BOTANY.—A Fusarium-like species of Dactylella capturing and consuming testaceous rhizopods.¹ Charles Drechsler, Division of Fruit and Vegetable Crops and Diseases, Bureau of Plant Industry.

Agar plate cultures, started from diseased rootlets or other decaying plant materials that previously have been in prolonged contact with the soil, usually allow the gradual multiplication of various species of testaceous rhizopods, some of which often attain large numbers in the course of two or three weeks. Once a population of these animals has become established, it is in general less subject to rapid decline than the populations of animal types multiplying more

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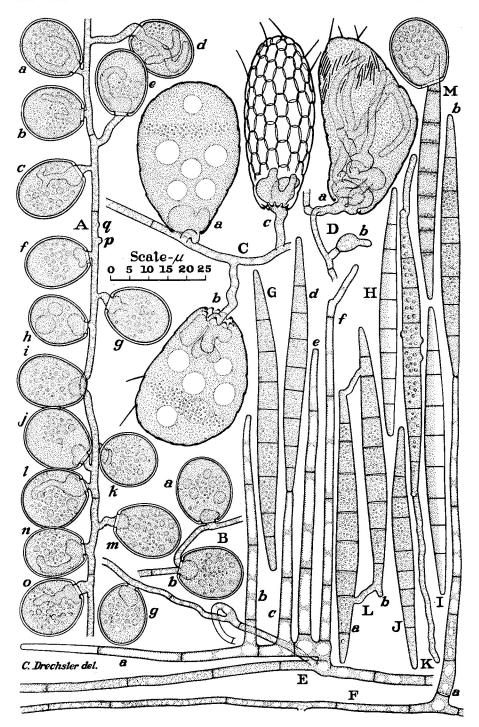


Fig. 1.—Dactylella passalopaga. For explanation, see opposite page.

rapidly in agar cultures, including, for example, many species of nematodes and many of the smaller amoebae. This lesser tendency toward abrupt reduction in number of living individuals, appears in considerable measure to be due to infrequence of destruction by parasitic or predacious fungi. In view of the disasters often overtaking populations of amoebae from the development of members of the Zoopagaceae (4, 5, 7) it might be expected that shelled rhizopods, whose protoplasmic bodies are necessarily partly protruded for feeding and locomotion, would suffer serious depredations from the same group of conidial Phycomycetes. Yet only two members of the Zoopagaceae, which will be described elsewhere, have so far been found to subsist on testaceous rhizopods. Difflugia globulosa Duj. and Trinema enchelys Ehrenb. were shown in an earlier paper (3) to be captured and consumed by Pedilospora dactylopaga Drechsl., a fungus referable to a quite different predacious series. This series, consisting of hyphomycetous forms belonging mostly to the genera Trichothecium, Arthrobotrys, Dactylaria and Dactylella (including Monacrosporium), is destructive mainly to nematodes. The biological relationship of P. dactylopaga would seem, therefore, to be a somewhat unusual one; as would also the similar relationship of an apparently allied fungus recently observed to subsist by the capture of two other species of shelled rhizopods.

The scanty vegetative mycelium of the fungus in question might readily be overlooked in a mixture of microorganisms but for the conspicuous alignment of captured prey in two ranks, with oral ends directed toward one another (Fig. 1, A-D). Because of the large numbers in which it develops in old agar plate cultures, the smaller

Fig. 1.—Dactylella passalopaga, drawn from material developed in mixed culture on maizemeal agar, with the aid of a camera lucida, at a uniform magnification; ×1000. A.—Portion of hypha on which fifteen specimens of Geococcus vulgaris, a-o, have been captured; the two slight protuberances p and q, possibly representing predactions modifications. B.—A short portion of hypha with two captured specimens of G. vulgaris; one, a, having been taken without positional disturbance of the filament; the other, b, having drawn the hypha partly into its mouth as in feeding. C.—Portion of hypha with three specimens of $Euglypha\ laevis$, each held by means of a lobed predactions gag; two of the animals, a and b, being shown mainly in optical section, the other, c, mainly in surface view. D.—Portion of hypha with (a) a captured specimen of E. laevis, within which are shown assimilative hyphae arising from the lobes of the predacious gag; and (b) an enlargement representing probably an outgrowth from which a rhizopod managed to escape. E.—Portion of mycelium showing an old, partly evacuated, prostrate conidiophore, a, that has given rise to four younger erect conidiophores, three of which, b, c and e, have each produced a single terminal conidium, and the other, f, in addition, a second conidium on the oblique distal prolongation; all the conidiophores being shown denuded except c, whereon conidium d is shown in position. F.—Portion of hypha with a conidiophore, a, bearing a conidium, b. G. H, I, J.—Detached conidia. L.—Two germinating conidia, a and b, the single germ tube from each having fused with a segment of the other conidium. M.—A conidium showing early predacious development following partial ingestion by a specimen of G. vulgaris.

rhizopod having a broadly ovoid, smooth test slightly thickened about the circular mouth, and otherwise corresponding well to Francé's description (8) of his Geococcus vulgaris, provides an especially striking display. Frequently the individual hyphae are beset for long stretches with the ovoid animals, here and there at such close intervals that the test of one will be in contact with that of its neighbor on either side (Fig. 1, A). A somewhat less abundant but still impressive display of predacious activity is furnished in the capture of an ovoid or often somewhat unsymmetrically bursiform species of Euglypha, measuring usually 35 to 50μ in length and provided with aperture scales noticeably thickened at their slightly incurved apices (Fig. 1, C, D). In morphology the animal evidently corresponds most closely to the description of E. laevis Perty as given in the accounts of Penard (13) and of Cash and Wailes (1); for though in some individuals a few rudimentary bristles may be present at the aboral end, a completely glabrous condition is by far more common.

Examination of tracts of mycelial filament free of the two species of rhizopods mentioned, has not revealed any distinct structure to which a special function in the capture of prey could be assigned. Some slight protuberances to be found now and then on vegetative hyphae (Fig. (1, A, p, q), or even on germinating conidia (Fig. 1, K), may possibly represent predacious modifications, but their meager differentiation is hardly at all suggestive of any important role. The swollen parts, sessile or stalked (Fig. 1, D, b), that are occasionally seen and that in some degree resemble the well defined predactious organs of Dactylella tylopaga Drechsl. (6) and of Pedilospora dactylopaga, are very similar to the processes formed after prey has been engaged, and in all probability represent outgrowths from which animals have managed to escape. An absence of definite organs of capture previous to encounter with prey, is unusual among the predactious Hyphomycetes, the only other example of such absence known in this series being found in the nematode-capturing species of Dactylella with quadrilobate conidia figured in another paper (2: Fig. 9, A, C).

The necessity for special organs to initiate capture is apparently obviated by the feeding habits of the animals on which the fungus preys. As *Geococcus vulgaris* is a relatively small testaceous rhizopod with a proportionately small aperture, it might be expected that feeding would be restricted to objects like bacteria and the more minute of fungus spores. Such limitation, however, does not actually prevail, for often the animal obtains its nourishment from objects as formidable as the oospore of *Pythium ultimum* Trow, which not only

exceeds it in size, but is surrounded, moreover, by the thick and thoroughly substantial oospore wall. Oospores of P. ultimum and of many congeneric forms are, of course, consumed by other rhizopods flourishing in agar plate cultures: some of the larger species of Amoeba often enveloping a specimen until the durable wall is broken down and the protoplasmic material assimilated; while the robust testaceous Arcella vulgaris Ehrenb., with its capacious oral aperture, often "imports" one specimen after another, so that three or four oospores in various stages of digestion may be seen inside. Neither of these more usual modes of ingestion is followed by G. vulgaris, which instead, applies its mouth flush to the oospore wall, calks the zone of contact with a yellow secretion apparently identical with the substance closing up the test during periods of encystment, and gradually perforates the delimited portion of spore wall, probably by some sort of digestive action. Once communication is established with the interior of the oospore, the granular contents, now visibly degenerating, are drawn into the test of the animal,—the movement of material appearing much the same as in the sucking of an egg.

When mycelium is attacked by Geococcus vulgaris the delay incident to the resistance of the thick oospore wall is obviated, and the sucking action becomes evident while the filament is still intact. No exception is made of the hyphae belonging to the predacious fungus herein under consideration, as a filament of this species is often to be seen drawn into the mouth of an animal (Fig. 1, A, i; B, b). To such undiscriminating voracity the fungus responds by rapidly proliferating from the partly ingested portion a bulbous outgrowth slightly larger than the oral aperture, so that the rhizopod is securely held. Indeed, more generally, the fungus meets the animal half way, by putting forth the expanded outgrowth before suffering any physical change itself. In many instances the expanded part is nearly sessile on the filament (Fig. 1, A, a, b, c, f, g, h, j, k, l, n, o; B, a), but in other instances it is formed on a short branch (Fig. 1, A, d, e, m). The rangier connection apparently is brought about when the animal, after making contact with the filament, moves away, and is pursued through elongation of the outgrowth until the expanded part has attained a width making further movement impossible.

The same sequence of events is followed also in the capture of *Euglypha laevis*. Because of the larger mouth of this rhizopod, a correspondingly bulkier gag is required to effect capture; the additional requirement being supplied through the proliferation of a number of expanded lobes (Fig. 1, C) in place of the simple distended part. Like-

wise, as might be expected, the assimilative hyphae thrust into the interior of the larger animal (Fig. 1, D, a) are longer and more numerous than those of the meager haustorial apparatus discernible, mostly with difficulty, in some specimens of *Geococcus vulgaris*. The exhaustion of materials from either rhizopod takes place without causing any sudden conspicuous change in appearance of the sarcode, the protoplasmic contents merely becoming more and more tenuous, much like the protoplasm of amoebae attacked by members of the Zoopagaceae, or like the contents of *Amoeba verrucosa* Ehrenb. attacked by *Dactylella tylopaga*.

After a mycelium has been nourished for some time, erect conidiophores arise singly (Fig. 1, F, a) or in small groups (Fig. 1, E, b, c, e, f) from the rangy prostrate filaments. They show unmistakable similarity to the homologous structures of Pedilospora dactylopaga, though noticeably stouter and shorter in stature. When growing in mixed culture in the presence of bacteria, the conidiophore usually concludes its development with the production of a single rather massive terminal conidium (Fig. 1, E, d; F, b). In some instances, however, it grows out from below the attachment of the first spore to produce a second farther on (Fig. 1, E, f); or, fairly often, it gives rise through lateral branching to one or more secondary conidiophores, under the increasing weight of which it is pressed down into a prostrate position. (Fig. 1, E, a). Though the conidium in its septation and elongatefusoid shape bears a suggestive resemblance to the conidia of some species of Fusarium, it lacks the distinctive basal modification frequent in that genus, and is never borne on a sporodochium (Fig. 1, G-J). Germination takes place readily, by the production usually of two germ tubes, one from each end (Fig. 1, K). Anastomoses of germ tubes with detached conidia (Fig. 1, L, a, b) or with mycelial filaments, and, indeed, vegetative fusions generally, are frequent in this species, as in other members of the predactious series of Hyphomycetes. Occasionally newly detached conidia are partly ingested by Geococcus vulgaris (Fig. 1, M), so that at times vegetative germination may be preceded by predacious development.

The morphology of its conidial apparatus makes the fungus clearly eligible for inclusion in the genus Dactylella Grove. Of the several forms described in this genus, D. minuta var. fusiformis Grove (9) offers apparently the closest resemblance, though the greater diameter (7 to 9μ) and more abundant septation (9 to 12) ascribed to the conidia of the British species, would seem to exclude any strong likelihood of identity. Similarity in varying degree is recognizable also

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when comparison is extended to the several species with narrow conidia that have been compiled in the genus Monacrosporium Oud. Thus M. subtile, as described and figured by Oudemans (12), approaches the predacious form under consideration in diameter of conidium, but presents fairly decisive differences in the clavate shape and more abundant septation of that structure. The pronouncedly clavate shape illustrated in Harz's original publication (10), together with the inferior length (35 to 38μ) and less abundant (3 to 5) septation, also sufficiently distinguishes the conidia of M. sarcopodioides (Harz) Berl. et Volg. On the other hand, the conidia of M. oxysporum Sacc. and March. (11) are described as being symmetrically spindleshaped; yet their very acutely pointed ends emphasized in Marchal's drawings, their greater length (96 to 105μ) and width (9 to 10.5μ), and their more frequent (10 to 12) septation, not to mention the greater length (120 to 170 μ) and width (4 to 5μ) of the supporting conidiophores, constitute details not reconcilable with the asexual reproductive apparatus found in my cultures.

The fungus so curiously adapted to prey on small-mouthed testaceous rhizopods is believed, therefore, to represent a new species, for which a name having reference to the gaglike predacious structure would seem appropriate.

Dactylella passalopaga sp. nov.

Mycelium sparsum, repens, parce ramosum; hyphis sterilibus $1.2-2.7\mu$ crassis, hyalinis, mediocriter septatis, ex latere in ores animalium ramulum trudentibus qui intus tumet et sic animalia tenet; hyphis fertilibus paucis, solitariis vel parum aggregatis, hyalinis, plus minusve erectis, saepe 2-5-septatis, $40-110\mu$ altis, basi $2.8-4\mu$ crassis, sursum attenuatis, apice $1.2-1.8\mu$ crassis, unicum conidium vel interdum secundum post incrementum ferentibus. Conidia hyalina, elongato-fusoidea, utrimque obtuse rotundata, $60-80\mu$ longa, $4.5-6\mu$ crassa, 6-8-septata.

Habitat in radicibus plantarum putrescentibus, in terra, saepe in humo silvarum, Geococcum vulgarem et Euglypham laevem capiens et consumens, prope Beltsville, Maryland.

Mycelium sparse, creeping, rather scantily branched; the vegetative hyphae 1.2 to 2.7μ wide, hyaline, septate at moderate distances, capturing some species of small-mouthed testaceous rhizopods by thrusting into the mouth of the individual animal a short lateral branch that expands inside to form a simple or lobed enlargement wider than the aperture; conidiophores usually few in number, scattered singly or in small groups, hyaline, more or less erect, mostly 2 to 5 (average 3.3) times septate, 40 to 110μ (average 69μ) in height, 2.8 to 4μ (average 3.3μ) wide at the base, tapering upward to an apical diameter of 1.2 to 1.8μ , bearing usually a single conidium and sometimes a second one on a distal prolongation originating immediately below the base of the first. Conidia hyaline, elongated spindle-shaped,

bluntly rounded at both ends, 60 to 80μ (average 69μ) long, 4.5 to 6μ wide, and divided usually by 6 to 8 (average 7.7) cross-walls.

Capturing and consuming Geococcus vulgaris and Euglypha laevis, it occurs in decaying plant roots, in soil, and especially often in leaf mold, near Beltsville, Maryland.

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