

TWO HYPHOMYCETES PARASITIC ON OOSPORES OF ROOT-ROTTING OOMYCETES

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When sizeable masses of tissue in the larger roots, as also in the basal portions of the stems of plants—more especially of herbaceous plants—are invaded and killed by phycomycetous parasites of the genera *Pythium*, *Phytophthora*, and *Aphanomyces*, they usually come to be permeated by an assortment of adventitious organisms wherein bacteria, fungi, protozoa, and nematodes are represented in greater or smaller measure. As these intrusive organisms cannot well be reached with surface disinfectants, isolation of the oomycetous pathogens primarily responsible for root rots needs to be accomplished in almost all instances through procedure that, except for some discouragement of bacterial multiplication at the beginning, cannot well aim at suppression of such forms of life as may be present (7). Accordingly, after a week or two, the isolation cultures started from the affected tissues often show luxuriant development of microscopic plants and animals, some of which then conveniently reveal on the transparent substratum characteristic parasitic, predacious, or other biotic relationships that undoubtedly prevail also on the natural substrata, but there ordinarily remain concealed from view because of the opaqueness of these materials.

OCCURRENCE, MORPHOLOGY, AND CULTURAL CHARACTERS OF DACTYLELLA SPERMATOPHAGA

Among the organisms thus appearing time after time, year in, year out, in isolation cultures of many species of *Pythium*, is a moniliaceous fungus that I first took for a type of *Fusarium* differing from the general run of forms referred to that genus in its slow growth and in the scanty production of its conidia singly on erect aerial conidiophores. It was noticed early that here and there a branch of the septate mycelium passed narrowly through the wall of an oospore, conidium, or zoosporangium belonging to the root-rotting phycomycete cultured, and, within the invaded reproductive body, terminated in swollen lobulate elements. Though the swollen elements clearly had the appearance of assimilative structures, their presence in itself could not be considered final evidence of parasitism, as the reproductive body might already have been dead at the time it was invaded. For abortive development of sexual apparatus occurs only too frequently in cultures of *Pythium*, often being traceable to such nutritional deficiencies as come into play when, for example, *P. arrhenomanes* Drechsl. (18), *P. periplocum* Drechsl., or *P. scleroteichum* Drechsl. (10) are grown on unmodified maize-meal agar or on potato agar; the contents of the degenerating oogonia and oospores then being frequently appropriated by such purely saprophytic fungi as may chance to be on hand.

That the moniliaceous form is indeed a parasite became increasingly evident from its constant recurrence in isolation cultures containing oospores or conidia of various species of *Pythium*; from which bodies it manifestly always derived its nourishment. Moreover, it regularly made its appearance in immediate proximity to the pieces of diseased material originally planted on the medium. With the slow extension of its mycelium throughout cultures containing abundant sexual apparatus wholly normal in structural detail, the widening tracts of occupied substratum showed always a steadily increasing proportion of degenerating oospores. This strongly suggested that the hyphomycetous fungus did not wait for the oospores to degenerate spontaneously, but invaded them in their healthy state and actively brought about their destruction.

Closer examination bore out this suggestion. Individual oospores could be found whose central reserve globule, parietal protoplasmic layer and globose or ellipsoidal refringent body still attested a thoroughly normal condition of the protoplast, even after an invading branch had narrowly perforated the enveloping oogonial membrane, had traversed the intervening space, and was perforating the oospore wall itself (Fig. 1, A). From the absence of protoplasmic degeneration previous to invasion, it may be presumed no readily diffusible toxic substance was operative that could be held at all comparable in action to the lethal principle investigated by Weindling (38) and by Weindling and Emerson (39) as a very effective agent in the parasitism of *Trichoderma lignorum* (Tode) Harz on *Rhizoctonia solani* Kühn. Once the invading branch has passed through the oospore wall and into the protoplasmic interior, pronounced changes in internal structure promptly took place. The rather uniformly granular parietal layer and the central reserve globule of homogeneous consistency were both replaced by an irregular arrangement of largish block-like lumps, each of the lumps containing numerous fatty globules of variable sizes. Within this confusion of lumps and granules the progress of invasion by the parasite was always badly obscured. For a period apparently of some duration, it was most difficult to distinguish the haustorial elements from the degenerating protoplasmic materials surrounding them (Fig. 1, H). Following depletion, in large part, of the host protoplasm, the haustorial apparatus could be plainly discerned as a somewhat massive structure composed usually of several swollen lobate elements extending well throughout the cavity of the oospore (Fig. 1, B-G). Once assimilation of the materials within the cavity had been completed, the protoplasmic contents of the haustorial system were withdrawn into the parent hypha, leaving only the empty branching envelope in the collapsing membranous remains of the evacuated sexual apparatus.

Chiefly because the widely distributed damping-off fungus, *Pythium ultimum* Trow, has been obtained more frequently from specimens of diseased plants than any other pathogenic phycomycete, I have observed the moniliaceous fungus most often parasitizing that species in isolation cultures. As might be expected the conidia usually formed in quantity by *P. ultimum* are

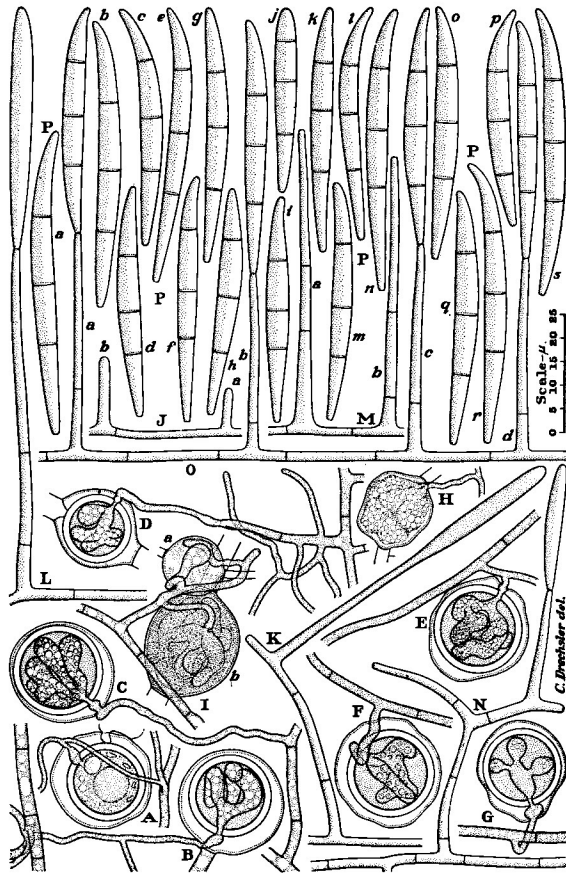


FIG. 1. *Dactylella spermatophaga*; drawn with the aid of a camera lucida to a uniform magnification, from material developed in an isolation culture permeated with *Pythium ultimum*; $\times 620$ throughout. A. Early stage in the invasion of a mature oospore of *P. ultimum* by a hyphal branch of the parasite; the branch having perforated the oogonial wall is penetrating the oospore wall, within which the contents show normal structure—the single large central reserve globule being surrounded by a parietal granular layer that has the single globose refringent body imbedded in it. B–G. Oospores of *P. ultimum* at later stages of invasion by the parasite; as the protoplasmic contents have largely been appropriated, the haustoria are clearly visible as branched lobate structures. H. Conidium of *P. ultimum* soon after invasion by the parasite; the haustorium being concealed in disorganized granular material. I, a, b. Two invaded conidia of *P. ultimum* from which the contents have been largely taken by haustorial elements of the parasite. J. Two young erect conidiophores, a and b, arising close together from the same mycelial filament. K. A mature conidiophore, which after producing and shedding one conidium, has given rise below its tip to a lateral branch whereon a second conidium is developing. L. Simple and relatively tall conidiophore bearing a young aseptate conidium. M. Two denuded simple conidiophores arising close together from the same superficial hypha. N. A branched conidiophore giving rise to its third conidium. O. A superficial hypha with four erect simple conidiophores, a–d, on each of which a mature conidium is borne. P, a–s. Mature conidia showing variations in size and shape.

destroyed much in the same manner as are the oospores, and, perhaps, in view of their less substantial walls, with greater readiness (Fig. 1, H; I, a, b). The parasite has also been observed operative in hundreds of isolation cultures of *P. debaryanum* Hesse, *P. irregulare* Buisman, and *P. mammillatum*

Meurs, always destroying oospores and zoosporangia in its gradual extension through the substratum. Often, too, it has been observed similarly destructive in isolation cultures of *P. butleri* Subr., *P. vexans* de Bary (= *P. complectens* Braun), *P. complens* Fischer, and *P. arrhenomanes*; as well as in isolation cultures of the species I have described elsewhere (8) under the binomials *P. salpingophorum*, *P. paroecandrum* and *P. oligandrum*. On the other hand, it has never appeared spontaneously in cultures of pythiaceus fungi started from pieces of diseased tissue excised from the interior of such massive plant structures as fruits of the watermelon, *Citrullus vulgaris* Schrad., or as the edible roots of the sweet potato, *Ipomoea batatas* Poir.

After the parasite has been nourished for some time through the destruction of reproductive bodies in isolation cultures of its phycomycetous hosts, it gives rise to scattered conidiophores and conidia. The conidiophores arise as simple erect hyphae (Fig. 1, J, *a, b*) that usually complete their development (Fig. 1, L; M, *a, b*; O, *a-d*) in producing a single elongate-fusoid tri-septate conidium (Fig. 1, P, *a-s*), sometimes straight but more often noticeably curved at the tip like the conidia of various species of *Fusarium*. Some conidiophores put forth a branch to produce individually a second conidium (Fig. 1, K); and, occasionally, the first branch gives rise to a second that then forms a third conidium at its tip (Fig. 1, N). Aside from its less abundant conidial septation, the fungus thus shows, at least in mixed bacterium-laden culture, a marked resemblance to *Dactylella passalopaga* Drechsl., a *Fusarium*-like hyphomycetous form capturing and consuming certain species of testaceous rhizopods (17).

The moniliaceous parasite was isolated by removing its conidia from the supporting hyphae directly to tubes of maize-meal agar; the removal being accomplished by means of minute slices of sterile agar held on a flamed platinum spatula, care being taken to avoid contact with the substratum. Growth on maize-meal agar, as also on other artificial media is relatively slow, radial extension usually not exceeding 1 mm. in 24 hours. The vegetative mycelium, which is almost wholly submerged in the substratum, consists of rather delicate, freely branching hyphae in moderately crowded arrangement. When examined with the naked eye it presents for the most part an irregularly cumulous appearance, except in the central portion, where a more uniformly dense texture is usual (Fig. 2, A-D). About a week after a culture has been started, the central portion begins to show a meager greyish or whitish aerial efflorescence that in the course of time is sparingly extended toward the periphery.

Under microscopic inspection this efflorescence is seen to be composed wholly of asexual reproductive apparatus. Successive production of conidia on individual conidiophores following repeated elongation of the fertile axis, encountered only now and then in bacterium-laden isolation cultures, here comes to elaborate expression. In cultures 30 days old, longish sporophoric hyphae may be found weighted down into somewhat procumbent postures by the conidia, often 10 to 20 in number, that are borne on them mostly at

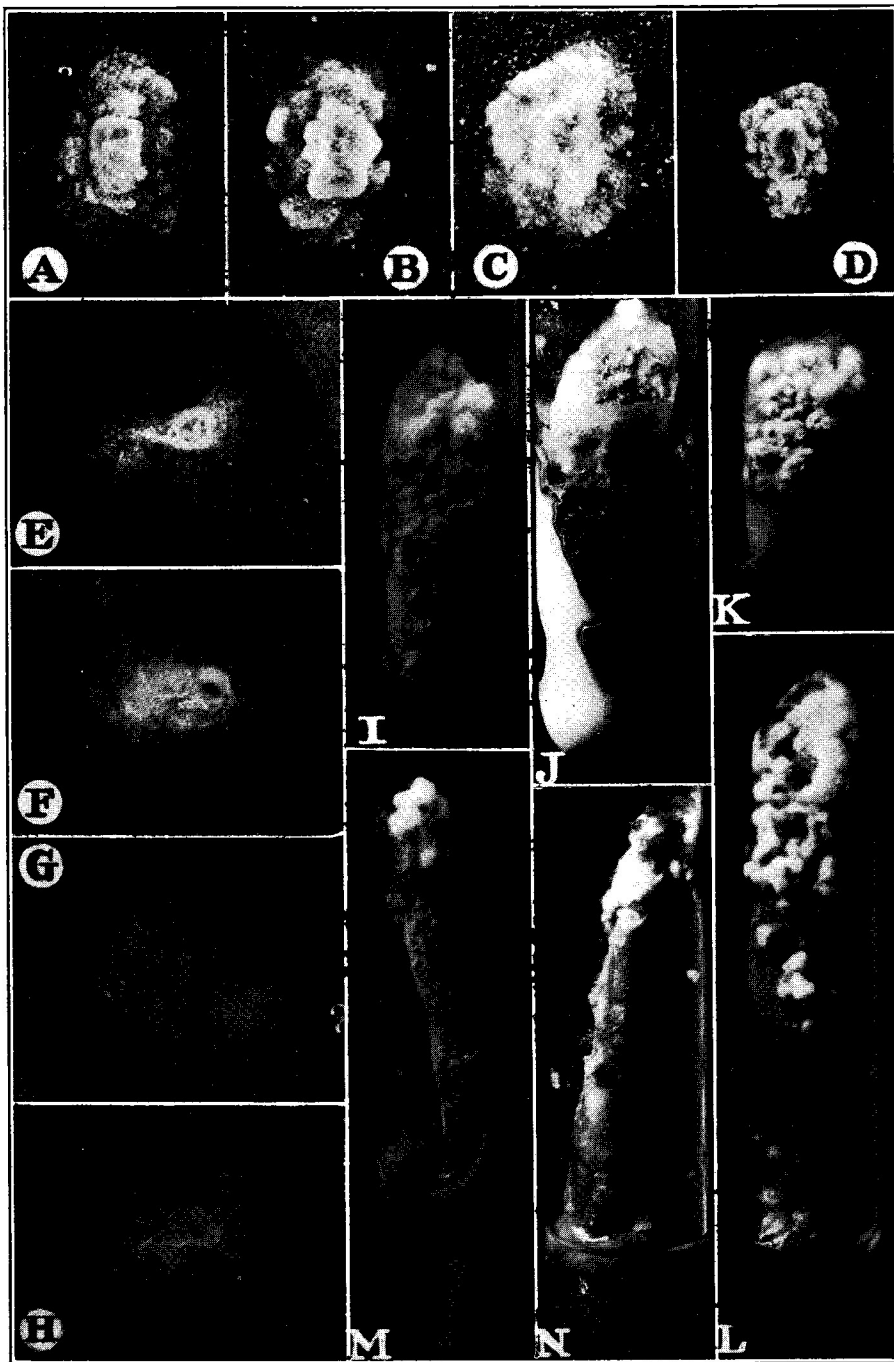


FIG. 2. *Dactylella spermatothaga* photographed from cultures after growing for 13 days at temperatures fluctuating between 25° and 33° C.; all approximately natural size. A-D. Mycelia from maize meal agar plate cultures, showing rather compact, cumulous texture. E-H. More diffuse mycelia of *D. spermatothaga* resulting from parasitic development in dual culture with *Pythium oedochilum*. I-K. Growth on steamed potato plugs. L-N. Growth on sterilized string-bean pods.

perceptible geniculations and in loose, irregularly spicate arrangement. Sometimes, as often when developing at temperatures between 20° and 25° C., the conidia are conspicuously abnormal in being of small size and irregular shape. Cultures kept at temperatures near 30° C. more often yield conidia similar in shape, size, and septation to those produced in isolation cultures, where, it may be presumed, conditions correspond approximately to those prevailing in nature.



FIG. 3. *Trinacrium subtile*; drawn with the aid of a camera lucida to a uniform magnification, from material developed in an isolation culture permeated by *Pythium butleri*; $\times 620$ throughout. A-F. Oospores of *P. butleri*, each occupied by one or two haustorial systems of *T. subtile*. G. A specimen of the shelled rhizopod *Geococcus vulgaris* invaded and parasitized by a hyphal branch of *T. subtile*. H. A portion of superficial filament bearing a young conidiophorous process, *a*, and also a conidiophore supporting a mature cruciform conidium, *b*. I. A well-developed conidiophore that after producing and shedding 4 conidia in succession, is giving rise to a fifth. J. Portion of superficial hypha with a conidiophore, *a*, bearing its first conidium, which is of cruciform design and immature, as is evident from the single septum; and close by, a second and denuded conidiophore, *b*, that has produced and shed two conidia. K. Portion of mycelium with a conidiophore bearing a somewhat immature conidium. L-P. Conidia, showing variations in dimensions, shape and septation. Q. A denuded simple conidiophore on which one conidium has been produced. R-T. Branched conidiophores whereon 3, 3, and 4 conidia respectively, have been produced.

On steamed potato plugs (Fig. 2, I-K) and on steamed pods of string bean (Fig. 2, L-N) the parasite likewise shows a slow rate of mycelial extension, but develops in more massive quantity. After 20 days the potato plugs reveal usually an irregularly sculptured, somewhat lichenoid growth, which is dull slaty grey where exposed. For the most part, however, it is clothed either sparingly with a sparse downy efflorescence, or slightly more profusely with a whitish velvety covering. On sterilized string-bean pods the aerial growth becomes aggregated here and there in somewhat raised, lichenoid or cartilaginous, waxy or pale flesh-color masses that, like the subjacent growth, may remain partly bare and partly become overspread with effuse or tufted, whitish or dirty greyish, aerial mycelium. In tubes with the bean pod partly immersed in water, a rather substantial cartilaginous, waxy or flesh-colored shelf may develop at the surface of the liquid. When planted in tubes of steamed rice, the fungus remains for some time scarcely perceptible, but, after 3 or 4 weeks, its development is clearly evidenced by a pale creamy coloration, by a matting together of the substratum, as well as by the presence of whitish downy aerial mycelium on the surface. Bright colorations, of the sort resulting from the growth of many of the familiar species of *Fusarium* associated with plant diseases, have never been observed in cultures of the parasite either on steamed rice or on the two other sterilized vegetable substrata. Neither conidia nor any other kind of reproductive bodies were ever produced in cultures employing one or another of the 3 vegetable materials.

OCCURRENCE OF TRINACRIUM SUBTILE RIESS AS A PARASITE ON OOSPORES

A mucedinaceous fungus, differing rather conspicuously from the one so far discussed, appeared in several maize-meal-agar plate cultures started with pieces of decaying tissue excised from the crowns of some potted spinach plants, *Spinacea oleracea* L., at Arlington Experiment Farm, Rosslyn, Virginia. After a protracted period of hot weather in June, 1936, these plants had become wilted one by one, the wilting in each instance having been followed soon by general collapse of the aerial parts, and death. From nearly all of the excised pieces of tissue, mycelium promptly grew out that in due course gave rise to lobulate zoosporangia and sex organs readily recognizable as those of *Pythium butleri*. To this fungus, often actively destructive in our middle latitudes during spells of high summer temperature, the spinach crown rot is manifestly to be attributed.

When the isolation cultures had become 10 days old, 5 among them showed in the agar adjacent to the tissue fragments numerous oospores of *Pythium butleri* being destroyed by a fungus that penetrated the oogonial and oospore walls and developed a swollen lobulate haustorial system within (Fig. 3, A-F), very much after the manner of the form with triseptate *Fusarium*-like conidia. A difference, apparently of somewhat incidental character, came to light in that the invading branch, after perforating the oogonial envelope, often became markedly inflated in the oogonial cavity, before

proceeding with the perforation of the oospore wall. From the original source in each of the 5 plate cultures the fungus continued to spread steadily until 15 days later it was present throughout the medium in the 100-millimeter Petri dishes, and had destroyed the innumerable oospores of *P. butleri* encountered in the course of its extension. In addition a few specimens of the ovoid testaceous rhizopod *Geococcus vulgaris* Francé were found parasitized by the fungus; a lateral hyphal branch evidently having grown through the mouth of each animal and then given rise inside to a number of swollen assimilative branches (Fig. 3, G).

Sporulation of the parasite took place in moderate quantity here and there over the surfaces of the 5 cultures. Though some of the conidia were elongate-fusoid in shape, they clearly exceeded those of the *Fusarium*-like form in dimensions, sometimes attaining as they did, a length of 115 μ and a diameter of 7.5 μ (Fig. 3, L). Instead of regularly showing 3 septa, these larger uniaxial conidia revealed as many as 13 (Fig. 3, M) or even 15 septa. By far the greater number of spores, however, did not consist of uniaxial bodies, but were branched in various ways. A very considerable proportion were bifurcate,—the proximal element, 4- to 8-septate and often between 40 and 60 μ long, terminating in 2 widely divergent elements, mostly up to 40 μ long and containing about 4 septa, to form a rather symmetrically triradiate structure (Fig. 3, N). An almost equally large number were of cruciform design,—bearing generally somewhat closer to the tip than to the base 2 lateral branches nearly at right angles with the main axis (Fig. 3, H, *b*; J, *a*). A smaller number terminated in 4 (Fig. 3, O) or even in 5 (Fig. 3, P) distal elements.

Conidial production was found to begin with the elongation of a fertile erect aerial outgrowth arising from a superficial mycelial filament (Fig. 3, H, *a*). When this outgrowth had attained approximately its definitive size and its definitive condition with respect to presence or absence of branches, a septum was inserted usually between 5 and 20 μ , often about 10 μ , from the base, thereby setting off stalk from young conidium (Fig. 3, J, *a*; K). Maturation of the delimited spores was accompanied by the insertion of usually 10 to 19 partitions, the number varying approximately with the combined length of the main axis and its branches. After a conidium was formed (Fig. 3, Q) the supporting stalk frequently grew out laterally to produce a second on a fertile extension from 5 to 20 μ in length (Fig. 3, J, *b*); repetition of the process yielding simple or variously branched conidiophores, from the successive geniculations of which the development of 3 (Fig. 3, R, S), 4 (Fig. 3, T), or 5 (Fig. 3, I) conidia could be inferred.

With respect to the morphology of its conidial apparatus the fungus agrees rather well with the description and figures of *Trinacrium subtile* published by Fresenius (23) in 1852. While the nearly symmetrically triradiate conidia (23, Pl. 5, Figs. 14, 15) of the design represented in figure 3, N, were apparently held typical of the species by the early mycologist, he included among his illustrations also a figure of a spore with 4 distal elements

(23, Pl. 5, Fig. 16). The limbs of the triradiate conidia were described as containing 3 to 6 septa and as measuring usually about 40 μ in length, though instances of the proximal limb measuring the equivalent of about 72 μ in length were acknowledged. It is perhaps significant that the species was first recorded as overgrowing the acervuli of another fungus, *Stilbospora* sp., and that the relevant figure (23, Pl. 5, Fig. 17) would seem strongly indicative of a parasitic relationship to the spores of the melanconiaceous form.

The literature bearing on *Trinacrium subtile* is relatively meager. Nearly 3 decades after its original description by Riess and Fresenius, Saccardo published additional figures of the species, wherein conidia of the same triradiate design held typical by Riess and Fresenius were shown both detached and in process of development on conidiophores arising directly from an insect egg (35, Tab. 966). Somewhat later, in a brief diagnosis (36) based more especially on his own material, he characterized the spore elements as being 4- to 5-septate, 25 to 30 μ long and 3.5 to 4 μ wide, and the conidiophores as filiform, 20 μ long and 2 μ wide. Oudemans observed *T. subtile* in a vertical strip of *Pleurococcus* on a beech trunk, *Fagus sylvatica* L., in the Netherlands, without being able to make out any evidence of parasitism. He described the conidia as triradiate; the constituent awl-like radial elements, 25 to 40 μ long, being stated in one account (31) to be divided by 3 or 4 septa into 4 or 5 compartments, and in another account (32) to be divided by 2 to 8 cross-walls into 3 to 9 cells. After Wildeman (40) had listed the fungus in a flora of Belgium, Magnus (30) recorded it on decaying *Berberis* twigs within the region embracing Tirol, Vorarlberg, and Liechtenstein; and more recently Rostrup (34) noted its occurrence on dead branches of *Betula* in Denmark.

The rather small measurements given by Saccardo for width of the radial elements in the conidium of *Trinacrium subtile*, suggests that possibly the Italian fungus recorded on insect eggs may have represented a species less robust than the one found destructive to the oospores of *Pythium butleri*. In any case, however, the oospore-destroying parasite conforms closely to the description and figures published by Fresenius; and its conidial septation shows a range of variation in fair consonance with Oudemans' somewhat variant statements regarding this feature. It is accordingly referred, at least provisionally, to the species originally discovered by Riess and adequately described by him in text quoted by Fresenius.

TAXONOMIC POSITION OF TRINACRIUM SUBTILE AND
DACTYLELLA SPERMATOPHAGA

The very evident parallelism in parasitic development between the two Hyphomycetes destructive to oospores leaves scarcely any doubt that they are closely related to one another. A presumption of intimate kinship is supported by the resemblance that the uniaxial conidia intermingled with the branching spores of *Trinacrium subtile* bear to the smaller triseptate conidia of the other species, and also by the similarity of the two species with

respect to the production of successive conidia following repeated elongation of the conidiophore. Now, in morphology of conidial apparatus the fungus with triseptate spores shows unmistakable parallelism and evident kinship especially with *Dactylella passalopaga*. Since *D. passalopaga*, as was pointed out earlier, manifestly belongs to an interrelated series of Hyphomycetes including in its known membership various species of *Trichothecium*, *Arthrobotrys*, *Dactylella*, *Dactylaria*, *Tripasporina*, *Pedilospora*, and *Tridentaria* predacious either on nematodes or on rhizopods, it follows that the 2 oospore-destroying forms must also belong in the same natural alliance, despite the generally different biotic relationship pertaining to both alike. For that matter, the divergence in biotic relationships is not so pronounced as to imply mutual exclusiveness in these relationships; reciprocal overlapping coming to light through the occasional parasitism on the one hand, of *T. subtile* on *Geococcus vulgaris*, and through occasional destruction (20, p. 510), on the other hand, of *Pythium* oospores by the nematode-capturing *Dactylella gephyropaga* Drechsl. Pertinent significance, moreover, may well attach to the fact that all known congeners of *Pedilospora dactylopaga*, a form I described (9) as predacious on the shelled rhizopods *Diffugia globulosa* Duj. and *Trinema enchelys* Ehrenb., were reported on other fungi—*P. parasitans* Höhn. (25) being recorded on *Helotium citrinum* (Hedw.) Fr., *P. ramularioides* Bubák (4) on *Bispora pusilla* Sacc., *P. episphaeria* Höhn. (26) on *Nectria cucurbitula* Fr., and *P. zacewskii* Gizhits'ka (24) on *Acrothecium tenebrosus* Preuss.

Considered from a morphological viewpoint, the 2 oospore-destroying fungi fit acceptably in the predacious series. The short conidiophores of *Trinacrium subtile* invite comparison with the similarly stubby fertile hyphae of the amoeba-capturing *Dactylella tylopaga* Drechsl. (14); its occasional uniaxial conidia suggest the elongated many-septate spores of *D. leptospora* Drechsl. (20); and its more numerous variously branched conidia recall the homologous branched structures of *Pedilospora dactylopaga*, *Tripasporina aphanopaga* Drechsl. (20), and *Tridentaria carnivora* Drechsl. (21). Repeated prolongation of conidiophores with the production of additional conidia, prevails in conspicuous measure among some of the capitate nematode-capturing forms, as notably in *Arthrobotrys superba* Corda, *A. oligospora* Fres., *A. conoides* Drechsl. (20), and *Dactylaria polycephala* Drechsl. (20); yet certainly, under especially favorable conditions, is not wholly absent among the predacious species of *Dactylella*, even though this genus is defined—and with respect to development on natural substrata, properly defined—as producing solitary acrogenous conidia. Indeed, such repeated prolongation is found not altogether rarely, even in bacterium-laden cultures of *D. passalopaga*, with which fungus, as has been stated, the smaller oospore-destroying parasite would seem most intimately allied. This parasite, having apparently not been described hitherto, possibly because its commonplace appearance and its very meager development of reproductive apparatus invite little attention, is accordingly presented as a new species of *Dacty-*

lella; a term meaning "eating seeds" being deemed a suitably descriptive specific name.

***Dactylella spermatophaga* sp. nov.**

Sparsa; mycelium ramosum, hyphis sterilibus hyalinis, .8–4 μ crassis, aliis angustis, flexuosis, filiformibus, parce septatis, aliis latioribus, torulosis, crebro septatis,—quibusvis ramulum tenuem in corpora perdurantia Pythiacearum saepe intrudentibus, haustorium obesum ramosum plerumque plus minusve lobosum intus evolventibus quod protoplasma assumit; hyphis fertilibus hyalinis, erectis, septatis, simplicibus vel interdum parce ramosis, vulgo 35–75 μ altis, basi 2.5–4 μ crassis, sursum leniter attenuatis, apice 1–2 μ crassis, ibi unicum conidium ferentibus, atqui subinde identidem repullulantibus, 10–15 additicia conidia deinceps gerentibus, tum usque 300 vel 500 μ longis et fere aliquid procumbentibus. Conidia hyalina, elongato-fusoidea, recta vel saepe praecipue in parte superiore curvata, basi rotunde truncata, apice rotundata, 35–65 μ (saepius circa 50 μ) longa, 3.8–5.2 μ (saepius circa 4.5 μ) crassa, vulgo triseptata, rarius biseptata vel quadri-septata.

Hyphas, conidia, zoosporangia, oogonia, praecipue oosporas multarum specierum Pythiacearum (magnam partem Pythii et Phytophthorae) interimens, habitat late in terra et in materiis plantarum putrescentibus, prope Beltsville, Maryland et in Arlington, Virginia.

Sparse; mycelium abundantly branched; vegetative hyphae hyaline, .8 to 4 μ wide, some narrow, flexuous, filiform and sparingly septate, others wider, toruloid and more closely septate,—whether of one type or the other, often thrusting a narrow branch into the resting reproductive bodies of Pythiaceae, and then, in each instance, giving rise inside to a rather bulky haustorium consisting of more or less lobulate branches usually 2 to 5 μ wide, yet sometimes as much as 6 or 7 μ in width; conidiophores, hyaline, septate, simple or sometimes somewhat branched, commonly 35 to 75 μ high, 2.5 to 4 μ wide at the base, tapering upward to a width of 1 to 2 μ at the tip, whereon is borne a single conidium,—but when developing under especially favorable conditions, often on repeated elongation giving rise at successive intervals to 10 or 15 additional conidia, thereby attaining lengths of 300 to 500 μ and becoming more or less procumbent. Conidia hyaline, elongate spindle-shaped, roundly truncate at the base, narrowly rounded at the tip, straight, or more especially in the distal portion, curved, 35 to 65 μ (average about 50 μ) long, 3.8 to 5.2 μ (average about 4.5 μ) wide, commonly containing 3, more rarely 2 or 4 cross walls.

Parasitizing hyphae, conidia, zoosporangia, oogonia and more particularly oospores of many species of Pythiaceae (mostly species of *Pythium* and *Phytophthora*), it occurs widely in the soil and in decaying plant remains near Beltsville, Md., and in Arlington, Va.

It must be admitted that with respect to reproductive habit neither *Dactylella spermatophaga*, nor certainly *Trinacrium subtile*, shows much direct resemblance to *Arthrobotrys oligospora* Fres., the species most familiarly exemplifying the predacious hyphomycetes; the connection being traceable only rather indirectly through a number of forms embodying transitional types of conidial apparatus. That the chain of similarities here concerned, though perhaps appearing at first somewhat far-fetched, is not beyond the scope of a well-integrated group, becomes manifest from its parallelism with an analogous train of resemblances extending more particularly through the noncatenulate members of the Zoopagaceae, an unquestionably natural family of conidial phycomyces destructive to nematodes and rhizopods. Thus, the branched conidium produced on the short conidiophore of *Trinacrium subtile*, shows an engaging analogy to the appendaged and virtually sessile conidium of *Acaulopage tetraceros* Drechsl. (12) or of *A. acanthospora* Drechsl. (22); the elongated conidium and moderately developed conidiophore of *Dactylella spermatophaga* recalls the similarly proportioned homologous structures of *Stylopage rhabdospora* Drechsl. (16); the broadly ellipsoidal or obovoid conidia and tall conidiophores of *Dactylella bembicodes* Drechsl. (20), *Dactylella gephyropaga*, and *Trichothecium polybrochum* Drechsl. (20) are

reminiscent of the conidial apparatus in *S. hadra* Drechsl. (13) and *S. leiohypha* Drechsl. (15); while to extend the correspondence, the monocephalous capitate moniliaceous forms as, for example, *Dactylaria candida* (Nees) Sacc. and *Arthrobotrys dactyloides* Drechsl. (20), show a striking similarity of habit to *S. cephalote* Drechsl. (22).

An alternative disposition of the two oospore-destroying forms is, of course, suggested by the remarkable structural resemblance that the conidia of *Dactylella spermatophaga* bear to the conidia of some species of *Fusarium*—a resemblance that gains in possible import from the known occurrence of many species of *Fusarium* on other fungi (41, pp. 302–305). However, assimilation of *D. spermatophaga* to *Fusarium* encounters a serious obstacle in the failure of the fungus to produce conidia otherwise than terminally on discrete aerial hyphae. Clements and Shear (6, p. 402), it is true, have ventured to subsume under *Fusarium* the genus *Rachisia* represented by a single species, *R. spiralis* Lindner, which, after developing endoparasitically in vinegar eels (*Anguillula aceti* Ehrenb.), produces falcate conidia laterally on external discrete rachiform filaments. Unfortunately, Lindner (28) omitted to state whether cross walls are present or absent in the hyphae and conidia of *R. spiralis*; yet, the rachiform conidiophores pictured by him reveal a most persuasive similarity to those of *Graminella bulbosa* recently described by Léger and Gauthier (27) from the rectal cuticle of *Bactis* larvae. Indeed, the resemblance is so striking that, until further information is obtained, Lindner's remarkable parasite might well be extricated from any association with *Fusarium* and placed, even if only somewhat tentatively, in the Harpellaceae, a singular family of conidial phycomycetes occurring especially on the peritrophic membrane and rectal cuticle of the aquatic larvae of various insects.

DACTYLELLA SPERMATOPHAGA IN DUAL CULTURE WITH VARIOUS OOMYCETES

After *Dactylella spermatophaga* had been obtained in pure culture, the scope of its parasitism was further explored by growing it in dual culture together more especially with different pathogenic oomycetes that had not previously been observed being attacked in isolation cultures. In order that spontaneous degeneration of the host fungi may not be held to have impaired the trustworthiness of observations recorded here, only results will be considered that could be obtained by the use of maize-meal agar media clear enough to permit satisfactory inspection throughout and thereby to make possible the confirmation of normal development in the particular oomycetes under trial. Among the species of *Phytophthora* thus tried out, oospores of undoubtedly normal structure were produced in quantity by *P. cactorum* (Leb. & Cohn) Schroet. and *P. megasperma* Drechsl. After their maturation the oospores of both species were successfully parasitized by *P. spermatophaga*, and that despite the thickness of their protective walls. The clustered globose chlamydospores of *P. cinnamomi* Rands were likewise abundantly

attacked and destroyed, as were also the more solitary globose thick-walled chlamydospores or "resting zoosporangia" of *P. parasitica* Dast.

In dual culture with *Dactylella spermatophaga*, oospores of *Aphanomyces euteiches* Drechsl., a pathogen often responsible for serious root rot of peas (*Pisum sativum* L.) during wet seasons, were freely invaded and exhausted of contents. Neither the thick oogonial membrane characteristic of this water mold, nor the substantial oospore wall, appeared to offer any effective barrier to entrance by the hyphomycetous parasite. Rather often, to be sure, the oospore was reached not by perforation of the oogonial envelope, but by penetration of the antheridial wall, followed by elongation of the infective hypha through the antheridial chamber and down the fertilization tube. This easier mode of invasion is apparently facilitated by the frequent presence of 3, 4, or 5 male organs about an oogonium, by the fairly large size of these organs, and by their retention, sometimes, of granular protoplasm, even at relatively late stages of development.

When *Pythium graminicolum* Subr., *P. dissotocum* Drechsl., and *P. peritium* Drechsl., each isolated (8, 18) from diseased roots of sugar-cane, *Saccharum officinarum* L., were grown in dual culture with *Dactylella spermatophaga*, the numerous oospores of correct internal structure produced by them were parasitized in large numbers. Such parasitism was evident also in dual cultures of *D. spermatophaga* and *P. myriotylum* Drechsl., a species occurring widely in our southeastern States as the cause of a blossom-end decay of watermelon fruits (8), as well as of a cottony rot of the fruits of cucumber, *Cucumis sativus* L., closely resembling "cottony leak" caused by *P. butleri*. With no less success *D. spermatophaga* likewise parasitized the oospores of *P. acanthicum* Drechsl. and *P. periplocum*, the 2 forms with characteristically spiny oogonia that are most frequently found associated with blossom-end rot of watermelon fruits in Maryland, Indiana, and Missouri (8). In dual culture on slightly acidulated maize-meal agar containing considerable maize-meal sediment in suspension, the hyphomycetous parasite abundantly destroyed the oospores of *P. scleroteichum*, one of the species frequently causing in edible sweet-potato roots the marbled decay known as "mottle necrosis."

Among morphological modifications to be observed in the sexual apparatus of oomycetes, few are more formidable in aspect or present more of an appearance suggesting a protective function than the sturdy, often characteristically mammiform protuberance normally besetting the oogonia (8) of *Pythium polymastum* Drechsl. and *P. mastophorum* Drechsl. Yet, *Dactylella spermatophaga*, in mixed culture with these impressive and rather rare representatives of the genus *Pythium*, thrusts its infective branches through the sturdily mamelonated oogonial envelopes without apparent difficulty, to reach the smooth, globose oospores within; the infective branches then, of course, individually perforating the oospore wall and extending a lobulate haustorium through the protoplasmic interior. Equally ineffective for protection against invasion by the hyphomycetous parasite is the prominently

echinate oogonial wall of *P. anandrum* Drechsl., a species remarkable alike for its consistent parthenogenesis and for the *Phytophthora*-like shape of its repeatedly proliferous sporangia (8). The handsome parthenospores of the species are readily invaded and destroyed on their development in dual culture with *D. spermatophaga*.

Further testimony to the efficiency of *Dactylella spermatophaga* in penetrating sturdy host structures is furnished by its more than ordinarily profuse development when grown in dual culture with any one of the 4 closely interrelated forms I described (8) under the names *Pythium helicoides*, *P. oedochilum*, *P. polytylum*, and *P. palingenes*. In their asexual reproduction these forms follow the development early set forth by de Bary (1) in the description of his *P. proliferum*, giving rise, as they do on appropriate irrigation, to repeatedly proliferous terminal sporangia that individually discharge their undifferentiated contents through an evacuation tube into a vesicle, there to be fashioned into zoospores (Fig. 4, A, B). Much greater distinctiveness attaches to their sexual apparatus, not only in that the elongated antheridia are applied lengthwise to the oogonium rather than apically, as in most species of *Pythium*, but, also, in that the mature oospore regularly reveals imbedded in its somewhat turbidly granular protoplasmic contents usually about a score of reserve globules and about a half dozen refringent bodies (Fig. 4, F, G), rather than only the single reserve globule and single refringent body more generally present elsewhere among the monospermous oomycetes of the genera *Pythium*, *Phytophthora*, *Aphanomyces*, and *Plectospora*. Of particular relevance to the present discussion is the fact that the oospore wall in each of the 4 species usually averages about 2.5 μ or more in thickness, besides presenting an appearance of marked induration through its frequently yellow or yellowish coloration. Yet, after penetration of the oogonial envelope, this conspicuously substantial wall is perforated without apparent difficulty by the invading branch of *D. spermatophaga*; extension of a massive lobulate haustorial system throughout the protoplasmic interior then ensuing (Fig. 4, H and K), as in the less stoutly incased oospores of the species more frequently isolated.

As *Pythium oedochilum*, when grown on maize-meal agar, is very dependable in producing—and rather abundantly, too—sexual apparatus of uniformly normal structure, it makes an especially satisfactory host in dual culture with the hyphomycetous parasite. On encountering a mycelium of *Dactylella spermatophaga*, many of its vegetative hyphae are invaded over stretches of variable lengths and locally exhausted of their contents (Fig. 4, C–E). With the appearance later of zoosporangia, these are parasitized (Fig. 5, A) no less successfully than are the hyphae and oospores. Thus richly nourished, the parasite gives rise to its most luxuriant display of simple or somewhat branched conidiophores (Fig. 5, B, C) bearing numerous conidia (Fig. 5, D, *a–n*) comparable in shape and size to those produced in pure culture only under exceptionally favorable conditions. Frequently the conidia anastomose with their supporting hyphae previous to normal dis-

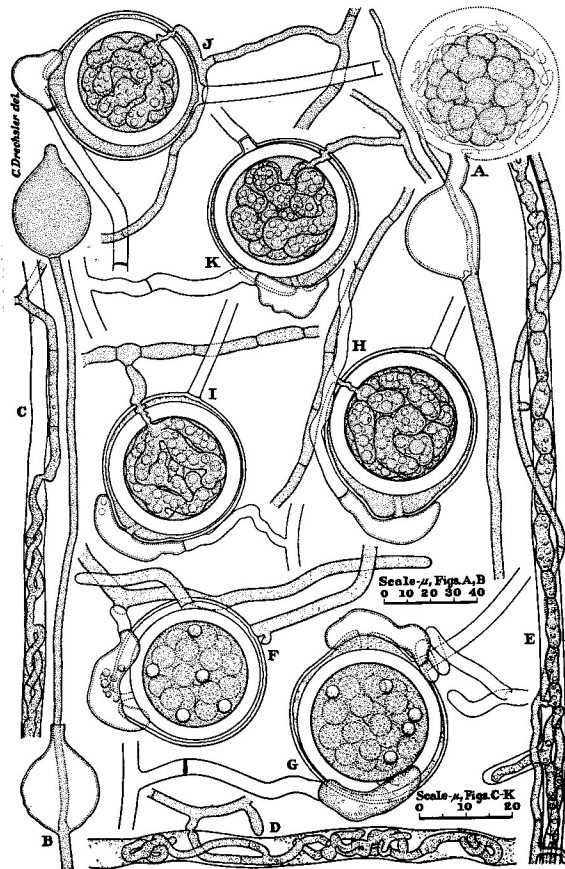


FIG. 4. *Dactylella spermatorhaga* and *Pythium oedochilum*; drawn with the aid of a camera lucida, mostly from material developed in dual culture on maize meal agar. A. A zoosporangium of *P. oedochilum* showing zoospores being formed in a vesicle at the tip of an evacuation tube; the supporting hypha is continuing growth from immediately below the sporangium; $\times 310$. B. Two zoosporangia of *P. oedochilum*, the distal one borne on an axial prolongation of the conidiophore supporting the proximal one; $\times 310$. C-E. Hyphae of *P. oedochilum* parasitized by filaments of *D. spermatorhaga*; $\times 620$. F, G. Normal mature sexual apparatus of *P. oedochilum*, showing the internal organization characteristic of the *helicooides* series in *Pythium*—multiple reserve globules and multiple refringent bodies being imbedded in murkily granular protoplasm; spiral involvement of the oogonial stalk by the branch supporting one of the antheridia, in the manner shown in G, occurs infrequently in the species, though regularly present in *P. helicooides*; $\times 620$. H-K. Infected sexual apparatus of *P. oedochilum*; the oospore in each unit having been occupied by a rather massive branching haustorium of *D. spermatorhaga*, after successive perforation of the oogonial and oospore walls; $\times 620$.

articulation (Fig. 5, E); or, falling on the substratum, unite vegetatively with one another (Fig. 5, F), sometimes to give rise to secondary conidia (Fig. 5, G). To the naked eye, as might be expected, the parasitic mycelia of *D. spermatorhaga* present a more diffuse appearance than mycelia developing in pure culture, rarely showing any suggestion of cumulous texture (Fig. 2, E-H).

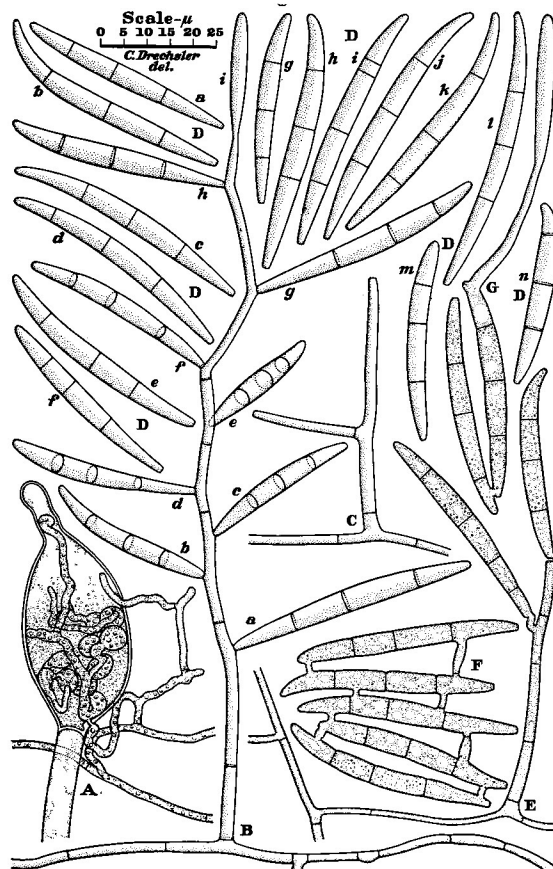


FIG. 5. *Dactylella spermatophaga*; drawn with the aid of a camera lucida to a uniform magnification, from material developed in dual culture with *Pythium oedochilum* on maize meal agar; $\times 620$ throughout. A. A sporangium of *P. oedochilum* invaded and nearly depleted of protoplasmic contents by the parasite. B. A conidiophore on which have been produced successively 8 conidia, *a-h*; a ninth conidium, *i*, being in course of development at the apex. C. Portion of hypha with a branched conidiophore denuded of its two conidia. D, *a-n*. Conidia, showing variations in size, shape and septation. E. Portion of mycelium with a conidiophore whereon have been produced 2 conidia, both of which have become united vegetatively with the supporting hypha previous to their disarticulation therefrom. F. Five conidia that after falling on the substratum have become united vegetatively through fusion by means of germ tubes. G. Two fallen conidia that have fused vegetatively; from one of them a conidiophore has been produced that is giving rise to a secondary conidium.

THE RÔLE OF DACTYLELLA SPERMATOPHAGA IN THE BIONOMICS
OF ROOT-ROTTING OOMYCETES

Though *Dactylella spermatophaga* is unquestionably capable of destroying mycelial filaments of numerous species of *Pythium*, the destruction of vegetative hyphae would seem on the whole far too meager to be of any great importance in the bionomics of the oomycetous hosts. Even the slower-growing species among the phycomycetes subject to attack show rates of mycelial extension from 10 to 15 times faster than that of the parasite, while some hosts, as, for example, *P. debaryanum*, *P. ultimum*, and *P. butleri*,

exceed the linear or radial growth of *D. spermatophaga*, 50 to 75 times. A mycelium extended by a pathogenic oomycete through a sizable portion of root or stem, or through any other rather bulky mass of substratum, would, for the most part, therefore, presumably have ample time to form reproductive bodies before it could be overtaken by the parasite.

Though *Dactylella spermatophaga* may appear rather innocuous in its occasional invasion of vegetative hyphae, as also in its occasional interception of reproductive development, its unceasing destruction of mature oospores and conidia must almost certainly reduce the longevity of its phycomycetous hosts. Evidently widely distributed in the soil, as well as in plant materials decaying moistly in contact with the ground, and freely attacking the most resistant of soil-borne reproductive bodies through which the many root-rotting oomycetes are enabled to persist from season to season, *D. spermatophaga* must be considered an organism with very real potentialities for promoting soil sanitation. Since, in the persistence of oospores, and accordingly also in programs of crop rotation governed thereby, periods of time reckoned in years rather than in days, weeks, or months, are involved, the relatively slow growth of the parasite would seem not seriously incompatible with its efficiency as a hygienic agent. Even in much shorter periods, oospores at first inaccessible to attack because of the massiveness of the phanerogamic structures occupied, become subject to invasion with the disintegration of the substratum. Thus, while the innumerable oospores formed by *Pythium acanthicum* and *P. periplocum* in diseased watermelon fruits may enjoy protection for perhaps a week or two, decomposition of the affected material soon exposes them to the action of the parasite.

OTHER ORGANISMS ANTAGONISTIC TO ROOT-ROTTING OOMYCETES IN ISOLATION CULTURES

Apart from *Trinacrium subtile* and *Dactylella spermatophaga*, oospores of root-rotting phycomycetes in isolation cultures have been found undergoing destruction by amoebae and shelled rhizopods. The various amoebae implicated vary greatly in size. Some are so small that after ingesting a single oospore of *Pythium ultimum* or *P. debaryanum* they appear individually as only a rather thin enveloping layer of protoplasm. Others are large enough to move about briskly after engulfing a dozen oospores of the two damping-off fungi mentioned. Somewhat curiously, the small species of *Amoeba* seem generally much more rapid in killing and digesting oospores devoured by them than are the larger congeneric forms. Oospores have likewise been found ingested by the robust, large-mouthed testaceous rhizopod *Arcella vulgaris* Ehrenb.; or, again, have been observed in process of being exhausted of their degenerating contents by the testaceous rhizopods *Geococcus vulgaris* Francé and *Euglypha denticulata* Brown, following, in each instance, perforation of the oospore wall within an area circumscribed by the mouth of the shelled animal orally applied to it (17, pp. 400-401; 19, p. 244). On the whole, however, the aggregate destruction of oospores seen accom-

plished in isolation cultures by all protozoans together, while sometimes not inconsiderable, seems hardly deserving of comparison with the destruction found achieved by *D. spermatophaga*.

Butler (5, p. 109) directed attention to the somewhat unexpected occurrence of chytridiaceous parasites in soil-inhabiting species of *Pythium*. The pure-culture technique whereby affected portions of root or stem are placed on firm agar culture media, ordinarily gives little encouragement to the development of any organisms able to spread only through locomotion of zoospores. Nevertheless, some slight opportunity for the development of such organisms is often provided by the accumulation of water in a minute pool immediately surrounding the planted decaying material. In the limited area covered by the pool, *Pleolpidium inflatum* Butl., with its large and immensely prolific zoosporangia, can sometimes be found actively parasitizing *Pythium* filaments. Very little free water would seem to suffice for the propagation of *Pleolpidium irregulare* Butl., as this species has been found extending itself successfully in maize-meal agar cultures of *Pythium irregulare* on the surface of which no deposit of liquid was visible. The chytridiaceous parasite was for years maintained in culture free of bacteria and all extraneous organisms by merely transferring it with its fungus host from one tube of firm agar medium to another. It singles out for invasion especially the growing oogonia, which organs are often conveniently identifiable by the characteristic digitations borne on them (5, Pl. 8, Fig. 11); so that its parasitism, if not effecting the destruction of oospores already formed, yet operates, in part, like the parasitism of *Dactylella spermatophaga*, by preventing their formation.

The generally unfavorable effect of bacterial contamination on cultures of most pythiaceous and saprolegniaceous fungi has long been annoyingly familiar both among students of the aquatic microflora and among investigators dealing with plant diseases. Such contamination, being here far more pertinacious than in cultures of most other fungi, usually requires extra effort for its elimination; wherefore, indeed, different special methods of purification have been devised, including some made known in recent years by Brown (3), Volkonsky (37), Machacek (29), Blank and Tiffney (2) and Raper (33). Yet in investigations on root rots and other related plant diseases, discomfiture more serious than any resulting from an unhappy intrusion of bacteria in isolation cultures, has often come in repeated failure to obtain on agar or other artificial medium any growth whatever of the causal parasite concerned; so that in the absence of any isolation culture from which a correct beginning might be made, either no likely pathogenic agent could be uncovered at all, or the disease was (and it may be suspected in many instances still is) wrongly attributed to an adventitious organism. According to the relevant literature, species of *Phytophthora* that in nature develop at relatively high temperatures in the softer succulent tissues of herbaceous or, for that matter, of woody plants, have often been found difficult to get started from pieces of diseased tissue placed on artificial sub-

strata; as have also most disease-producing species of *Aphanomyces* and some root-rotting species of *Pythium* other than the common damping-off forms distinguishable among phycomycetous parasites for their vigorous and extensive extramatrical growth—*P. ultimum*, *P. debaryanum*, *P. irregulare*, *P. mammillatum*, and *P. butleri*.

Microscopic examination of tissues undergoing active invasion by species of oomycetes, not readily started in isolation cultures, has very generally shown the difficulty to lie in a debilitated condition of the parasitic mycelium, evidently attributable, in the main, to the presence of putrefactive bacteria. During warm periods especially, the motile saprogenous bacteria that habitually accompany the phycomycetous filaments in their courses through host tissue, become so active that often many can be seen swarming about the very tips of the invading hyphae, just as under similar conditions they swarm about the tips of superficial hyphae of growing mycelia in isolation cultures. Now, whereas on firm agar media development of bacteria is limited, for some time at least, to the surfaces, so that submerged filaments are protected from the products of putrefaction save as these gradually diffuse through the intervening gel, in invaded plant tissues the multiplying bacteria permeate the substratum throughout, thereby exposing all filaments to direct contact with the saprogenic substances. As a result protoplasmic degeneration becomes evident everywhere except in the youngest hyphae in the forefront of the advancing mycelium. Sometimes, in fact, bacterial development appears to overcome even the filaments in the van of an infection; partly decayed specimens of watermelon fruits, for example, having been found wherein the advance of one or another of the different parasitic *Pythium* species causing blossom-end rot seemed to have been stopped outright. Where remnants of mycelium survive in the marginal portions of a lesion, they nearly always can be induced to grow out conveniently into an agar substratum if first the accumulated products of putrefaction are leached away by bathing the affected tissues in several changes of fresh water, and bacterial development, after the transfer to agar, is discouraged through the removal of all free water previously by pressing the material between pieces of sterilized filter paper (7).

Indeed, within their host plants no less than in artificial culture, the whole behavior of pythiaceous and saprolegniaceous parasites betrays, as a general fundamental character, an incapacity for thriving, or even for long enduring vegetatively in a fouled substratum. With their markedly rapid rate of mycelial extension some species of *Pythium* are enabled to thrust their assimilative hyphae into fresh unfouled masses of plant material, moribund or newly dead, ahead of competing fungi of slower growth, and there to build up a vegetative thallus of sufficient bulk for the development of oospores before the increasing putrefaction brought on by the accompanying bacteria causes protoplasmic degeneration on a serious scale. Despite their sensitiveness to putrefaction such fast-growing species of *Pythium* frequently occur, therefore, in semi-parasitic and saprophytic relationships as well as in truly

parasitic relationships resulting from the invasion of succulent living structures. It may be presumed, on the other hand, that species of *Phytophthora* with their slower mycelial growth are at a great disadvantage in any competitive invasion of plant tissues normally moribund or otherwise deprived of effective resistance; and are consequently, for the most part, limited in their development under natural conditions to tissues newly invaded and freshly killed by them. Their ready saprophytic development in pure culture on a wide variety of artificial and natural substrata, yet always in the absence of putrefactive organisms, must accordingly not be considered inconsistent with their habitual occurrence in nature as parasites. With respect to nutrition, then, the root-rotting oomycetes in general seem comparable to the predacious hyphomycetous fungi and the two related oospore-destroying forms herein discussed; though a notable difference is presented in that, while the hyphomycetous fungi apparently cannot take nourishment from a foul substratum, their mycelia readily endure immersion in putrescent slime. As was pointed out earlier (11) *Pythium anandrum*, *P. mastophorum*, and *P. polymastum* are appreciably less sensitive to bacterial contamination than the main mass of root-rotting oomycetes; their capacity for producing zoospores in water rather generously laden with bacteria, as well as their somewhat aberrant morphology, perhaps being indicative of special ecological relationships. However, the moderate tolerance of these species to bacterial contamination is not to be confused with the thoroughgoing adaptation to foulness shown by members of the truly saprophilous genus *Pythiogeton*, which grow luxuriantly and produce zoospores abundantly in heavily putrescent slimes.

From some writings on damping off the suggestion is conveyed that addition of stable manure is undesirable, not only because infectious material may be introduced and tender growth favorable to infection encouraged thereby, but also because after such addition the seedling parasites might be able to permeate the soil more readily by developing on the bits of dung distributed through it. Misgivings on the latter score would seem excessive, as certainly the behavior of the pythiaceous damping-off organisms in the laboratory is not such as to justify any fear that they might spread anywhere on a substratum as foul as dung. On the contrary, their behavior suggests that if a seedbed could be kept continuously infiltrated throughout with putrescent substances, development of destructive mycelia from resting conidia and oospores might be effectively prevented. Indeed, it appears within the realm of possibility that where soil sterilization by steam or chemicals is inexpedient, some control of damping off might be achieved by watering seedling flats exclusively with a putrescent infusion not objectionably rich in nitrogenous substances, such as could be conveniently prepared by the retting of herbaceous waste materials.

SUMMARY

Of 2 moniliaceous fungi found vigorously parasitic on oospores of pythiaceous root-rotting organisms, one with mostly triradiate and cruciform

conidia is identified as *Trinacrium subtile*; the other with regularly trisepate *Fusarium*-like conidia is described as a new species under the binomial *Dactylella spermatophaga*. Despite conspicuous differences in conidial design, the 2 hyphomycetous parasites appear closely related to one another. Because of its failure to produce compound conidial apparatus, and in view of its resemblance to *D. passalopaga*, a rhizopod-capturing form, as well as to *D. leptospora*, a nematode-capturing species, *D. spermatophaga*, together with *T. subtile*, is considered related taxonomically to the predacious series of hyphomycetes rather than to the genus *Fusarium*.

Dactylella spermatophaga has been observed to appear spontaneously in numerous isolation cultures started from diseased portions of many host plants obtained in a number of different localities representing collectively a wide variety of environmental conditions. In these cultures it was found destroying oospores of *Pythium arrhenomanes*, *P. butleri*, *P. complens*, *P. debaryanum*, *P. irregulare*, *P. mammillatum*, *P. oligandrum*, *P. paroecandrum*, *P. salpingophorum*, *P. ultimum*, and *P. vexans*. Grown in dual culture with other oomycetes it parasitized abundantly also the oospores of *Pythium acanthicum*, *P. anandrum*, *P. dissotocum*, *P. graminicolum*, *P. helicoides*, *P. mastophorum*, *P. myriotylum*, *P. oedochilum*, *P. palingenes*, *P. peritium*, *P. periplocum*, *P. polymastum*, *P. polytylum*, *P. scleroteichum*, *Phytophthora cactorum*, *Phytophthora megasperma*, and *Aphanomyces euteiches*. Infection is accomplished by perforation successively of the oogonial and oospore walls, followed by development within the oospore of a branched, somewhat lobate, and rather massive haustorium that appropriates the protoplasmic contents.

Because of its evident capacity for widespread destruction of oospores, on which bodies root-rotting oomycetes mainly depend for survival from season to season, *Dactylella spermatophaga* presumably serves as an effective agent in promoting soil sanitation over extended periods of time. A similar rôle in the long-time bionomics of soil-borne oomycetes is played by various amoebae and testaceous rhizopods. Parasitic chytrids, on the other hand, operate not so much to destroy oospores already formed, as they operate to prevent their development; while putrefactive bacteria exert a pervasively debilitating effect on the mycelium of root-rotting oomycetes,—an effect entailing, under natural conditions, the virtual restriction of slow-growing oomycetous forms to strictly parasitic relationships, though permitting the occurrence of faster-growing forms in saprophytic and semiparasitic as well as wholly parasitic relationships.

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