. Again, instead of increasing numerically by repeated fission during the earlier stages of invasion, the infective cell of *M. asterospermum* grows into a stout massive hypha before division by deposition of cross walls takes place preliminary to disjunction.

If among the groups of phycomycetes mainly endoparasitic on animals and reproducing asexually by immotile aerial spores the Delaware fungus is brought into alignment with the Entomophthoraceae by virtue of its ready fissiparous multiplication, it is through this same feature of vegetative development estranged from the Zoopagaceae; since in the latter family thallodic or mycelial disjunction is wholly unknown, and apart from the septa associated with reproduction, transverse walls are laid down within thallus,

hypha, or germinating conidium solely as retaining walls to mark successive stages in the evacuation of these structures. Then, too, the contents of the disjointed vegetative cells show sharp contrast between the sappy protoplasmic matrix and the granules scattered through it in moderate numbers, whereas the denser protoplasmic matrix in the thalli and vegetative hyphae of the Zoopagaceae often obscures the granular constituents rather markedly. Although in the Delaware fungus the spores usually do not appear spatially separated from the membrane of the hyphal outgrowth within which they are formed, their visible movement upward through the lumen of the membranous envelope gives ample evidence of their endogenous origin. Among the Zoopagaceae, on the other hand, movement of spores within the membrane of a parent hyphal element has never been observed. Except for the empty membranous appendages borne on the conidia of some species, the spores throughout that family are indistinguishably fused with the membrane originally surrounding them; and after disarticulation each spore retains the adnate portion of original membrane as an integral part of its wall. Even the restricted analogy in sporulation offered by the three catenulate genera of the Zoopagaceae is absent in the five zoopagaceous forms that have so far been described as parasitic or predaceous on nematodes, since none of these five forms produce their spores in chains. However among the fungi found destructive to nematodes in agar-plate cultures planted with decaying vegetable materials catenulate sporulation very similar to that known in the Zoopagaceae occurs in representatives of the group of minute aerially sporiferous organisms that have been customarily referred to *Actinomyces,* though a genus of less ambiguous application is now available—if the lack of a Latin diagnosis can be overlooked—in *Streptomyces* Waksm. & Henr. (43). These organisms, which from their morphology seem best referable to the Phycomycetes, include not only many species parasitic on nematodes (*Bunonema* is attacked especially often) but also species destructive to various amoebae and to testaceous rhizopods of such genera as *Euglypha, Geococcus, Heleopera, Sphenoderia,* and *Trinema.*

Truly endogenous development of reproductive bodies in linear arrangement within basally attached unbranched filaments occurs certainly in a group of curious animal-inhabiting organisms, somewhat unfamiliar to mycologists though presumably referable to the Phycomycetes, of which the first representatives were made known by Leidy (24, 25, 26, 27) nearly a century ago in his original descriptions of *Enterobryus elegans, Enterobryus spiralis, Enterobryus attenuatus, Eccrina longa,* and *Eccrina moniliformis,*—all based on specimens found in the alimentary canals of different arthropods. *Enterobryus elegans* offers particular interest here as it was not only found attached to the mucous membrane of the small and the large intestine of its millipod host, *Julus marginatus* Say, but was also observed growing

from the exterior of the three nematode species—*Ascaris infecta* Leidy, *Streptosomum agile* Leidy, and *Thelastosomum attenuatum* Leidy—infesting the cavities of the viscera mentioned. Despite the development of *E. elegans* on nematodes, Leidy's account of this organism can hardly be considered directly suggestive of the Delaware fungus since in the relevant figures (27, pl. 1, fig. 1, e, f, i; pl. 4, fig. 28, b, c) its very few large propagative bodies, or "secondary cells" would seem to be formed through *Oidium*-like segmentation; and similar segmentation would likewise seem illustrated in the figures relating to "secondary-cell" production in *E. spiralis* (27, pl. 1, fig. 4, d) and *E. longa* (27, pl. 5, fig. 1–6). Closer resemblance to the Delaware fungus is, however, evident in the illustrations pertaining to asexual reproduction in some of the organisms more recently described, again from the digestive tubes of arthropods, as members of the group Eccrinides erected in 1905 by Léger and Duboscq (17) to include besides Leidy's two genera the type genus *Arundinella* (now *Arundinula*) then newly erected by them. This group, subsequently augmented through assimilation of *Amoebidium* Cienk. (4) and through addition (18, 19, 20, 21, 22, 23) of eight new genera, including three contributed by Poisson (32, 33, 34, 35, 36, 37), was in 1929 ranked by its authors (22) apparently as a subclass (Eccrinideae) in the Phycomycetes under which were subsumed two separate orders, the Eccrinales with three families and the Amoebidiales with one family. From the descriptions and figures given by Léger and Duboscq and by Poisson, the spores of the Eccrinales are formed endogenously. The "macroconidia" of these authors, though apparently corresponding to Leidy's "secondary cells," seem much less suggestive of oidia. Where the French investigators show relatively short thalli in process of forming the small reproductive bodies designated by them as "microspores," as, for example, in a specimen of *Parataeniella intermedia* delineated by Poisson (35, p. 205, fig. XX, E), it is easy to recognize general similarity to hyphal outgrowths of the Delaware fungus, such as those illustrated herein in figures 4, 10, 11, 12, and 13. Since my fungus has so far not been seen to produce any spores of strongly indurated character, grounds are lacking for any comparison with the seriately arranged, transversely oriented, thick-walled reproductive bodies of the Eccrinales, which the French writers term "spores durables," and which Poisson (36, p. 60, 65) took occasion to distinguish from the "cysts" of Thaxter's *Enterobryus compressus* (42) as well as from the "oospores" of Hauptfleisch's *Astreptonema longispora* (15), a related species first placed in the Saprolegniaceae but later (16) surrendered to the protozoologists. My fungus has shown nothing in its sporangial outgrowths analogous to the expanded terminal "gland" present in some members of the Eccrinales, which by breaking down permits apical liberation most usually of microspores; and the disintegration of its

sporangial membrane seems too rapid and disorderly to afford any very close parallelism with the manner of dehiscence by lateral apertures that occurs among the Eccrinales more especially in the liberation of macrospores and resting spores. Further, the well-developed endoparasitic thallodic cells of my fungus have no recognizable equivalent in the Eccrinides, as the tubular thalli of those organisms are only slightly inserted into the host tissues, more or less after the manner familiar in the genus *Harpochytrium* Lagerheim; while *Asellaria Caulleryi,* a somewhat related branching parasite described by Poisson (37) from the intestines of isopods has no attachment at all. Production of amoebospores in addition to immobile spores, such as occurs in *Amoebidium parasiticum* Cienk. (4), where according to Cienkowski's account the amoebospores after their encystment may form several curved immotile spores endogenously, is wholly alien to my fungus. This distinctive type of reproduction, which led Bütschli (3, p. 611–614) and Minchin (31, p. 313–314) to subsume *A. parasiticum* under the Protozoa, is present in the genus *Paramoebidium* Lég. & Dub. (23) to the exclusion of endospore formation; and though absent throughout the order Eccrinales is held to be of primary significance in considerations touching the fundamental character and taxonomic relationships of the entire group.

The Delaware parasite, as has been intimated, appears best interpretable as a primitive member of the Entomophthoraceae. To provide a suitable place for it, a new genus is proposed under a name compounded of two words meaning "fertile" and "hair," respectively.

Gonimochaete Drechsler, gen. nov. Parasitus intra animalia viventia crescens; cellulis nutritis juvenilibus ejus septo in duos loculos identidem se dividentibus, his loculis inter se disjungentibus, itaque stato assumenti postremo ex corporibus unicellularibus disjunctis incoloratis constante; post mortem animalis corporibus vulgo globosis vel ellipsoideis, quoque omne protoplasma tradente dum hypham fertilem extra integumentum saepe in aerem rarius in materiam subjacentem vel ambientem proferente; quaque fertili hypha sporas immotas incoloratas in unicam seriem penitus gignente denique eas expellente simul membrana ipsius in parte superiore evanescente, tamen parte inferiore ascendente sursum muro clausi saepe paulo longius persistente.

Parasite growing within minute animals, its assimilative cells early in development repeatedly becoming divided by a cross-wall, and the two segments in each instance separating from one another, so that eventually the vegetative state consists of disjointed colorless unicellular bodies; the bodies commonly globose or prolate ellipsoidal in shape, each of them yielding all its protoplasm in putting forth a filamentous hypha which after emerging from the host integument most often projects into the air, though at times creeping over or extending into the surrounding material; each hypha producing internally a row of colorless immotile spores, then expelling them while simultaneously the upper portion of hyphal membrane collapses and vanishes, though the lower portion often becomes closed by a distal wall and then persists some time longer in an ascending posture.

Gonimochaete horridula Drechsler, sp. nov. Corpora assumentia incolorata, multa (saepius 15–80) in vermiculo nematoideo oriunda, in maturitate globosa vel elongato-ellipsoidea, plerumque 6–33 μ longa, 5.5–10.5 μ crassa, primo protoplasmatis disperse granulosi repleta, deinde ex uno extremo hypham fertilem promittentia itaque omnino se exinanientia; hyphis fertilibus incoloratis, vulgo plerumque ascendentibus (itaque conjunctim horridulis), 10–100 μ longis, 2.8–5 μ crassis, 2–12 sporas immotas intus gignentibus, binas vel ternas vel quaternas leniter eas deinde expellentibus, postremo eas apice clausa partis inferioris vacuae 5–80 μ longae sustinentibus; sporis incoloratis, cylindraceis, utrimque inaequaliter rotundatis vel oblique rotundo-truncatis, 4–9.5 μ longis, 3–4.2 μ crassis, dejectis gemmam glutinosam 1.5–2.5 μ longam 1.5–2 μ crassam saepe oblique ex uno extremo emittentibus.

Habitat in *Acrobeloideo* sp. in foliis *Aceris rubri* putrescentibus prope Georgetown, Delaware.

Assimilative bodies colorless, often developing in numbers from 15 to 80 in an individual nematode host, when full grown mostly 6 to 33 μ long and 5.5 to 10.5 μ wide, at first filled with dispersedly granular protoplasm, each later becoming completely evacuated in giving rise from one end to a single hypha; the hyphae colorless, often mostly ascending (and thus collectively offering a bristling appearance), 10 to 100 μ long, 2.8 to 5 μ wide, individually producing 2 to 12 immotile spores internally, then expelling them weakly mostly 2 or 3 or 4 at a time, and afterwards often holding them aloft at the closed tip of an empty lower part 5 to 80 μ in length; spores colorless, cylindrical, mostly rather irregularly rounded or somewhat obliquely truncate at both ends, 4 to 9.5 μ long, 3 to 4.2 μ wide, each eventually when lying on the substratum budding forth a bulbous adhesive protuberance, 1.5 to 2.5 μ long and 1.5 to 2 μ wide, usually somewhat obliquely from one of its ends.

Destroying nematodes belonging to a species of *Acrobeloides* it occurs in decaying leaves of *Acer rubrum* near Georgetown, Delaware.

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