

Reprinted from MYCOLOGIA, Vol. XXXII, No. 4, 448-470, July-August, 1940
Printed in U. S. A.

**THREE NEW HYPHOMYCETES PREYING
ON FREE-LIVING TERRICOLOUS
NEMATODES**

THREE NEW HYPHOMYCETES PREYING ON FREE-LIVING TERRICOLOUS NEMATODES

CHARLES DRECHSLER

(WITH 3 FIGURES)

In an earlier paper (8) was given a comparative account of 18 interrelated mucedinaceous fungi found to subsist habitually on nematodes that they capture by means of vegetative parts variously adapted for prehension. These fungi had come to light in agar cultures started from discolored rootlets or from other affected vegetable materials, and later often further planted with pinches of friable leaf mold. Similar cultures prepared as circumstances permitted during the last few years have revealed 3 additional mucedinaceous forms obviously belonging in the same series as those previously discussed, and like them observed subsisting by the capture of free-living terricolous eelworms. As the forms appear not to have been recorded hitherto in mycological literature, they are described herein as species new to science.

A SECOND SPECIES OF *DACTYLELLA* WITH CONSTRICTING RINGS

A fungus more similar to *Dactylella bembicodes* Drechsl. than to any other known predaceous form appeared in numerous maize-meal-agar plate cultures that, after serving in the isolation of various species of *Pythium* from diseased plant tissues, had received, in addition to material put on them originally, some pinches of friable leaf mold collected near Butternut, Wis., in September 1938. The mycelial hyphae of the mucedinous species in question invariably grew out from the deposits of forest detritus to ramify rather sparsely through the adjacent substratum. On the hyphae were borne at intervals three-celled predaceous rings closely resembling the constricting rings produced by *D. bembicodes*, *Arthrobotrys dactyloides* Drechsl., *Dactylaria brochopaga* Drechsl., and *Trichothecium polybrochum* Drechsl., the general similarity in cel-

lular make-up being clearly revealed in specimens jostled into nearly horizontal positions by passing nematodes (FIG. 1, *A, a; B, a, b; C, a, b; D*). In such positions the three component cells usually display a median thickening that bulges toward the center of the ring. As is evident even when the rings are examined in their normal positions at approximately right angles to the parent filament (FIG. 1, *E; F; G, a; I, a, b; J, a*), the supporting stalk here, while also consisting regularly of two cells, is perceptibly longer than in any of the four other species with constricting organs. The incidental difference in structural detail does not make for any difference in operation; for the rings of the present fungus, like those of the constricting species previously described, capture intruding nematodes by abrupt contraction and swelling of their component cells, which then send haustorial filaments into the interior of the disabled prey to appropriate its fleshy contents (FIG. 1, *G, b; H; I, c; J, d*). Likewise, as in the other constricting species, closed rings holding no prey are to be seen near captured animals, their closure having apparently resulted from proximity to captured eelworms (FIG. 1, *J, b, c*).

Since captured eelworms lash about violently in their efforts to free themselves, it is not unnatural to presume that the stimulus effective in the unprofitable closure of constricting rings within the orbit of their struggles may be one of mechanical irritation. An instance of such closure incidentally shown in a figure of *Dactylaria brochopaga* (8: p. 515, fig. 13, *D, e*) was accordingly explained (8: p. 549) as having apparently been brought about by lashings from two specimens of *Diploscapter coronatus* (Cobb) Cobb that were found captured in rings nearby. Experimental evidence that a tactile stimulus is generally operative in closure of constricting rings has recently been supplied by Comandon and de Fonbrune (3, 4), who worked mainly with *D. brochopaga* and in lesser measure with *Dactylella bembicodes*. On gently irritating with a microneedle any one of the 3 arcuate cells on its inner or central side, they obtained motion pictures that recorded pronounced centripetal dilation of the irritated cell ensuing in the course of .1 second, followed a fraction of a second later by similar abrupt dilation of the other 2 cells; the intruding needle being thereupon found engaged so firmly that it could not easily be withdrawn.

However, Couch (5), working with *D. bembicodes*, found that movement of a fine glass rod on the inner surface of the open predaceous ring resulted in only slight swelling, and concluded therefore that mechanical irritation plays a very small, if any, part in closure of the loops. Heat, whether supplied from a hot scalpel or in water having a temperature of 33° to 75° C., he found consistently effective in springing the traps; though, as was recognized by him, a thermal stimulus can hardly be postulated in the normal entrapment of cold-blooded animals.

The divergence between Couch's findings and those of Comandon and de Fonbrune suggests that further inquiry into the physiology of the constricting ring—assuredly one of the most remarkable of plant structures—might not be misdirected. Occasion may be taken to explain in this connection that for lack of a micromanipulator my own observations on the closure of the strangulating organs have been limited so far to three instances of capture; two of these instances having occurred in cultures of *Arthrobotrys dactyloides*, the other in a culture of *Dactylaria brochopaga*. The abrupt initial closure, whereby the animal was held fast, did not seem in these few instances to effect constriction in definitive measure. Appearances indicated rather that in the region where the captured nematode was encircled its body had been squeezed to approximately one-fourth of its normal compass, so that in the beginning musculature and organs, though rather severely compressed, were by no means severed. During a period of approximately 30 minutes further constriction appeared to ensue, bringing about injury to internal parts of the animal, and consequently causing its disablement. Strangulation of prey in constricting rings was therefore considered as taking place, in some measure, progressively. Since the heavy musculature, especially of the larger sturdier nematodes, might well offer appreciable resistance to compression until its tone has become impaired by excessive exertion, partly progressive strangulation may, indeed, not be wholly at variance with complete initial closure of the predaceous ring under experimental conditions where, in the absence of a sizeable, reluctantly yielding animal body, closure is unopposed.

In an earlier paper (6) I recorded my failure to see any adhesive substance present on the constricting rings of the four fungi

then known to produce such predaceous organs. Rather unexpectedly some evidence of a glutinous secretion was found in examining a culture of the fungus under consideration. A completely closed ring in which no nematode had been captured was found connected with the head of a living nematode by a delicate filament of an extremely elastic substance. The animal repeatedly stretched this filament to a length of approximately $10\ \mu$, then being apparently unable to increase its pull, it held the filament under tension for a few seconds before relaxing. On cessation of the strain, the animal's head was promptly drawn back close to the swollen ring, through contraction of the elastic tether to a length of about $1\ \mu$. After several seconds of rest the nematode again stretched its leash with the same futile outcome as before. The effort was repeated some hundreds of times in the course of an hour. The curious gymnastic exercise appeared of little significance, except in showing vividly that an elastic adhesive substance was somehow present on the inner surface of the ring. As adhesive material would seem superfluous for detaining eelworms caught in a swollen ring, it may conceivably function in ordinary instances of capture as part of the mechanism that springs the annular trap.

When amply provided with nourishment from captured nematodes, the mycelium of the fungus gives rise to scattered erect conidiophores, each bearing a single terminal conidium (FIG. 1, *K, L, M*). This asexual reproductive apparatus reveals morphological features distinctive of the species. While in all congeneric predaceous forms previously described the conidiophore tapers continuously from base to apex, in the present fungus it expands at the apex into a knob-like termination (FIG. 1, *N, O*). Contrary to expectations that might be entertained under the circumstances, attachment of the conidium to this distended apex (FIG. 1, *K, L, M*) is not appreciably wider than in related species where no terminal modification is present. After disarticulation of the conidium its base does not show the somewhat convexly rounded truncate outline usual in related forms, but commonly retains a noticeably concave profile with rather sharp demarcation between peripheral wall and basal membrane (FIG. 1, *P, a-s, v*). This aberrance in proximal outline of the asexual spore may possibly be traceable to a somewhat different manner of conidial abjunction

from that prevailing in other species; a close juxtaposition of two septa observable at the base of some spores (FIG. 1, *P, t, u*) suggesting that abjunction may be accomplished here through separation of two distinct partitions rather than by median splitting of a single partition. Some little encouragement for such an interpretation is supplied in the fact that the conidia regularly contain only two septa, which delimit a small basal cell and a small apical cell from a large ventricose median cell; whereas the conidia of similar conformation in *Dactylella bembicodes* and *Dactylaria thaumasia* Drechsl. regularly contain three septa, spaced so as to delimit two rather small cells below and a small apical cell above a large ventricose penultimate cell. It must be admitted, of course, that the presence of a concave basal outline in the three-septate conidia occasionally produced by the form under discussion (FIG. 1, *P, v*), and the absence of such an outline in occasional two-septate spores of *D. bembicodes*, *D. thaumasia*, and *Arthrotrrys dactyloides*, argue somewhat against the suggested interpretation.

Uniseptate conidia (FIG. 1, *P, r, s*) are somewhat more frequently observed in cultures of the fungus than triseptate specimens, though their maturity and even more the maturity of undersized conidia devoid of cross-walls (FIG. 1, *P, q*) is naturally subject to doubt. The biseptate condition, in any case, predominates so strongly that it must be considered characteristic of the species. With respect to their main dimensions the conidia show rather moderate ranges of variation. The relevant metric data included in the diagnosis were derived from 100 measurements of biseptate conidia selected at random in equal numbers from nematode-infested cultures and from pure cultures showing abundant sporulation. These measurements gave a distribution of values for length, expressed to the nearest micron, as follows: 28 μ , 2; 29 μ , 3; 30 μ , 2; 31 μ , 3; 32 μ , 11; 33 μ , 19; 34 μ , 16; 35 μ , 21; 36 μ , 7; 37 μ , 11; 38 μ , 4; 39 μ , 1; and a distribution of values for width expressed to the nearest micron, as follows: 15 μ , 1; 16 μ , 1; 17 μ , 3; 18 μ , 9; 19 μ , 26; 20 μ , 31; 21 μ , 14; 22 μ , 11; 23 μ , 3; 24 μ , 1.

After a conidiophore has served its primary function it frequently declines to the substratum, and gives rise, often from one of its basal cells, to a secondary conidiophore (FIG. 1, *O*) whereon

another conidium is borne. Instances of somewhat different repetitive development are found occasionally when conidia, after falling on a stale substratum, germinate by the production of a delicate, erect conidiophore (FIG. 1, *Q*) that in due course bears a secondary conidium.

On fresh agar media the conidia germinate promptly by the more commonplace production of germ hyphae, which readily grow out to form extensive mycelia. Pure cultures of the fungus, free of bacterial contamination, have been obtained conveniently by removing newly formed asexual spores from the tall hyphae supporting them, to tubes of sterile maize meal agar; the removal being accomplished by means of slabs of a sterile agar medium held on a flamed platinum spatula. In these pure cultures tall conidiophores and bisepitate ventricose conidia, much like those produced by predaceous mycelia, were always formed abundantly, often with a relatively small number of hyaline conidioid bodies apparently not corresponding to any structures hitherto observed in related species. Apparently the bodies in question are never borne on tall conidiophores of the same type as those bearing the ventricose conidia, but instead are produced singly on short, erect, slightly tapering, hyaline branches, often once or twice septate, and usually measuring 10 to 20 μ in length, 3 μ in width at the base, and about 1.5 μ in width at the apex (FIG. 1, *R-U*). They are mostly of a more or less cylindrical shape, bluntly rounded at the apex and usually tapering somewhat toward the basal end (FIG. 1, *R-U*; *V*, *a-h*). They commonly measure 20 to 40 μ in length and 6 to 8 μ in width. Although occasional specimens, presumably representing early stages of development, contain vacuolate protoplasm (FIG. 1, *V*, *f*) not markedly different from that of young conidia, most of the bodies (FIG. 1, *V*, *a-e*, *g*, *h*) are largely filled with globules of nearly uniform size that appear arranged in transverse layers somewhat like bullets in canister shot. Many of the bodies (FIG. 1, *R*; *S*; *T*; *V*, *h*), including especially the shorter ones, appear almost certainly to be continuous; others show vague indications of an approximately median septum (FIG. 1, *U*; *V*, *a-e*, *g*), though owing to the difficult optical conditions associated with the globulose internal structure I have so far not been able to satisfy myself that a cross-wall is actually present.

The production of the elongated spore-like bodies in addition to large ventricose conidia might possibly be considered expressive of a tendency toward dimorphism comparable yet opposite to the tendency toward conidial dimorphism in *Arthrotrrys dactyloides*; for with respect to dimensions and shape the bodies resemble the uniseptate elongated conidia usually produced by *A. dactyloides*, while the swollen biseptate conidia occasionally produced by that species are not dissimilar to the ventricose spores typical of the present fungus. However, in *A. dactyloides* the conidia of the more exceptional type are borne on the same tall conidiophores as those of the usual type, and the two types show no marked difference either in the organization of their contents or in their readiness to germinate. Any presumed analogy with *A. dactyloides* is thus seriously disturbed; and it remains very uncertain whether the elongated bodies can be at all closely homologized with the ventricose conidia.

Of the several morphological features that might suggest a suitable epithet for the species, the bulbous apical modification of the conidiophore appears least apt to convey an objectionable connotation. At the risk, perhaps, of some exaggeration the fungus is described under a name compounded of two words meaning "pestle" and "form" respectively.

***Dactylella doedycoides* sp. nov.**

Mycelium effusum; hyphis hyalinis, septatis, plerumque 2-4 μ crassis, laqueos circulares 20-36 μ latos in 3 cellulis arcuatis 16-28 μ longis medio 4-7 μ , extremo 2.5-5 μ crassis consistentes ex ramulo biloculari circa 10-20 μ longo 2.5-4 μ crasso proferentibus; his laqueis vermiculos nematodeos illaqueantibus, deinde tum per contractionem et inflationem trium cellularum animalia magnopere comprimentibus, ita haec trucidantibus, statim integumentum perforantibus, hyphas intus evolventibus quae carnem exhauriunt. Hyphae fertiles hyalinae, erectae, septatae, plerumque 225-500 μ altae, basi 5-8 μ crassae, sursum leviter attenuatae, prope apicem 2-3 μ crassae, apice abrupte tuberantes, ibi 3-5 μ crassae et unicum conidium ferentes. Conidia hyalina, turbinea, apice rotundata, deorsum paulum attenuata, basi abrupte truncata vel saepe aliquantulum cavata, 28-39 μ (saepe circa 34 μ) longa, 15-24 μ (saepe circa 20 μ) lata, vulgo biseptata—loculo infimo obconico, 4-10 μ (saepe circa 6.6 μ) longo; loculo medio dolioformi, ventricoso, 16-26 μ (saepe circa 22.7 μ) longo; loculo summo 2.5-7 μ (saepe circa 4.7 μ) longo.

Vermiculos nematodeos multarum specierum usque .6 mm. longos laqueans consumensque habitat in humo silvestri prope Butternut, Wisconsin.

Mycelium spreading; vegetative hyphae hyaline, septate, mostly

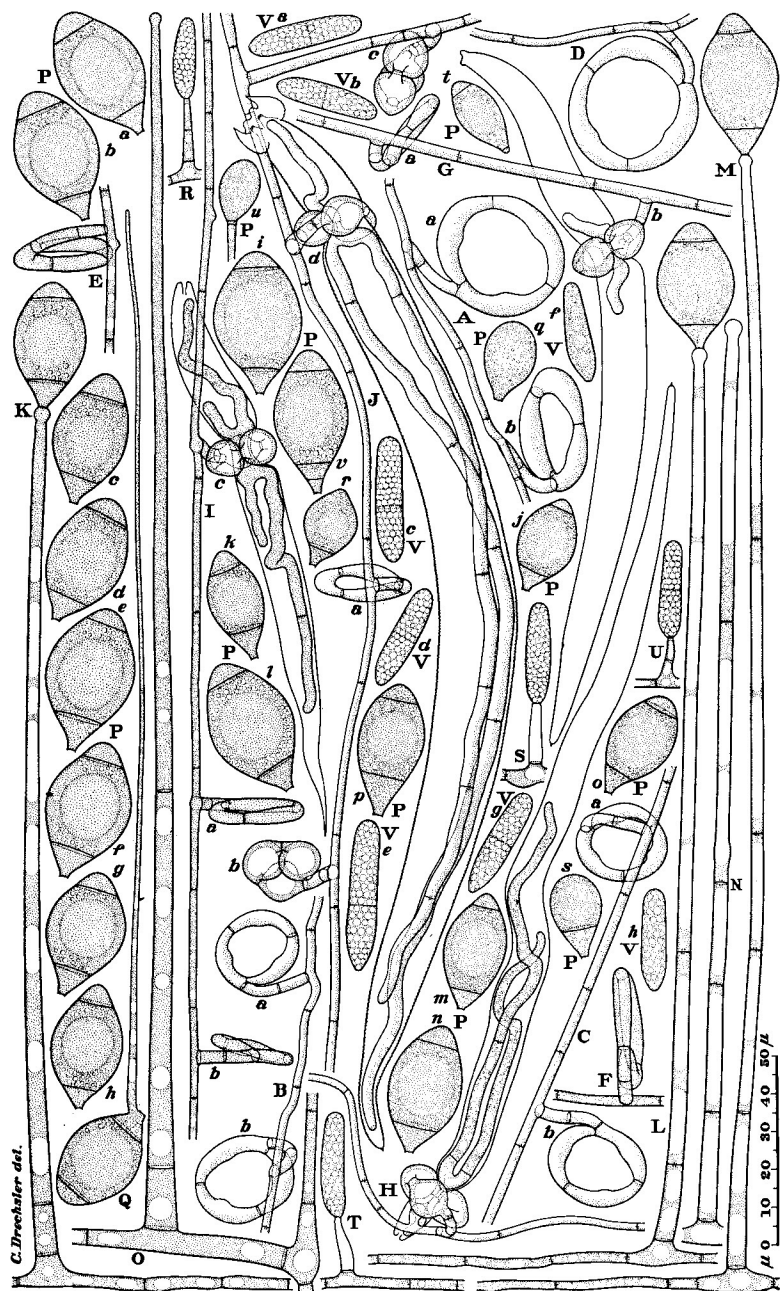


FIG. 1. *Dactylella doedycoides*.

2 to 4 μ wide, often, especially in the presence of nematodes, producing mostly underneath and at right angles to their axes approximately circular rings 20 to 36 μ in outside diameter, composed individually of 3 arcuate cells 16 to 28 μ long, 4 to 7 μ wide in the middle, and 2.5 to 5 μ wide at the ends—the first and third of the cells being united usually to each other as well as to the distal end of a somewhat curved or straight supporting branch 10 to 20 μ long, 2.5 to 4 μ wide, and consisting usually of 2 cells; following ensnarement of a nematode the individual ring through contraction and inflation of its component arcuate cells constricting the animal to death or into a state of reduced activity preceding death, then perforating the integument and extending lengthwise through the body assimilative hyphae that appropriate the fleshy contents. Conidiophores hyaline, erect, septate, 225 to 500 μ high, 5 to 8 μ wide at the base, tapering gradually upward to a diameter of 2 to 3 μ , then expanding abruptly into a knob-like tip 3 to 5 μ wide, whereon is borne a single conidium. Conidia hyaline, somewhat top-shaped, often tapering noticeably toward the abruptly or somewhat concavely truncate base, 28 to 39 μ (average 34 μ) long, 15 to 24 μ (average 20 μ) wide, usually divided by 2 septa into 3 cells—the basal obconical cell then measuring 4 to 10 μ (average 6.6 μ) in length, the middle swollen barrel-shaped cell measuring 16 to 26 μ (average 22.7 μ) in length, and the terminal cell measuring 2.5 to 7 μ (average 4.7 μ) in length.

Capturing and consuming nematodes measuring up to .6 mm. in length, referable to such genera as *Aphelenchoides*, *Plectus*, *Rhabditis*, *Diploscapter* and *Wilsonema*, it occurs abundantly in leaf mold in deciduous woods near Butternut, Wis.

A SPECIES OF DACTYLARIA WITH STALKED ADHESIVE KNOBS

Among several cultures of nematode-capturing fungi that Dr. M. B. Linford (12) isolated from Hawaiian soils and very kindly sent to me late in 1937 was a species of *Dactylaria* conspicuously different from any of the similarly predaceous hyphomycetous forms with which I had at the time become acquainted. Although the species had not been seen in the many cultures prepared, as occasion offered during the preceding four years, mainly with decaying vegetable refuse collected near Washington, D. C., it appeared in May, 1938, in a number of *Pythium* cultures to which had been added small pinches of somewhat woody, friable remnants from rotting stems of the giant ragweed, *Ambrosia trifida*

L., collected in Arlington, Va., a few weeks earlier. Addition of the ragweed detritus afforded development of bacteria in such meager quantity that nematodes addicted to ingestion of bacterial slime multiplied only sparingly, while forms equipped with a stylet and subsisting on protoplasm sucked from living *Pythium* filaments attained appreciably greater numbers. By far the most numerous of the eelworms expropriating the oomycetous mycelium was a species apparently identifiable as *Aphelenchoides parietinus* (Bastian 1865) Steiner 1932, whose frequent parasitism on fungus hyphae has been set forth by Christie and Arndt (2). Because of its abundance this species provided the chief source of nourishment for the new *Dactylaria*, which, wherever observed, was always found to have extended its mycelium from a deposit of ragweed refuse into the surrounding agar substratum. Other nematodes, including representatives of the genus *Rhabditis*, were also utilized by the fungus, suggesting that its development in the cultures was perhaps encouraged more by the relative freedom of the substratum from growth of putrefactive bacteria than by the taxonomic relationships of the eelworms available for consumption.

Although the new species of *Dactylaria* is correctly to be reckoned among the predaceous fungi, its attack on nematodes in my cultures was for the most part that of a parasite; for in most instances the animals were invaded by germ-tubes from adhering conidia. Usually several conidia were found attached to the anterior end of a nematode undergoing infection, so that as the encumbered animal continued to move about it gave somewhat the appearance of being provided with excessively long cephalic processes (FIG. 2, A). Infection was accomplished by narrow perforation of the integument, and extension into the animal of a germ tube from each conidium. The germ tubes continued their growth lengthwise through the nematode as branching hyphae, their advance being marked by fatty degeneration of musculature and internal organs. After appropriating the degenerating materials the internal hyphae would break through the integument and extend themselves into the surrounding substratum as new mycelial filaments on which would be borne at intervals stalked globose knobs (FIG. 2, B-G) generally similar to the predaceous knobs of *Dactylella ellipsospora* Grove and *D. asthenopaga* Drechsl. Much

as in these two species the globose knobs were functional in the capture of prey by means of a transparent adhesive substance secreted by them. A process arising from the individual knob would grow through the cushion of adhesive substance, narrowly perforate the animal's integument, and intrude a subspherical body that would disable the animal, thereby rendering it subject to invasion and expropriation by haustorial filaments.

With ample nourishment being supplied by captured animals, the fungus produces erect conidiophores that are shorter and more delicate than those of any other hyphomycetous form now known to prey on nematodes. Following development of a first conidium (FIG. 2, *H*) the axis of the conidiophore often elongates to produce a second one farther on, the first being pushed into a lateral position. Repetition of the process results in the development of several conidia in a loosely radiating head. The conidia are relatively uniform in structural design (FIG. 2, *N*, *a-s*; *O*, *a-s*; *P*), in nearly all instances being divided by four transverse septa into five cells. Four of these cells, approximately cylindrical in shape and nearly equal to one another in length, make up the main part of the spore. The fifth cell terminating the conidium is of a prolate ellipsoidal shape like the predaceous knobs borne on the mycelial hyphae. Though noticeably smaller than those knobs, it is nevertheless similarly adhesive, and functions in attaching the conidium to any active eelworm that may chance to come in contact with it. Occasionally a second adhesive knob may be found present at the proximal end of a detached spore (FIG. 2, *O*, *a, l, p*); its development possibly having taken place subsequent to disarticulation. Now and then a conidium may contain as many as eight cylindrical segments (FIG. 2, *O, k*), following division of some or all of the four cylindrical segments ordinarily present by median septa.

On removing its conidia from the conidiophores to sterile agar media by means of a small agar slab held on a flamed platinum spatula, the fungus may often be brought directly into pure culture, though at times further procedure may be necessary to remove contaminating bacteria. Even in the absence of extraneous organisms the mycelium is extended rather slowly on maize meal agar, and when extended, is usually somewhat inconspicuous, owing

to meager development of aerial elements. Besides the hyphal anastomoses frequent in related species, the fungus shows in pure culture scattered knots composed of irregular hyphal branches intricated with one another. Sporulation is usually somewhat tardy, yet after several weeks numerous conidiophores are often present, many of them bearing individually 10 to 15 conidia in loose capitate arrangement (FIG. 2, *I, J*) on a sporiferous tip modified with slight geniculations and an occasional spur (FIG. 2, *K, L, M*). The conidia thus produced, like those found in nematode-infested cultures, are always provided distally with a globose adhesive knob.

In no other fungus so far known to prey on nematodes is the conidium consistently furnished with a special adhesive part at the time of its development. The nearest approach to such consistent modification is shown in *Dactylella leptospora* Drechsl., which often in pure culture and occasionally in nematode-infested cultures gives rise to conidia bearing terminally a globose knob. In *D. leptospora*, it is true, the conidial knobs have not been seen operative in attaching spores to active eelworms; whereas in the fungus under consideration the homologous modifications are conspicuously efficient in promoting a parasitic mode of attack. Presumably, however, this marked difference in observed usefulness derives from a difference in suitability of some agar substrata for the operation of the conidial knobs produced by the two species, rather than from any essential difference in function.

A term compounded of two words meaning "to fasten" and "seed" respectively, is deemed an appropriate specific epithet for the fungus.

***Dactylaria haptospora* sp. nov.**

Mycelium effusum; hyphis sterilibus septatis, hyalinis, 1.3–4.5 μ crassis, bullas globosas vel ellipsoideas 6–10 μ longas, 5–8.5 μ crassas, ex ramulo recto vel curvato, saepius 4–30 μ longo, circa 1.5–2.5 μ crasso, continuo vel 1–3-septato emittentibus; his bullis ad vermiculos nematodeos inhaerentibus, ita animalia tenentibus, integumentum eorum perforantibus, hyphas intrudentibus quae carnem exhauriunt. Hyphae fertiles hyalinae, erectae, septatae, 50–150 μ altae, basi 1.7–2.7 μ crassae, sursum leviter attenuatae, apice circa 1.5 μ crassae, ibi plus minusve geniculatae interdum parce ramosae, 1–15 conidia in capitulum laxum singulatim deinceps gerentes. Conidia hyalina, elongato-cylindrata, in toto 35–60 μ longa, medio 2.2–3.2 μ crassa, vulgo in 5 cellulis consistentia: cellula summa globosa vel ellipsoidea, 3–5 μ longa,

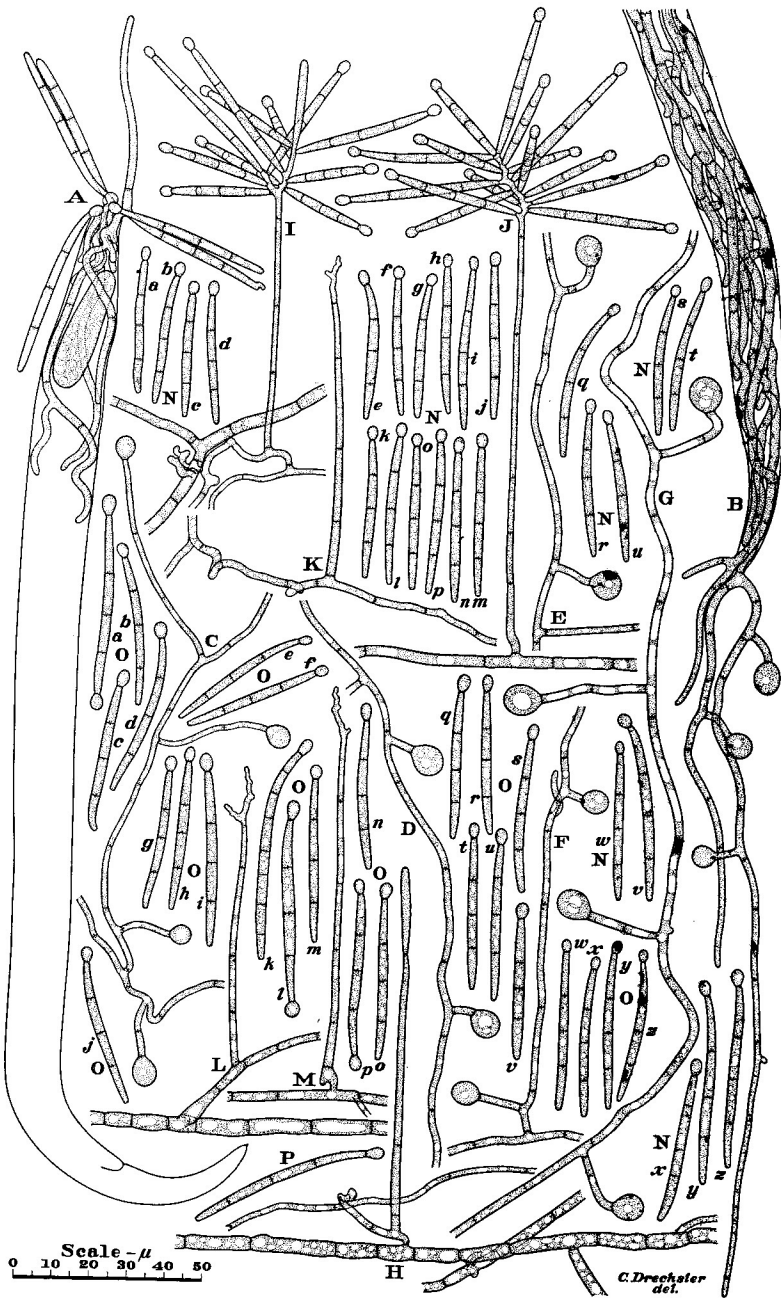


FIG. 2. *Dactylaria haptospora*.

2.5–3.7 μ crassa, glutinosa itaque saepe ad vermiculos nematodeos inhaerente: 4 alteris cellulis inter se subaequalibus, conjunctim partem cylindratam saepius sursum et deorsum plus minusve attenuatam conficientibus. Conidia rarius 5–8-septata, atque rarius non modo apice sed etiam basi cellula glutinosa instructa.

Vermiculos nematodeos diversos interficiens habitat in caulibus putrescentibus *Ambrosiae trifidae* in Arlington, Virginia, item in terra agresti in Hawaii.

Mycelium spreading; the vegetative hyphae hyaline, septate, 1.3 to 4.5 μ wide, often, especially in the presence of nematodes, giving rise here and there on stalks frequently straight or somewhat curved, 4 to 30 μ long, 1.5 to 2.5 μ wide, continuous or containing 1 to 3 septa, to unicellular adhesive knobs subspherical or prolate ellipsoidal in shape, 6 to 10 μ long and 5 to 8.5 μ wide; the knobs holding fast to nematodes, individually perforating the integument of the adhering animal, and intruding haustorial filaments lengthwise through its body to appropriate the fleshy contents. Conidiophores hyaline, erect, septate, 50 to 150 μ high, 1.7 to 2.7 μ wide at the base, very gradually tapering upward to a width of about 1.5 μ , then terminating often in a slightly branched more or less geniculate sporiferous part formed by repeated elongation following successive apical production of conidia up to 15 in number in loosely capitate arrangement. Conidia hyaline, elongated cylindrical, 35 to 60 μ long, 2.2 to 3.2 μ wide in the middle, usually divided by 4 septa into 5 cells: the distal cell globose or prolate ellipsoidal, 3 to 5 μ long, 2.5 to 3.7 μ wide, often adhering to a nematode and directly operative in causing its infection; the other 4 cells approximately equal to one another in length, together making up an elongated part often tapering more or less both toward its base and toward the tip. Conidia more rarely containing 5 to 8 cross-walls, and more rarely, too, provided with an adhesive globose cell not only at the apical end but also at the basal end.

Destroying various species of nematodes it occurs in decaying woody remnants of *Ambrosia trifida* in Arlington, Va., and also in field soils in Hawaii.

A SPECIES OF TRIDENTARIA PREYING ON WEAKENED EELWORMS

A fungus of unusual predaceous behavior made its appearance in a maize-meal-agar plate culture originally used in isolating a species of *Pythium* from some discolored roots of a smartweed (*Persicaria Hydropiper* L.) plant dug up in a moist field near

Butternut, Wis., early in September, 1938. When the culture was several days old and completely permeated with *Pythium* mycelium, it had been further planted with pinches of leaf mold taken from deciduous woods near Butternut, Wis., early in September, 1938. Thirty days after this final addition of vegetable material a tract of the substratum embracing about 100 square millimeters and adjacent to one of the leaf-mold deposits was found sparsely permeated by a delicate septate mycelium reminiscent of the sparse mycelium of *Triposporina aphanopaga* Drechsl. The fungus had evidently grown out from the forest refuse, and seemed to be wholly dependent for nourishment on the nematodes captured by it.

Destruction of nematodes by the fungus was on a relatively small scale; the number of animals consumed altogether probably not exceeding five hundred. All of the eelworms examined soon after their capture, before their morphological features had become obliterated beyond recognition, appeared to belong to a single species tentatively identified as *Aphelenchoides parietinus*. The captives, whether large or small, invariably showed rather extensive infection, especially in their median and posterior parts, by an organism producing aggregations of subspherical spore-like bodies about 1.5μ in diameter, each containing a somewhat eccentrically placed refractive globule approximately $.6 \mu$ in diameter. Continued accumulation of these minute bodies, which in shape and structure appeared closely comparable to some of the spores observed in nematodes by Micoletzky (13: p. 285-286, Taf. XI, 49 c; 50 c, d), was accompanied by progressive enfeeblement and finally complete disablement of the animal. Only nematodes already much enfeebled by the internal parasite were taken by the fungus.

This limitation in predaceous activity has its cause apparently in the meager differentiation of the mycelial elements operative in effecting capture. Repeated examination failed to disclose any evidence that vegetative filaments ever give rise to structures recognizable as predaceous apparatus previous to the moment prey is engaged and held; though, to be sure, captured nematodes are usually found encircled by a hyphal branch (FIG. 3, A-D) in a manner recalling the encirclement of eelworms by non-constricting rings of *Dactylella leptospora* and *Dactylaria candida* (Nees)

Sacc. In some instances the encircling element may even constitute a ring with a closure of contact if not of anastomosis (FIG. 3, *A*). More frequently, however, the tip of the element is definitely free, and the impression given is that encirclement came about through growth of the branch around the animal after its capture (FIG. 3, *B*; *C*; *D*, *c*, *d*). Unless appearances are misleading the animal is held at the beginning merely by adhesion to the distal part of a hyphal branch. If the branch is not already wider than the parent mycelial filament, it undergoes some widening subsequently, either throughout its length, or at times more especially in its distal portion. As the thickened branch continues its growth somewhat laterally in giving rise to the encircling element, its adhering tip narrowly perforates the integument of the captive and sends haustorial hyphae lengthwise through the fleshy interior. Some nematodes (FIG. 3, *D*, *b*) are captured and encircled by two separate branches (FIG. 3, *D*, *c*, *d*); and, again, a branch (FIG. 3, *D*, *c*) after participating in the capture of one eelworm (FIG. 1, *D*, *b*) may continue growth and capture a second (FIG. 1, *D*, *a*). Development of haustorial filaments is very often noticeably less abundant than in nematodes preyed upon by other hyphomycetes—the more meager development having an obvious explanation in the partial appropriation of available materials by the minute parasite.

Conidiophores were found arising here and there from the tract of mycelium (FIG. 3, *E*–*J*). In stature they show closest similarity to the fertile hyphae of *Dactylella tenuis* Drechsl. The conidia (FIG. 3, *K*, *a*–*z*, *L*) produced on them singly are of unusually distinctive make-up, being composed as a rule of a short obconical two-celled basal part together with three digitate or prong-like distal parts, each of which is divided by three to five transverse septa into four to six cells. In number of conidial prongs the fungus at once recalls *Tridentaria carnivora* Drechsl., a member of the predaceous series that was described in an earlier paper (9) as subsisting by the capture of the testaceous rhizopod *Difflugia constricta* (Ehrenb.) Leidy. However the relationship of the prongs to the basal part is different in the two species; for in *T. carnivora* the basal part is prolonged directly into one of the prongs, whereas in the present species it bears all three prongs

alike as terminal branches in isogonal arrangement. Accordingly, while the conidia typical of *T. carnivora* are symmetrical with reference to only one plane, those of the present species are symmetrical with reference to three planes.

The isogonal branching evident in conidia of the fungus under consideration is more closely approximated in the tridental conidia (7: p. 396, fig. 1, *Q*, *R*) occasionally produced by *Pedilospora dactylopaga* Drechsl., a hyphomycetous form which I first described as predaceous only on the testaceous soil rhizopods *Difflugia globulosa* Duj. and *Trinema enchelys* Ehrenb., but which I have since found preying also on *Sphenoderis dentata* Pen. (10: p. 405-406) and *Geococcus vulgaris* Francé. Similarity in angular relationships is likewise apparent when the symmetrically two-pronged conidia typical of *P. dactylopaga* are compared with the two-pronged conidia (FIG. 3, *K*, *f*, *z*) produced occasionally by the present fungus. The symmetrical dichotomy in the bidentate conidia of both these forms is readily distinguished from the monopodial branching evident in the bidentate conidia produced now and then by *Tridentaria carnivora* (9: p. 392, fig. 1, *I*).

Germination of the curiously designed asexual spores takes place by the production of germ-tubes from the basal end and from the tips of the prongs (FIG. 3, *M*). As in other members of the predaceous series of hyphomycetes, anastomoses of fallen conidia with mycelial hyphae occur frequently (FIG. 3, *N*).

The fungus is referred to *Tridentaria* Preuss, a genus so poorly defined by its author (14) that misgivings as to the wisdom of retaining it have been expressed (11). When earlier I nevertheless ventured to commit *T. carnivora* to this little esteemed taxonomic repository, I was persuaded as much by the realistic appropriateness of the generic term invented by Preuss as by the sketchy definition presumably intended to govern its application. The term appears, if anything, even more felicitous in relation to the conidium of the present species, especially when this structure is considered in combination with the supporting conidiophore. A word meaning "encircling," which it is hoped may prove conveniently suggestive of the unusual predaceous behavior of the fungus, is proposed as a suitable specific name.

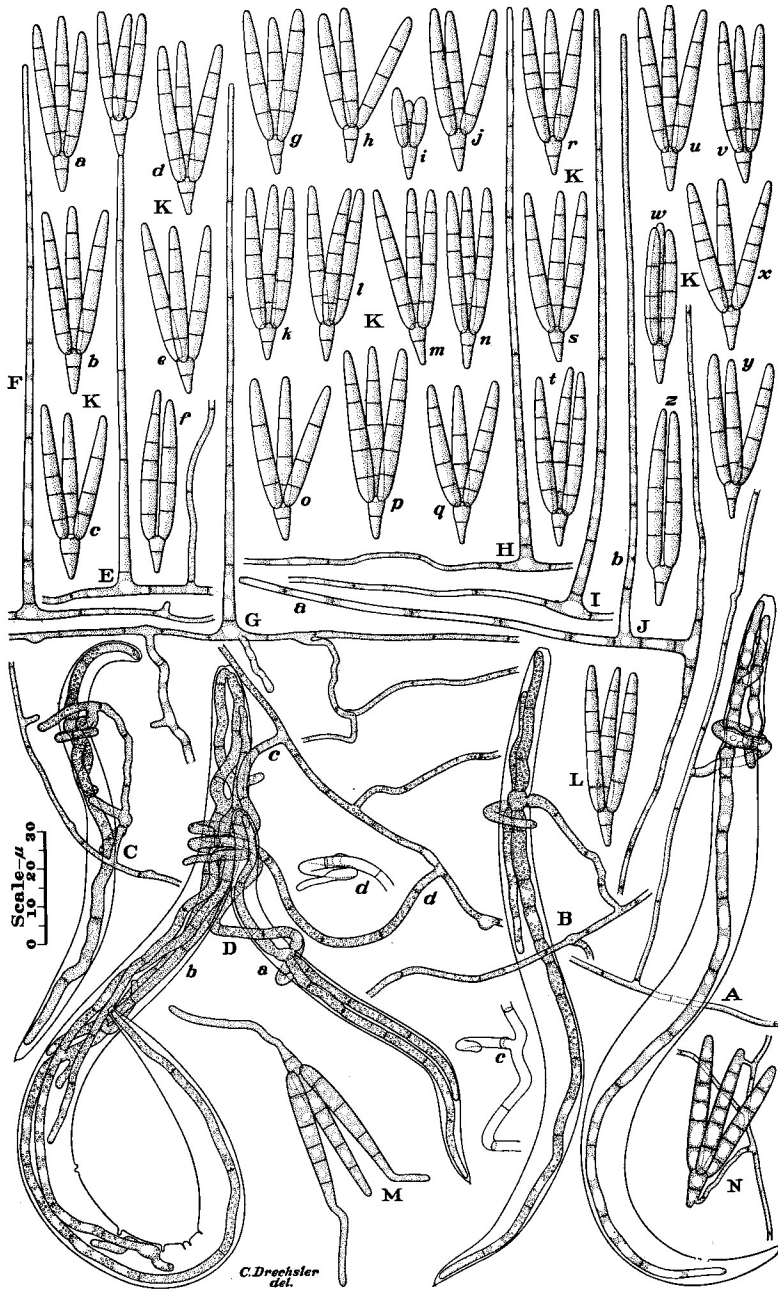


FIG. 3. *Tridentaria implicans*.

Tridentaria implicans sp. nov.

Mycelium sparsum; hyphis sterilibus hyalinis, parce ramosis, mediocriter septatis, vulgo 1–2.5 μ crassis, ramos saepius 15–75 μ longos, 2–3.5 μ crassos gerentibus—his crassioribus ramis vermiculos nematodeos attingentibus et haerendo tenentibus, animalia implicantibus, integumentum eorum perforantibus, hyphas usque 4 μ crassas intrudentibus quae carnem exhauriunt. Hyphae fertiles erectae, hyalinae, septatae, simplices, 100–200 μ altae, basi circa 3.5 μ crassae, sursum leviter attenuatae, apice circa 1.5 μ crassae, unicum conidium ferentes. Conidia hyalina, raro bifurca in modum conidiorum generis *Pedilosporae*, vulgo ex 4 partibus ad instar fuscinae composita—parte infera quae hastile fuscinae facit obconica, uniseptata, basi 1–1.5 μ crassa, sursum latescens, apice rotundata, 4–5.5 μ crassa, ibi 3 dentes aliquantulum divaricatos ferente; dentibus digitiformibus, 12–42 μ saepissime 30–40 μ longis, 3.5–5 μ crassis, plerumque 3–5-septatis, basi rotundatis, sursum nonnihil attenuatis.

Vermiculos nematodeos debilitatos capiens consumensque habitat in humo silvestri prope Butternut, Wisconsin.

Mycelium in mixed culture on agar substrata rather meager; vegetative hyphae hyaline, sparingly branched, septate at moderate intervals, commonly 1 to 2.5 μ wide, giving rise here and there to slightly differentiated branches often 15 to 75 μ long and 2 to 3.5 μ wide; these branches capturing nematodes by adhesion, then individually continuing growth to encircle the captive in 1 to 1.5 turns while narrowly perforating its integument and extending lengthwise through its interior assimilative hyphae up to 4 μ wide that appropriate the fleshy contents. Conidiophores erect, hyaline, septate, simple, 100 to 200 μ high, usually about 3.5 μ wide at the base, tapering gradually upward to a width of 1.5 μ at the tip, and there bearing a single conidium. Conidia hyaline, now and then bifurcate in the manner typical for conidia of the genus *Pedilospora*, but usually composed of 4 parts in trident-like arrangement—the basal part corresponding to the shaft of a trident being obconical, transversely uniseptate, 1 to 1.5 μ wide at the base, widening upward to a diameter of 4 to 5.5 μ at the bluntly rounded apex whereon are borne in isogonal arrangement the other 3 slightly divergent digitate parts corresponding to prongs of a trident; the prong-like parts 12 to 42 μ (usually 30 to 40 μ) long, 3.5 to 5 μ wide, individually tapering noticeably upward from a broadly rounded basal end, and divided by 3 to 5 transverse septa into 4 to 6 cells.

Capturing and subsisting on weakened nematodes it occurs in leaf mold of deciduous woods near Butternut, Wis.

CORRECTIONS CONCERNING DACTYLARIA BROCHOPAGA AND
ARTHROBOTRYS SUPERBA CORDA

An incidental comment in a recent review (1: lines 20, 21) calls attention to an error of more than ordinary seriousness in my earlier paper on nematode-capturing hyphomycetes. The species which I intended to name *Dactylaria brochopaga*, and to which I referred in all other connections by that binomial, was, owing to a lapse of the pen, presented in its formal diagnosis under the binomial *Dactylella brochopaga* (8: p. 517, line 7). Despite the unhappy *lapsus calami* the species has fortunately been cited under its correct generic name by Comandon and de Fonbrune (3, 4), as well as by Roubaud and Deschiens (15). It is hoped that the binomial *Dactylaria brochopaga* will continue to be used in all future references to the fungus.

Rather curiously the somewhat troublesome similarity in spelling between the generic names *Dactylaria* and *Dactylella* is associated with an equally troublesome morphological intergradation between those members of the two genera that constitute members of the predaceous series. When developing on natural or on nematode-infested agar media, the fungi in question offer little difficulty, since on these materials their conidiophores ordinarily bear either a solitary terminal conidium or a terminal cluster of conidia. The generic difference tends to become more or less obliterated when some of the fungi are grown in pure culture on agar media; for a number of capitate forms, including *Dactylaria brochopaga*, then often produce their plural conidia in extended arrangement, and certain forms more usually seen with solitary conidia, as, for example, *Dactylella spermatophaga* Drechsl., then likewise often produce plural conidia in extended arrangement on a conidiophore successively prolonged. On the other hand, two capitate forms, namely *Dactylaria thaumasia* and *Dactylaria haptospora* Drechsl., often appear somewhat more pronouncedly capitate when grown in pure culture, owing to a more copious production of conidia.

In my earlier paper, too, similarity of spelling facilitated an error (8: p. 454, line 28) resulting in a rather obvious misstatement concerning the conidia of *Arthrobotrys superba*. This mis-

statement is to be remedied by substituting for the unintended "uniseptate" the correct word "unseptate."

DIVISION OF FRUIT AND VEGETABLE CROPS AND DISEASES,
BUREAU OF PLANT INDUSTRY,
U. S. HORTICULTURAL STATION,
BELTSVILLE, MARYLAND

LITERATURE CITED

1. [Anonymous.] Rev. Appl. Mycol. **18**: 251. 1939.
2. **Christie, J. R. & C. H. Arndt.** Feeding habits of the nematodes *Aphelenchoides parietinus* and *Aphelenchus Avenae*. Phytopath. **26**: 698-701. 1936.
3. **Comandon, J. & P. de Fonbrune.** Recherches expérimentales sur les champignons prédateurs de nématodes du sol. Conditions de formation des organes de capture. Les pièges garrotteurs. Les gluaux ou pièges collants. Compt. Rend. Soc. Biol. Paris **129**: 619-625. 1938.
4. —. De la formation et du fonctionnement des pièges de champignons prédateurs de nématodes. Recherches effectuées à l'aide de la micromanipulation et de la cinématographie. Compt. Rend. Acad. Paris **208**: 304-305. 1939.
5. **Couch, J. N.** The formation and operation of the traps in the nematode-catching fungus *Dactylella bembicodes* Drechsler. Jour. Elisha Mitchell Soc. **53**: 301-309. 1937.
6. **Drechsler, C.** Organs of capture in some fungi preying on nematodes. Mycologia **26**: 135-144. 1934.
7. —. *Pedilospora dactylopaga* n. sp., a fungus capturing and consuming testaceous rhizopods. Jour. Washington Acad. Sci. **24**: 395-402. 1934.
8. —. Some hyphomycetes that prey on free-living terricolous nematodes. Mycologia **29**: 447-552. 1937.
9. —. A species of *Tridentaria* preying on *Diffugia constricta*. Jour. Washington Acad. Sci. **27**: 391-398. 1937.
10. —. Five new Zoöpagaceae destructive to rhizopods and nematodes. Mycologia **31**: 388-415. 1939.
11. **Lindau, G.** Die Pilze Deutschlands, Oesterreichs und der Schweiz. VIII. Abteilung: Fungi imperfecti: Hyphomycetes (erste Hälfte). In Rab. Krypt.-Fl. Ed. 2. 1^s: —. 1904-1907.
12. **Linford, M. B.** Stimulated activity of natural enemies of nematodes. Science **85**: 123-124. 1937.
13. **Micoletzky, H.** Die freilebenden Süßwasser- und Moornematoden Dänemarks nebst Anhang über Amöbospodien und andere Parasiten bei freilebenden Nematoden. Danske Vid. Selsk. Skr. VIII. **10**: 57-310. 1925.
14. **Preuss, G. T.** Uebersicht untersuchter Pilze, besonders aus der Umgegend von Hoyerswerda. Linnaea **25**: 71-80. 1852.
15. **Roubaud, É. & R. Deschiens.** Capture de larves infectieuses de nématodes pathogènes par des champignons prédateurs du sol. Compt. Rend. Acad. Paris **208**: 245-247. 1939.

EXPLANATION OF FIGURES

FIG. 1. *Dactylella doedycoides*; drawn to a uniform magnification with the aid of a camera lucida; $\times 500$ throughout. *A, B, C*, Portions of mycelial hyphae, each bearing two open constricting rings, *a* and *b*, that have been jostled by passing nematodes from their original approximately vertical positions into more nearly horizontal positions where their cellular make-up is better revealed. *D*, Portion of a mycelial hypha bearing an unusually large open predaceous ring that has been jostled into a nearly horizontal position. *E, F*, Portions of mycelial hyphae, each bearing an open predaceous ring apparently in its original position. *G*, Portion of mycelial hypha bearing two predaceous rings, one of them, *a*, being shown open, the other, *b*, having strangled a small nematode possibly identifiable as a larva of *Aphelenchoides parictinus*, and intruded into the captive two short haustorial branches. *H*, Portion of mycelial hypha bearing a predaceous ring that has strangled a nematode possibly referable to *Plectus parvus* Bastian, and extended two haustorial filaments through half the length of the animal. *I*, Portion of mycelial hypha bearing two open predaceous rings, *a, b*, apparently in their original positions, and a third ring, *c*, that after capturing and strangling a small specimen of *Rhabditis dolichura* Schneider has invaded the captive by means of four haustorial filaments. *J*, Portion of mycelium bearing one open predaceous ring, *a*, two predaceous rings, *b, c*, that have closed without capturing prey, and a fourth ring, *d*, that after strangling an eelworm probably referable to *Wilsonema* sp., has extended haustorial hyphae throughout the length of the captive. *K, L, M*, Portions of hypha, each with an erect conidiophore whereon is borne a mature conidium. *N*, Conidiophore denuded of the conidium it produced. *O*, A denuded conidiophore that was produced from the basal portion of an older one, which now is in contact with the substratum. *P*, Conidia: *a-p*, mature specimens of usual type with two septa and more or less concave basal end; *q*, non-septate specimen that probably became detached while still immature; *r, s*, small specimens, apparently mature, though containing only one septum; *t*, small specimen with two septa, the proximal being so close to the convex basal end that it may possibly correspond to the usual basal membrane; *u*, young specimen set off from the sporophore by two septa very close together, the upper one possibly corresponding to the usual basal membrane, the lower one possibly corresponding to the basal membrane in exceptional specimens such as *t*; *v*, large mature specimen with septation unusual for the species, the three cross-walls showing the positional arrangement most frequent in conidia of *Dactylella bembicodes* and *Dactylaria thaumasia*. *Q*, Conidium germinating by production of a delicate erect germ sporangiophore. *R-U*, Short erect sporophores, each bearing an elongate spore that shows globulose internal structure and apparently is not homologous to a conidium. *V, a-h*, Elongate spores detached from erect sporophores, all of them except the apparently immature specimen *f*, showing characteristic globulose internal structure.

FIG. 2. *Dactylaria haptospora*; drawn to a uniform magnification with the aid of a camera lucida; $\times 500$ throughout. *A*, Specimen of *Aphelenchoides parictinus* invaded at its anterior end by infection hyphae coming from five conidia adhering to the head; one of the conidia having apparently

germinated before becoming attached to the animal. (The oblong body shown in the nematode is a young thallus of the phycomycetous parasite *Haptoglossa heterospora* Drechsl.) *B*, Portion of a specimen of *A. parietinus* permeated with mycelium of the fungus; from the tail-end of the animal have grown out a few vegetative hyphae whereon are borne three stalked adhesive knobs. *C*, Portion of mycelium with four adhesive knobs. *D*, *E*, *F*, Portions of mycelium, each bearing two stalked predaceous knobs. *G*, Portion of hypha with four stalked predaceous knobs. *H*, Portion of mycelium with an erect conidiophore, which terminates in an immature conidium, the first to be produced by it. *I*, Portion of mycelium with an erect conidiophore on which are borne 11 mature conidia, a twelfth conidium being in process of development. *J*, Portion of hypha from which has arisen an erect conidiophore bearing 15 mature conidia. *K*, *L*, *M*, Portions of mycelium, each bearing a denuded conidiophore. *N*, *a-z*, *O*, *a-z*, *P*, Conidia showing variations in shape, dimensions, septation and number of adhesive organs.

FIG. 3. *Tridentaria implicans*; drawn to a uniform magnification with the aid of a camera lucida; $\times 500$ throughout. *A*, *B*, *C*, Nematodes, possibly referable to *Aphelenchoides parietinus*, that after being weakened through extensive infection by a minute internal parasite, were captured individually by adhesion to a branch of the fungus, entwined by a hyphal prolongation, and invaded by haustorial filaments. *D*, Portion of mycelium with two captured nematodes *a*, *b*—nematode *a* having been captured, enveloped, and invaded by the distal part of branch *c*; while nematode *b* was captured, enveloped, and invaded conjointly by the branches *c* and *d*; the portions of branches *c* and *d* enveloping nematode *b* being also shown separately for clearness. *E*, Portion of hypha with an erect conidiophore on which a conidium is borne. *F-I*, Portions of mycelium, each with an erect denuded conidiophore. *J*, Portion of a hypha on which was produced a conidiophore, *a*, that after serving its primary function, declined to the substratum and gave rise to a secondary conidiophore. *K*, *a-z*, *L*, Conidia showing variations in number and dimensions of shaft and prongs, and in abundance of septa. *M*, Conidium germinating by production of germ tubes from base of shaft and from tips of two prongs. *N*, Conidium anastomosing with branches of a vegetative hypha.