A NEW SPECIES OF CONIDIAL PHYCOMYCETE PREYING ON NEMATODES

CHARLES DRECHSLER

(WITH 1 TEXT FIGURE)

Although the Zoopagaceae hitherto observed in Petri dish cultures started from decaying plant materials consist preponderantly of forms destructive to *Amoebae*, at least several fungi undoubtedly referable to the same taxonomic group have been found that evidently subsist entirely by capturing and consuming nematodes. Of these several fungi the one whose morphology and predacious habit were briefly set forth in the text and synoptic illustrations of an earlier summary (**1**, *p. 140, lines 6 to 13; p. 139, fig. 8, A, C*) has made its appearance by far most frequently. In the vicinity of Washington, D. C., it seems to be present on leaf mold wherever in parks on other wooded tracts this material has had opportunity to accumulate in deposits deep enough to retain some moisture during periods of dry weather. When a pinch of leaf mold from such a deposit is added to an agar plate culture already well infested with nematodes, the fungus develops with considerable regularity, giving rise within 5 to 15 days to a growth, which, if ordinarily too scanty to be readily noticed with the naked eye, is fairly conspicuous under a microscope of low magnification.

MORPHOLOGY, DEVELOPMENT, AND DESCRIPTION

The rather meager mycelium thus revealed is composed of originally continuous hyphae approximately equal in width to the hyphae of the more familiar species of *Aphanomyces, Pythium* and *Phytophthora* occurring in diseased vegetable tissues (FIG. 1, A–E). Variations in width are neither frequent nor pronounced, a branch being generally of about the same diameter as the parent filament, and maintaining this diameter without marked diminution well toward its growing tip. Branching occurs at irregular intervals and often at angles approaching a right angle, thus bringing about a characteristically stiff haphazard arrangement of the vege-

tative thallus. The living uninjured hyphae are filled with moderately and uniformly densely granular material, comparable in texture with the protoplasmic contents of the coarser species of *Pythium,* or, perhaps, intermediate in consistency between the protoplasmic material of the genus *Pythium* considered as a whole, and that of the genus *Phytophthora.* The older portions of the mycelium, as in many other filamentous Phycomycetes, undergo progressive evacuation, the retreating contents leaving behind thickish septa at intervals in the empty hyphal envelopes (FIG. 1, C, D). Similar evacuation and deposition of cross-walls takes place also in portions of younger hyphae that have become injured through the protracted and often very violent struggles of captured nematodes (FIG. 1, A).

Capture of prey is effected by means of a yellow adhesive substance similar in appearance to that secreted by the species of *Acaulopage* and *Stylopage* destructive to *Amoebae* (**5**). Operating in conjunction with this material are definitely differentiated structures in the form of largish globose protuberances (FIG. 1, A, *a, b, c*). Apparently these protuberances, unlike the stalked adhesive organs of *Dactylaria condida* (Nees) Sacc., are not formed beforehand to await the passage of suitable animals. As they have been found only where nematodes had already been caught, it would seem that their development follows rather than precedes contact with prey. As far as can be determined the animal is first held fast by a local deposit of a sticky substance secreted by the vegetative hypha at a place not otherwise markedly differentiated. In the course of time, as the animal struggles to free itself, there is thrust through the adhesive cake a lateral process, which, upon reaching the integument of the nematode, expands into the globose protuberance. Evidently the thick yellow wall of the protuberance is copiously covered over with adhesive material; so that with the extensive contact afforded by the expanded surface, the animal is held securely. Frequently two or more protuberances participate in catching a nematode (FIG. 1, A, *a, b*).

Although capture is thus accomplished altogether through adhesion without structural involvement, vigorous eelworms up to 0.5 mm. in length referable to such genera as *Rhabditis, Cephalobus, Diplogaster, Diploscapter, Acrobeles,* and *Acrobeloides,* are

held in spite of violent attempts at liberation. In contrast to most nematode-capturing Hyphomycetes, which in a few hours bring about the death of their prey by severing its organs either through intrusion of a bulbous outgrowth, or, more amazingly, through the strangulating action of constricting loops, the present fungus employs no special means of hastening the end of a captured animal. Extensive invasion is therefore of necessity delayed until the captive, after many hours of exertion, has become somewhat quiescent, in the main apparently from exhaustion. Eventually the animal's integument is perforated, and from the adhesive protuberance is intruded an outgrowth that immediately gives rise to hyphae which soon elongate and ramify to permeate the fleshy interior throughout (FIG. 1, A, *d*). The advance of the endozoic hyphae, which are about half as wide as the mycelial filaments, is everywhere reflected in visible degeneration of the organs and musculature of the eelworm. Gradually the degenerated contents become more and more attenuated, until finally they vanish completely. When this process of absorption is nearing completion, the protoplasm in the haustorial filaments begins to migrate back into the mycelial hypha, laying down rather widely spaced septa in its retreat (FIG. 1, B). As the evacuated haustorial system soon becomes largely if not wholly invisible, in the end only the empty and mostly collapsed integument of the nematode is to be seen adhering to the one or more protuberances, which are now walled off from the haustorial elements they had earlier put forth (FIG. 1, A, *e*).

Once a mycelium attains some size it gives rise to a scattering of tall erect conidiophores. These often conclude their development in producing individually a single large obovoid conidium (FIG. 1, C); but with more abundant nourishment they may continue growth from below the first conidium to produce a second farther on (FIG. 1, D, E), and sometimes after repeated elongation to a third, and occasionally even to a fourth. The conidia at maturity (FIG. 1, L–W) drop off on slight disturbance, and then usually without much delay germinate individually by the production of a stout hypha from the apex or from the zone immediately surrounding the basal hilum (FIG. 1, F–K). Despite the readiness with

which the conidia germinate, attempts at growing the fungus in pure culture on maizemeal agar have not been successful.

The development of the asexual reproductive apparatus manifestly reveals a close correspondence with the homologous phase in the development of the three known amoeba-capturing species of *Stylopage*. Because of the frequent production of more than one conidium on a single conidiophore the parallelism with *S. lepte* Drechsl. is especially complete. The great disparity in dimensions might at first seem to compel interpretation of this close parallelism as being fortuitous. However, the differences in size appear far from impossible to reconcile with close relationship of the two fungi, after consideration of *S. araea* Drechsl. In the latter species are expressed, on the one hand, unquestionable similarities in general dimensions and predacious relationships to *S. lepte;* and, on the other, obvious even if only partial approximation to the nematode-capturing form with respect to stature of conidiophore as well as to size and shape of conidium. The fungus predacious on nematodes is therefore assigned with reasonable assurance to the genus *Stylopage*. A term having reference to its robust stature is deemed appropriate as specific name.

Stylopage hadra sp. nov.

Sparsa; hyphis sterilibus incoloratis, 3.5–5.5 μ crassis, tubera orbicularia flavida glutinosa usque 15 μ lata et longa evolventibus; his tuberibus animalia tenentibus, integumentum perforantibus, hyphas 2–2.5 μ crassas intus evolventibus, carnem exhaurientibus. Hyphae fertiles 200–400 μ altae, basi 4–5.5 crassae, sursum attenuatae, apice 2–2.5 μ crassae, unicum conidium vel interdum usque 3–4 conidia post incrementa repetita ferentes; conidiis incoloratis, obovoideis, 20–45 μ longis, 13–23 latis. Zygosporae ignotae.

Habitat in terra, in materiis plantarum putrescentibus, praecipue in humo silvarum, nematoda diversa usque .5 mm. longa capiens et consumens, prope Washington, D. C.

Sparse; vegetative hyphae colorless, 3.5 to 5.5 μ wide, forming yellow adhesive orbicular protuberances up to 15 μ in diameter, by means of these protuberances holding nematodes, perforating the integument of each, inside producing hyphae 2 to 2.5 μ wide and assimilating the fleshy contents. Conidiophore 200 to 400 μ high, 4 to 5.5 μ wide at the base, tapering upward, 2 to 2.5 μ wide at the tip, bearing a single conidium, or often producing up to 3 or 4 conidia one by one after repeated elongation. Conidia colorless, obovoid, 20 to 45 μ long and 13 to 23 μ wide. Zygospores unknown.

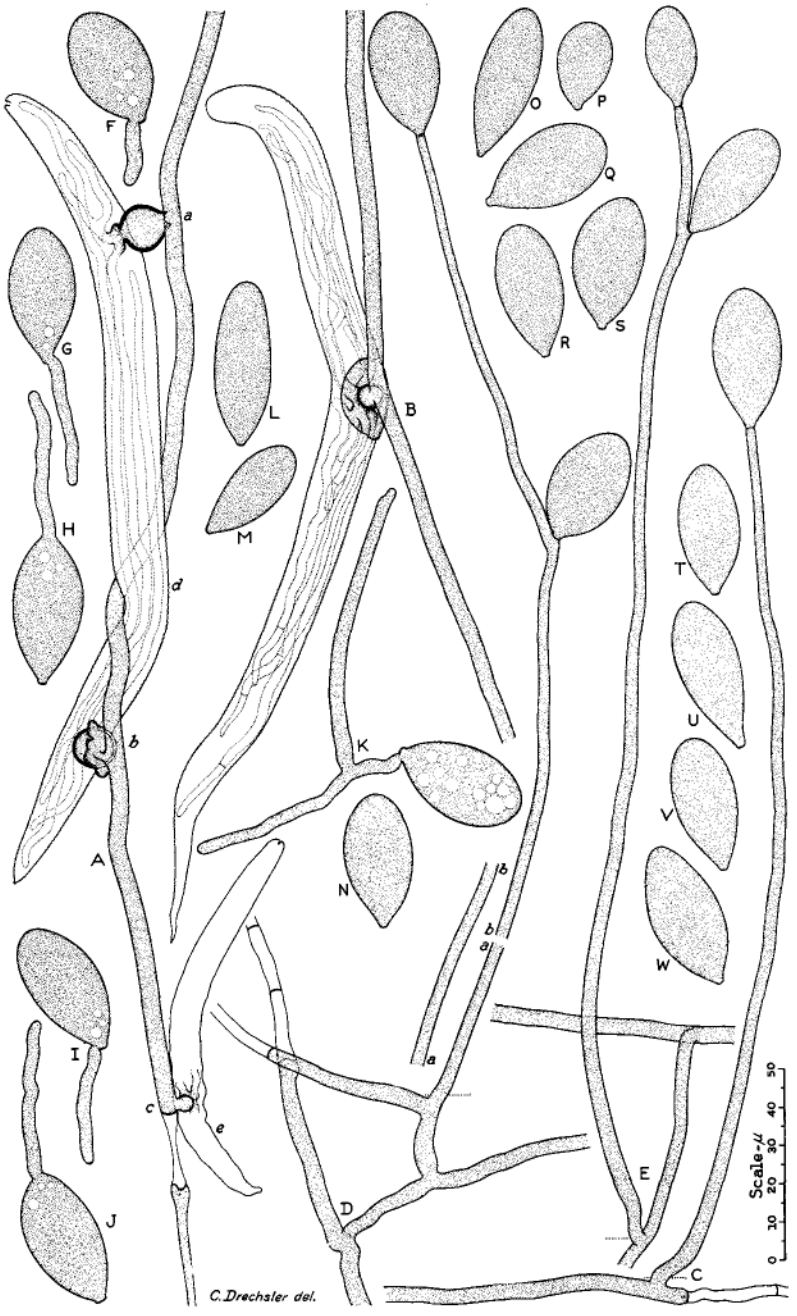

FIG. 1. *Stylopage hadra.*

Occurring in soil, in decaying plant materials but especially abundantly in leaf mold; capturing and consuming nematodes up to .5 mm. long belonging to various species of *Rhabditis, Cephalobus, Diploscapter, Diplogaster, Acrobeles* and *Acrobeloides,* near Washington, D. C.

TAXONOMIC CONSIDERATIONS

The species is apparently not the only representative of its group subsisting on nematodes. Similarities in character of vegetative mycelium and in mode of capture give reason to believe that the predacious fungus with *Pythium*-like intercalary chlamydospores figured earlier (**2**, *fig. 15, D, C*) may be closely related to it. A fungus not hitherto referred to, which likewise captures nematodes through adhesion to a continuous mycelium, and which on a short prolongation from the union of two branches coming from separate hyphae gives rise to a zygospore about 15 μ in diameter within a closely fitting zygosporangial wall irregularly sculptured with yellow incrustation, undoubtedly represents another member of the group. From these two species, which it is hoped may be more fully discussed after their asexual stages are more completely known, *Stylopage hadra* differs in the moderate and sometimes even rather meager development of its mycelium. This inextensive development finds a plausible ecological explanation in the evident adaptation of the fungus for the capture of the larger and correspondingly more vigorous nematodes. The brisk locomotor movements of these animals insures, on artificial substrata, and presumably also in nature, adequate encounter with prey notwithstanding the moderate extension of the predacious apparatus. Once a relatively powerful animal has been engaged, however, physical sturdiness is required both to hold it securely and to endure the inevitable violence without incurring too severe injury. For although the predacious Hyphomycetes suffer little damage when their organs of capture, together often with connected portions of mycelium, are uprooted, a phycomycete would obviously be more seriously affected if portions of its non-septate thallus were constantly being torn away. Indeed, in spite of the considerable measure of sturdiness attained at the expense of a wider extension, local damage is very frequently plainly evident.

The somewhat inextensive mycelial development, whatever its explanation, brings about an appearance vaguely suggestive of some members of the Entomophthorales. This suggestiveness is sustained in the large size of the conidia, and their similarity in shape to the ovoid conidia described and figured by Thaxter (**11**) in the presentations more particularly of his *Empusa americana, E. montana,* and *E. echinospora.* Occasionally, too, the hypha of germination from a conidium gives rise to a second conidium with so little intervention of a purely vegetative phase that the repetitional development of secondary conidia frequent in many species of the Entomophthorales is approximated. As such repetitional development is fairly widespread among various groups of fungi, occurring for example, in conspicuous measure in many of the predacious hyphomycetous forms referable to *Monacrosporium* and *Dactylaria,* its importance as an indication of affinity hardly merits emphasis. Yet in the absence of all intimate parallelism with any other of the older established groups within the Zygomycetes, the suggestive correspondencies with the insectivorous Entomophthorales, among which a semi-predacious habit of fixing their enfeebled prey to the substratum by means of adhesive substance is frequent, are at least deserving of mention.

Its frequent occurrence in leaf mold and in similar nematode-infested decaying materials, together with the large dimensions of its conidia and conidiophores, would make it seem unlikely that *Stylopage hadra* could have remained unobserved by the numerous mycologists that have devoted themselves to the study of fungi appearing on animal refuse and on decomposing plant remains. Once observed, it might be supposed that the fungus would almost certainly have evoked more than ordinary interest by virtue of morphological features, which, while obviously pertaining to a member of the Phycomycetes, do not conform to those of any of the groups long recognized in that class. That such interest failed to develop may perhaps be attributed less to the fungus having been overlooked than to its probably having been confused with nematode-capturing Hyphomycetes, and of these more particularly with two forms with which it appears in almost habitual association: the fungus with swollen 3-septate conidia and constricting loops figured previously (**3**, *fig. 17, A, C*), and possibly

to be identified as *Monacrosporium elegans* Oud. (**8**); and the fungus with somewhat fusiform 4-septate conidia and stalked adhesive knob-cells (**1**, *fig. 7, A, B, C*) corresponding well to Grove's (**6**) description of his *Dactylella ellipsospora* (**4**). Very curiously, whether through morphological accident, or, more probably, through what would seem to constitute a remarkable instance of convergence resulting from similarity in predacious relationship, the two Hyphomycetes mentioned show approximate similarity to *S. hadra* in the dimensions and erect posture of their conidiophores, as well as in the dimensions and shape of their conidia. Their conidiophores, moreover, like the homologous structures of predacious Hyphomycetes generally, show few septa, and often do not develop these until a relatively late stage. On closer inspection of material in agar cultures, the presence of numerous cross-walls dividing adjacent living cells in the mycelial filaments, and the nearly homogeneous consistency of the protoplasm surrounding the well defined largish vacuoles, are easily recognized as features alien to the fungus under consideration. But when the vegetative mycelium is concealed in an opaque natural substratum, the similarities in habit of the erect aerial parts are brought into deceptively strong relief; so that the conidial apparatus of the Phycomycete might then readily be mistaken for immature apparatus of either of the two Hyphomycetes often accompanying it.

In 1851 Preuss (**9**) described and figured under the binomial *Menispora ellipsospora* a fungus he found on decaying needles of Scotch fir where it formed thinly effuse growths consisting of white erect non-septate conidiophores bearing individually a single terminal large elliptical spore. According to the description a large oil globule occupied the entire lumen in the median portion of the conidium, which thus came to reveal toward each of its ends a curved contour extending entirely across its width. No mention was made of septa occurring in the conidia of either this species or of *Menispora pyriformis,* which Preuss described at the same time; nor were such septa shown in any of the accompanying figures. The non-septate condition ascribed to the conidia of *Menispora ellipsospora* and *Menispora pyriformis* was emphasized by Oudemans (**8**) in distinguishing his *Monacrosporium elegans*

from these species despite the similarity in habit clearly recognized by him. Grove (**6**) on the other hand considered *Menispora ellipsospora* identical with his *Dactylella ellipsospora,* and therefore cited Preuss' binomial as a synonym. Later Saccardo (**10**, *p. 194*) transferred also *Menispora pyriformis* to the genus *Dactylella.* Lindau (**7**, *p. 411–412*), though adopting the transfers thus made, commented on the uncertain status of *D. pyriformis,* stating that not even the condition of the conidia, whether continuous or septate, was definitely known.

Since in Preuss' account of *Menispora pyriformis,* at least the conidiophores were described as sometimes containing septa, Lindau's doubts might with even more justification have been directed at *Menispora ellipsospora.* Certainly in its main features the original description of the latter fits *Stylopage hadra* better than *Dactylella ellipsospora* or, for that matter, than any similarly septate hyphomycetous form. However, vacuoles of any considerable size are not usually discerned in the conidia of *S. hadra,* nor in those of the three amoeba-capturing species of *Stylopage;* whereas, very large vacuoles regularly are found in the inflated median cells in the well matured conidia of various predacious Hyphomycetes. In any case the vacuolate condition figured by Preuss, which would perhaps need to be considered rather extreme even for a species of *Trichothecium, Monacrosporium,* or *Dactylaria,* appears very definitely foreign to the nematode-capturing phycomycete herein described. This difference in the internal structure of the conidium precludes identification of the fungus with *Menispora ellipsospora* hardly less decisively than the presumptive difference in condition of the conidiophore relative to septation precludes identification with *Menispora pyriformis.* Apart from the two binomials mentioned, the established application of the genus *Menispora* to a distinctive group in the Dematiaceae obviates the possibility of further nomenclatorial or taxonomic involvement with *Stylopage.*

LITERATURE CITED

1. **Drechsler, C.** Morphological diversity among fungi capturing and destroying nematodes. Jour. Wash. Acad. Sci. **23**: 138–141. 1933.
2. ——. Morphological features of some more fungi that capture and kill nematodes. Jour. Wash. Acad. Sci. **23**: 267–270. 1933.

3. ——. Several more fungi that prey on nematodes. Jour. Wash. Acad. Sci. **23**: 355–357. 1933.
4. ——. Organs of capture in some fungi preying on nematodes. Mycologia **26**: 135–144. 1934.
5. ——. Some non-catenulate conidial phycomycetes preying on terricolous *Amoebae*. Mycologia **27**: 1935.
6. **Grove, W. B.** New or noteworthy fungi:—Part III. Jour. Bot. **24**: 129–137, 197–206. 1886.
7. **Lindau, G.** Die Pilze Deutschlands, Oesterreichs und der Schweiz. VIII. Abteilung: Fungi imperfecti: Hyphomycetes (erste Hälfte). In Rabenh. Krypt.-Fl. Ed. 2, 1^8: 1904–1907.
8. **Oudemans, C. A. J. A.** Aanwinsten voor de flora mycologica van Nederland, IX en X. Nederl. Kruidk. Arch. II. **4**: 203–278. 1885.
9. **Preuss, C. G.** Die Pilze Deutschlands. *In* Sturm, Deutsch. Fl. III. Abtheil. **6**(29, 30): 93–96. 1851.
10. **Saccardo, P. A.** Syll. Fung. **4**. 1886.
11. **Thaxter, R.** The Entomophthoreae of the United States. Mem. Boston Soc. Nat. Hist. **4**: 133–201. 1888.

EXPLANATION OF FIGURE

Fig. 1. *Stylopage hadra;* drawn with aid of camera lucida at a uniform magnification; × 500. *A*, Portion of hypha on which have been developed three adhesive protuberances, *a–c*; two of which, *a* and *b*, have been operative in the capture and invasion of a rather large nematode, *d*, referable apparently to *Acrobeloides Bütschlii* (De Man, 1885) Thorne, 1925; and the third, *c*, has captured a small nematode evidently of the same species, depleted its contents, and withdrawn the protoplasm from the haustorial elements by means of which the depletion was accomplished. *B*, Portion of hypha with an adhesive protuberance, on which has been captured a nematode belonging to *Cephalobus* sp.; the eelworm is thoroughly permeated with haustorial hyphae, from which, following depletion of the fleshy tissues, the protoplasmic contents are being withdrawn, as is indicated by the appearance of septa near the hyphal ends. *C*, Portion of prostrate hypha bearing a relatively short conidiophore which has given rise to a single conidium. *D*, Portion of mycelium, and arising from it, a conidiophore whereon two conidia have been produced successively; owing to its length the conidiophore is shown in sections, on which *a* and *b* represent corresponding points. *E*, Portion of mycelium from which arises a conidiophore bearing two conidia. *F–K*, Germinating conidia. *L–W*, Conidia showing variations in size and shape.