## A NEW MUCEDINACEOUS FUNGUS CAPTUR-ING AND CONSUMING AMOEBA VERRUCOSA

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(WITH 1 TEXT FIGURE)

In an earlier summary setting forth the morphological features of some fungi that had been found capturing and consuming Amoebae in agar plate cultures started from plantings of diseased rootlets and other decaying vegetable materials, was included a brief characterization (3, p. 200, lines 19 to 34; p. 201, fig. 1, A, B) of a septate species predacious on an Amoeba then provisionally determined as Amoeba verrucosa Ehrenb. The determination can advantageously be retained, since the protozoan, in its relatively large dimensions, its single ellipsoidal nucleus, its slow movement, and its extraordinarily thick pellicle, agrees well with Leidv's description (10) of A. verrucosa. Though the animal might also be referred to A. terricola Ehrenb. in the broad sense in which that species was understood by Penard (14), it is apparently not identical with any one of the three separate forms to which I have elsewhere (6) applied this binomial together with the numerals I, II, and III, respectively. Of these three forms, it most nearly resembles the one designated as A. terricola II, being distinguished therefrom, however, by a different distribution of dark material within the nucleus, and by a much greater thickness of the pellicle (FIG. 1, A). It has been found to develop rather rarely on plate cultures, probably requiring conditions for multiplication not often provided by agar substrata. Owing apparently to this infrequent development, the septate fungus that lives, as far as has been observed, entirely by the capture of the protozoan in question, has put in appearance only a few times.

The mycelium on a transparent substratum like maizemeal agar is similar in general aspect to the mycelium of *Pedilospora dacty-lopaga* Drechsl., a mucedinaceous fungus known to subsist on shelled rhizopods (5). It reveals a similar sparsely effuse habit

with approximately equally meager branching. The hyphae, which follow rather straightforward courses, in large part on the surface of the substratum, while somewhat wider than the hyphae of P. dactylopaga, contain like these, cross-walls separating adjacent living cells, which are filled, except for occasional vacuoles, with protoplasm of fairly homogeneous consistency. At irregular intervals on the hyphae are borne prolate ellipsoidal protuberances that although slightly longer and noticeably more obese obviously correspond to the digitate or elongate-elliptical protuberances of P. dactylopaga both in morphology and in function.

An animal on coming in contact with one of the protuberances remains adhering to it, evidently being held by means of glutinous material. Whether the captive makes any effort to escape, apart from movements normally entailed in locomotion, remains uncertain. In any case the substantial pellicle of the animal is perforated when the protuberance puts forth a filamentous outgrowth that penetrates deeply into the protoplasmic interior, at the same time widening gradually in its course. On attaining definitive length, the outgrowth branches dichotomously; the resulting elements very soon bifurcating again (FIG. 1, B), often in planes at right angles to the primary dichotomy (FIG. 1, A). Repeated dichotomous branching follows until the central portion of the animal is occupied by a rather elaborately ramifying apparatus (3, fig. 1, B). This apparatus at first is continuous but later becomes divided by septa into a number of variously shaped segments (Fig. 1, C, a). From these segments, on the depletion of the animal's protoplasmic materials, are put forth narrow hyphae that pass out through the pellicle to extend the predacious mycelium or to give rise to conidiophores and conidia. The pellicle eventually collapses, and persists long as a wrinkled mass testifying to the destructive efficacy of the fungus.

Usually after a few animals have been consumed, conidiophores are produced in small groups scattered here and there on the substratum (Fig. 1, D; 3, fig. 1, A). Relatively short and sparingly branched, they present an atrophied appearance little reminiscent of the stately conidiophores characteristic of most of the nematodecapturing species of *Trichothecium*, *Arthrobotrys*, *Dactylella*, *Monacrosporium* and *Dactylaria*. And the narrow conidia (Fig.

1, D, a; E, a-e; 3, fig. 1, A) borne on these meager reproductive hyphae are correspondingly little suggestive of the conidia produced by the more robust of the hyphomycetous forms preying habitually on eelworms. The empty distal appendage present on the conidium finds no homologue among any of the other Hyphomycetes now known to be predacious, providing instead a striking parallelism with some Amoeba-capturing Phycomycetes described elsewhere (7) as members of the genus Acaulopage.

Yet the dissimilarities in outward form just noted are hardly such as to preclude a fairly close taxonomic relationship. In the group of Amoeba-capturing Phycomycetes, species with well developed conidial appendages are most obviously closely connected with species having only rudimentary appendages, and even with species altogether devoid of such modifications. If the conidiophores of the fungus under consideration are unimpressive in comparison with those of Pedilospora dactylopaga, they would seem, judging from Höhnel's original account (9), quite comparable with the conidiophores of P. parasitans, a form whose intimate relationship to P. dactylopaga cannot readily be questioned. The thoroughgoing resemblance to the latter species with respect to mycelial characters, may therefore be presumed with a fair degree of certainty to indicate membership in the group of closely interrelated predacious Hyphomycetes most familiarly exemplified in Arthrobotrys oligospora Fres.

In considering an appropriate disposition of the fungus, this presumptive relationship deserves to be taken into account. If the conidium is regarded as being composed of two cells, it would be difficult to avoid assignment to *Trichothecium*, of which genus three established species, *T. obovatum* (Berk.) Sacc., *T. piriferum* (Fries) Sacc., and *T. inaequale* Mass. & Salm., would seem from their resemblance in habitat, habit, and morphology to the nematode-capturing form figured earlier (2, fig. 10, A, C), to represent members of the same predacious series. However, with respect to shape of conidium and to position of the septum within the conidium, these species diverge markedly from the one under discussion. Assignment to *Trichothecium* is further discouraged from the fact that this genus has in large part become familiar to mycologists generally through *T. roseum* Link, a widespread sapro-

phyte and plant parasite that has revealed no predacious tendencies whatever under experimental conditions, and that in morphology is plainly alien to the predacious series.

A more apt disposition in the genus Dactylella or Monacrosporium is feasible if, as seems permissible, the empty distal conidial appendage is construed as a third cell. Both these genera were erected on species that may rather safely be presumed to belong to the predacious series: D. minuta Grove (8) presenting strong similarities in habitat, habit, and morphology to known nematodecapturing forms; while the description of M. elegans Oud. (13) except for a somewhat greater length of conidium, applies very well to one of the most abundant and widespread of nematode-capturing forms figured earlier (4, fig. 17, A, C). Like the three established species of Trichothecium mentioned, these broad-spored type-species show little family resemblance to the Amoeba-capturing fungus; nor is such resemblance greatly evident in the broadspored nematode-capturing D. ellipsospora Grove (= M. leporinum Bubák), or in the similarly broad-spored and presumably similarly predacious D. rhombospora Grove and M. ovatum Petch (15). A closer approximation in general make-up is apparent in the allied forms with narrower conidia, including more particularly D. minuta var. fusiformis Grove, M. subtile Oud. M. oxysporum Sacc. & March., and M. sarcopodioides (Harz) Berl. & Vogl., which from their resemblance in habitat, habit and morphology to the somewhat Fusarium-like nematode-capturing fungus figured earlier (4, fig. 16, A-C) must be reckoned among the presumptive members of the predacious series.

Saccardo (17, p. 193) early recognized the affinity between Dactylella and Monacrosporium, but nevertheless held the latter genus distinct from the former because of the presence of copious mycelium. Lindau (11, p. 412) properly regarded the distinction based on the presence of copious mycelium as in itself insignificant, yet adopted it in the belief that whereas the species of Monacrosporium probably constitute conidial stages of the coprophilous Sordariaceae, Dactylella might more likely be referable to other Pyrenomycetes. An understanding of the predacious habits of the fungi in question places in a different light the substratum relationships on which Lindau's tentative assumption of divergent

pleomorphic connections must have been founded. Moreover, since in pure cultures of such of the predacious forms under discussion as have been isolated, the relative abundance of aerial mycelium is often hardly of sufficient distinctiveness to merit attention in the separation of species, its utility for the separation of genera seems exceedingly doubtful.

The equivalence of the two genera was disturbed more recently when Boedijn (1) extended the application of *Monacrosporium* by describing under the name *M. megasporum* a fungus producing conidia somewhat similar to those of *M. elegans*, but bearing them in closely capitate arrangement. However, as the fungus, evidently an authentic member of the predacious series, answers exactly to the definition of the genus *Dactylaria*, within which it would have found at least one closely related predacious congener in *D. candida* (Nees) Sacc., and perhaps others in *D. acicularis* Rostrup (16) and *D. pulchra* Linder (12), the extension seems hardly possible of adoption.

In assigning the *Amoeba*-capturing fungus, considerations of priority dictate a preference for *Dactylella*, erected in 1884, over *Monacrosporium*, proposed in 1885 (not apparently in 1884 as is often stated). A term having reference to the knoblike organs of capture is deemed appropriate as specific name.

## Dactylella tylopaga sp. nov.

Mycelium sparsum, repens, parce ramosum; hyphis sterilibus  $1.5{\text -}3~\mu$  crassis, hyalinis, mediocriter septatis, hinc inde tubera ovoidea vel ellipsoidea 4–7.5  $\mu$  longa,  $3.5{\text -}5.5~\mu$  crassa, verisimiliter glutinosa, primo hyalina mox flavida emittentibus, his tuberibus animalia capientibus, pelliculam perforantibus, ramum intus evolventibus; ramo primo hyalino, mox saepe flavente, ad centrum animalium penetrante, sursum paulatim latescente, ramos  $2.5{\text -}6~\mu$  crassos repetite dichotomos mox septatos gerente; his ramis protoplasma consumentibus, hyphas mycelii extus evolventibus. Hyphae fertiles paucae, hyalinae, assurgentes, saepe plus minusve ramosae,  $15{\text -}50~\mu$  altae, basi  $3{\text -}5~\mu$  crassae, sursum attenuatae, apice  $1{\text -}1.3~\mu$  crassae, conidia singulatim gerentes; conidiis hyalinis, in totum  $30{\text -}50~\mu$  longis, parte supera eorundem vacua itaque appendicula marcida  $13{\text -}23~\mu$  longa, basi  $1{\text -}1.5~\mu$  lata, sursum attenuata, apice  $.5{\text -}1~\mu$  lata facta; parte infera in cellulas duas subaequales, protoplasmatis repletas,  $9{\text -}17~\mu$  longas,  $2.5{\text -}3.5~\mu$  latas, divisa.

Habitat in humo silvarum Amoebam verrucosam capiens et consumens prope Washington, D. C.

Mycelium sparse, creeping, meagerly branched; vegetative hyphae hyaline, 1.5 to 3  $\mu$  wide, moderately septate, at intervals bear-

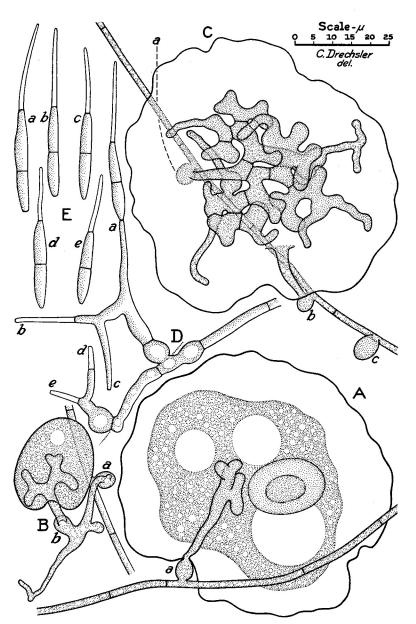


Fig. 1. Dactylella tylopaga.

ing ovoid or ellipsoid, apparently adhesive, and ultimately yellowish protuberances, 4 to 7.5  $\mu$  long and 3.5 to 5.5  $\mu$  wide; by means of these protuberances capturing animals, perforating the pellicle of each and developing a branch inside; the branch at first hyaline, often turning yellowish after penetrating toward the center of the animal while widening in its course, then giving rise to repeatedly dichotomous branches  $2.5-6 \mu$  wide, which, though originally continuous, after consuming the animal's protoplasm finally become septate and emit vegetative filaments. Conidiophores few, hyaline, ascending, often more or less branched, 15 to  $50 \mu$  high, individually 3 to  $5\mu$  wide at the base, tapering upward, 1 to  $1.3\mu$ wide at the tip. Conidia borne singly, 30 to  $50 \mu$  in total length, the upper part of each empty and accordingly present as a withered appendage 13 to 23  $\mu$  long, 1 to 1.5  $\mu$  wide at the base, tapering upward to an apical width of .5 to  $1 \mu$ ; the lower part divided into two subequal cells filled with protoplasm, each 9 to 17  $\mu$  long and 2.5 to  $3.5 \mu$  wide.

Occurring in leaf mold, capturing and consuming Amoeba verrucosa near Washington, D. C.

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## EXPLANATION OF FIGURE

Fig. 1. Dactylella tylopaga drawn with aid of camera lucida at a uniform magnification; × 1000. A, Portion of hypha with an adhesive protuberance, a, from which a widening branch has been intruded into a captured specimen of Amoeba verrucosa. B. Portion of hypha with an adhesive protuberance, a, that has proliferated an irregular outgrowth bearing a second protuberance, b, from which a dichotomously branching process has been thrust into a captured specimen of A. verrucosa. C, Portion of hypha with three adhesive protuberances, a-c, whereof two, a and b, have captured a specimen of A. verrucosa, invaded it extensively, and completely consumed its contents, leaving only the thick empty pellicle; septa have been inserted in the dichotomously branching system, and some of the delimited segments have begun to proliferate ordinary hyphae. (For the sake of clearness the branching development from protuberance b is omitted.) D, Superficial hypha with two conidiophores, one with three branches, a-c, the other with two branches, a and b; branch a being filled with protoplasm and bearing a mature conidium; branches b, d, and e having been partly evacuated. E, Mature conidia, a-e, showing variations in size and shape.