Reprinted from MYCOLOGIA, Vol. XXIX., No. 4, 447–552, July–August, 1937
Printed in U. S. A.

SOME HYPHOMYCETES THAT PREY ON FREE-LIVING TERRICOLOUS NEMATODES

CHARLES DRECHSLER

(WITH 18 FIGURES)

In several preliminary summaries (**12**, **13**, **14**) published a few years ago, were set forth synoptically the morphological features of 16 fungi observed to subsist by the capture of free-living nematodes infesting old agar plate cultures started from various decaying plant materials. Little attention was then given to the relationships of the different fungi to species previously described, only one among them, the widely familiar and well characterized *Arthrobotrys oligospora* Fres., whose predacious behavior had been impressively recorded by Zopf (**72**) nearly a half century earlier, being mentioned by name. In a subsequent paper (**15**), consideration of special organs developed by nematode-capturing fungi entailed identification of two other of the 16 forms; one being recognized as *Dactylaria candida* (Nees) Sacc., the other as *Dactylella ellipsospora* Grove. The remaining 13 fungi, with the exception of two species belonging in the Phycomycetes, could be referred to (**16**, **18**, **20**) only rather cumbersomely as members of an interrelated series of Hyphomycetes distributed in large part among the genera *Trichothecium*, *Arthrobotrys*, *Dactylella* (including *Monacrosporium*), *Dactylaria* and *Pedilospora*.

Although some of the mucedinous forms known to capture nematodes are dealt with under established binomials, usage regarding these binomials has not always been consistent. The species concerned are therefore given comparative treatment herein together with the more numerous related species of like biological habit that seem hitherto to have remained undescribed, including four discovered since the summaries were written. In addition there are appended brief accounts of two fungi, which so far have not been seen to capture or parasitize animals of any kind, yet which in all probability represent members of the predacious series, and, perhaps, under suitable conditions may prove destructive to other organisms.

Indeed, with better adapted cultural methods and employment of materials from more varied sources, many other vermivorous Hyphomycetes will undoubtedly be brought to light. A dozen species have been cited elsewhere (18), which from their descriptions alone would seem to belong in the predacious series; the sturdier ones among them, as notably *Trichothecium inaequale* Mass. & Salm., *Monacrosporium elegans* Oud., *M. megasporum* Boed., *M. ovatum* Petch, *M. oxysporum* Sacc. & March., *Dactylella minuta* Grove, *D. minuta* var. *fusiformis* Grove, and *Dactylaria pulchra* Linder, showing in their reproductive structures such close resemblance to species known to prey on roundworms that similarity in trophic relationships is strongly suggested. The suggestion loses little plausibility through the absence of supporting testimony in the relevant literature; for in the opaque solid substrata on which the enumerated fungi were reported, microscopic animals, apparatus of capture, and all evidence of predacious activity are only too effectively concealed from view. Precisely because of such concealment *Arthrobotrys oligospora* continued for decades to be regarded as primarily a saprophytic or coprophilous plant, even among mycologists who encountered it almost daily and to whom Zopf's findings concerning it were well known. On transparent artificial substrata, however, this fungus and its vermivorous allies are readily shown to be decidedly lacking in saprophilous traits. When sizable portions of their mycelia are transferred from pure culture to maizemeal agar well permeated with saprogenous bacteria but devoid of nematodes, development in any significant measure fails to take place; whereas extensive development ensues following transfer to agar both permeated with saprogenous bacteria and well infested with active nematodes. Evidently the predacious Hyphomycetes, like the Zoöpagaceae, absorb only water from their putrescent substrata, obtaining their nourishment entirely from the unfouled materials in the animals freshly killed by them.

In their choice of prey the nematode-capturing fungi show rather little discrimination between species of animals except such as may result from the physical limitations of their own predacious apparatus. Capable of holding eelworms up to 500 or 600 μ in length, the retiary as also the constricting forms destroy promiscuously nearly all nematodes that ordinarily multiply abundantly in agar plate cultures, including besides a few semi-parasitic forms as, for example, *Aphelenchus Avenae* Bastian and *Cephalobus elongatus* de Man, many saprophilous species of *Acrobeles, Acrobeloides, Cephalobus, Diplogaster, Diploscapter, Plectus* and *Rhabditis*.[1] The three more delicate fungi with non-constricting rings are usually limited in their destructiveness to animals not exceeding 350 or 400 μ in length. In general, even smaller dimensions are characteristic of the prey taken by the two fungi provided only with stalked adhesive knobs; one of the two, *Dactylella asthenopaga,* often restricting its predacious activity to specimens referable to the genus *Bunonema,* which, somewhat curiously, are not frequently caught by other fungi. Except in their earlier stages of development, the more robust species of eelworms that in agar cultures soon attain lengths in excess of 600 or 700 μ, are mostly immune from capture. Yet, now and then, powerful specimens of *Dorylaimus* have been found succumbing to infection from an uprooted hyphal network that they had failed to shake off; and, occasionally, constricting rings, though torn from their stalks, have been observed inexorably bringing to an appropriate end the predatory careers of encircled specimens of *Mononchus* as much as 1 mm. in length.

The nematode-capturing Hyphomycetes are most readily isolated through removal of conidia directly from the fertile hyphae to agar plates. This is conveniently accomplished, especially in forms with tall sporophores, by bringing a small slab of agar held on a flamed platinum spatula into contact with the spores, care being taken to avoid contact with the bacterium-laden substratum. As the conidia when produced usually carry no bacteria, cultures free of all contamination are often obtained without any further operation. Except in *Dactylella bembicodes* and *Triposporina aphanopaga* vegetative growth is moderately rapid and results in a rather dense mycelium composed of branching filaments usually

[1] For identification of nematodes I am greatly indebted to Dr. G. Steiner, Principal Nematologist in Charge, Division of Nematology, Bureau of Plant Industry, Washington, D. C.

more or less abundantly anastomosed. As in other members of the predacious series, a peculiar odor is given off in varying strength on different media. Organs of capture are regularly absent in pure culture, the production of such structures usually being indicative of invasion by mites. The retiary forms, all of which generally sporulate well on nematode-infested substrata, sporulate even better in pure culture. When protected from excessively rapid evaporation, the four polycephalous species and the two more nearly monocephalous species, *Arthrobotrys cladodes* and *Dactylaria thaumasia,* develop reproductive apparatus in spectacular luxuriance. The annulose and knobbed forms sporulate moderately in pure culture much as on wormy substrata, though a few of the species behave even more capriciously here, sometimes failing to give rise to any conidiophores at all until after exposure to strong light.

ARTHROBOTRYS SUPERBA Corda

The fungus referred to earlier (**12**: p. 138, lines 29–31; p. 139, fig. 2, A, B) as differing from *Arthrobotrys oligospora* in the smaller size and more nearly equal partitioning of its conidia, occurs widely in decaying vegetable materials. It has been found to develop now and then in agar plate cultures started from pieces of roots or of other underground structures decaying as a result of invasion by phycomycetous parasites. More frequently it has made its appearance on maizemeal agar cultures to which, following infestation with saprophilous nematodes of such genera as *Acrobeles, Acrobeloides, Cephalobus, Diplogaster, Plectus* and *Rhabditis,* had been added pinches of leaf mold from supplies of this material gathered in deciduous woods near Beltsville, Md., Cumberland, Md., Butternut, Wis., and Madison, Wis., as well as in Arlington, Va.

A general similarity to *Arthrobotrys oligospora* at once becomes evident as the fungus extends its mycelium sparsely through a nematode-infested culture. If, on the whole, the filaments are slightly narrower than in the species described by Fresenius, the difference is certainly not pronounced. On the hyphae is borne the predacious apparatus, which consists of anastomosing bails or loops often compounded in some number to form here and there networks of variable extent (FIG. 1, *A, a, b; B*). Capture of prey

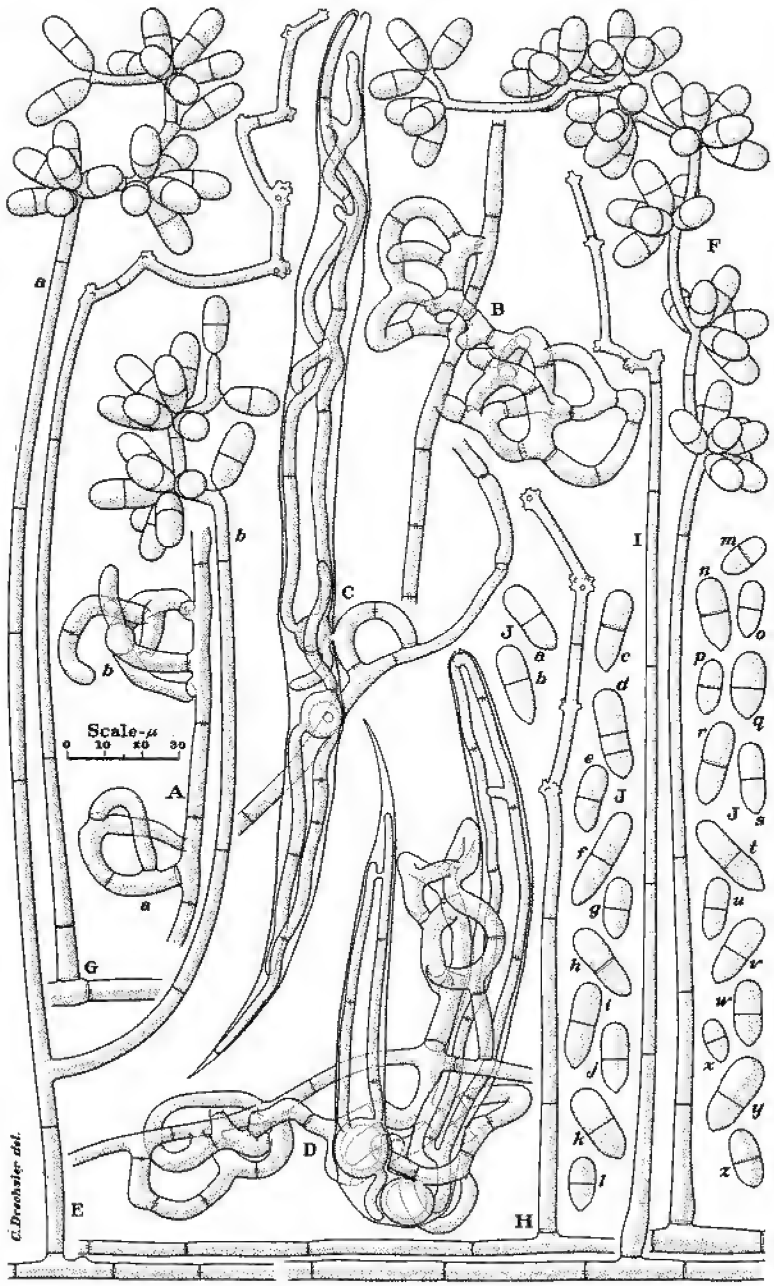

FIG. 1. *Arthrobotrys superba.*

can, of course, be effected by a single arch; sometimes, indeed, being accomplished merely through adhesion of the animal to the outer rim of the hyphal bail (FIG. 1, *C*). Instances of such capture without enmeshment are often very frequent in moist agar cultures; the bacterial slime usually covering the smooth surface here, apparently affording the animal so little hold on the substratum that it can exert no effectual leverage to pull itself away. Under drier conditions, or in the presence of bits of solid material, the struggles of the nematode are not attended with disadvantages quite as serious; so that except for the smaller larvae, adhesion in itself proves insufficient, but needs to be supplemented by enmeshment, whether in a single loop or in a more extensive anastomosed network (FIG. 1, *D*).

Soon after capture is effected the animal's integument is penetrated at a place median in the region of contact by a process about $2\,\mu$ wide thrust out from the predacious element. On reaching the fleshy parts within, this process gives rise to a globose structure that increases in size until after an hour or two it comes to occupy a cross-section of the interior either wholly (FIG. 1, *D*) or in large part (FIG. 1, *C*). The virtual severance of the captive's body accomplished in this way, is promptly reflected in diminution of its movements. When these movements have become relatively sluggish, a number of hyphae arise from the subspherical structure and extend themselves throughout the fleshy interior, their advance being marked by conspicuous degeneration of musculature and organs, with production of very numerous globules consisting presumably of some fatty material. The contents become more and more attenuated from progressive absorption by the permeating hyphae, until finally nothing remains but the diaphanous integument collapsed about the evacuated and very inconspicuous envelopes of the assimilative filaments.

Frequently a nematode is penetrated in two (FIG. 1, *C*, *D*) or more places, and a corresponding number of globose bodies and haustorial systems are intruded to share in the appropriation of its fleshy substance. As was intimated earlier (12), there can scarcely be any doubt that the special function of the globose bodies produced in this species, as also in allied retiary and knobbed forms, is to kill the animal quickly and thus without much delay to make it suitable for invasion by the assimilative hyphae. Certainly the rapid death of captured roundworms achieved by means of the intruded bodies, offers a marked contrast to the lingering decline of nematodes captured by the two Phycomycetes I have described elsewhere under the binomials *Stylopage hadra* (**17**) and *S. leiohypha* (**19**), neither of which develop anything that could be considered a special mortiferous structure.

On developing in agar plate cultures infested with saprophilous nematodes, and therefore in the presence of other fungi as well as of bacteria and a miscellaneous assortment of microscopic animals, the fungus gives rise to conidiophores scattered sparsely over the substratum. The individual conidiophore, arising always as an erect aerial branch from a prostrate mycelial filament, here measures mostly from 100 to 300 μ in height and from 3 to 5 μ in width at the base, whence it tapers upward to a diameter varying between 2 and 3.5 μ. At the tip it is slightly expanded and bears in capitate arrangement usually from 4 to 10 conidia, each of which on falling off leaves behind a short stumpy sterigma. Occasionally, after elongation of the conidiophore, a second head of conidia is formed (**12**: p. 139, fig. 2, A). Three successive conidial clusters have never been seen produced on the same sporophoric axis in nematode-infested cultures.

Much more luxuriant development of conidial apparatus ensues when the fungus is grown in pure culture on some suitable artificial medium as, for example, maizemeal agar. The rapidly growing mycelium then begins to produce numerous conidiophores within a few days after planting; through repeated elongation straightforward or at variable angles, these continue to give rise to successive conidial heads (FIG. 1, *E-I*), until more than a score of clusters may have been formed on a single irregularly geniculate, nodose axis. Besides, the sporophores may give off one (FIG. 1, *E*) or more branches, likewise bearing from one to a dozen conidia at successive nodes. Naturally the very rangy, heavily laden fertile hyphae assume a somewhat procumbent habit and thereby become confusingly entangled with one another. After about 15 days, production of conidia comes to an end, probably as a result of staling. Degeneration becomes increasingly evident, especially in widespread germination of the conidia in place, the germ tubes anastomosing with one another, with neighboring conidia, with conidiophores, or with mycelial hyphae. Very frequently through such vegetative union the conidia of the individual heads become joined to one another and to the distal portion of the conidiophore; and are then supported approximately in their original positions in spite of disarticulation from their sterigmata. In 30 days after planting, cultures of the fungus rather characteristically show extensive evacuation of the vegetative hyphae, evacuation and general collapse of the conidiiferous filaments, germination of the conidia everywhere, accompanied often by their complete or partial evacuation, and widespread promiscuous anastomosis of germ tubes, sporiferous hyphae and vegetative filaments—giving altogether an appearance of pronounced debilitation.

Although in their continued growth and production of successive conidial heads, the sporophores of the fungus resemble those of *Arthrobotrys oligospora*, they differ markedly from the latter in their smaller diameter and generally less robust aspect. A comparison between the conidia of the two species reveals even more decisive differences. In the fungus under discussion these structures are mainly cylindrical, usually tapering only slightly toward the basal end, which is frequently little less bluntly rounded off than the distal end (FIG. 1, *J*, *a-z*). Often, indeed, the proximal half of the conidium is fully as wide as the distal half, and occasionally may even be somewhat wider. A single septum, which is sometimes placed at a slight constriction in the outer contour, and sometimes is unassociated with any external modification, divides the conidium into two approximately equal cells. While a uniseptate conidium is generally to be regarded as immature, it yet appears probable that in many instances a partition is never formed. Conidia with two cross-walls are definitely exceptional (FIG. 1, *J*, *d*). For the most part the spores vary between 12 and 23 μ in length, and between 6.5 and 9.5 μ in diameter, though specimens as much as 28 μ in length, and as much as 10 μ in diameter, have been found. The average values for these dimensions, 16.8 μ and 7.8 μ respectively, that were computed from measurements of 200 specimens taken at random from several lots of material, would seem approximately representative of the species.

In morphology of reproductive apparatus the present fungus agrees better than any other species known to me, with Corda's original description (**10**) of *Arthrobotrys superba;* the correspondence in production of successive heads, in general shape of the conidia, and in their division into two approximately equal cells, being especially persuasive. A tolerably satisfactory agreement with regard to spore dimensions would, moreover, seem to follow from Corda's statement that the conidia of his fungus measured "biz 0,0006 P. Zolltheile" in length. The expression, if interpreted as referring to the old Prussian "Zoll," equivalent to 2.615 cm., would indicate a maximum conidial length of 15.69 μ. Writing only 13 years later, when presumably the linear unit concerned could hardly yet have become entirely unfamiliar, and possibly may even have still been in common use, Fresenius (**23**) converted Corda's expression to "$\frac{1}{55}$–$\frac{1}{59}$ mm." or 18.2–16.9 μ.

It must be admitted, however, that departures from the description of *Arthrobotrys superba* are not wanting. In Corda's figures the conidia are shown more deeply constricted at the septum and more acutely pointed at the base than is usual in my fungus; the sterigmata at the same time being represented as acutely pointed and as spirally arranged on the separate nodes, rather than as bluntly truncate and irregularly arranged. Moreover, the conidiophores, figured consistently with branching rhizoidal systems, are set forth in the text as being provided at the base with an "ästiges, feinfaseriges, strahliges Wurzelgeflechte." The discrepancies in finer details of conidium and sterigma are perhaps to be accounted for partly in the imperfections of the microscopes used a century ago, and partly in an artistic idealism that lacked such restraint as is now usually imposed by the general use of the camera lucida. A tree-like rooting habit appears to have been attributed more often in earlier times than at present to erect sporiferous elements, possibly from a natural though frequently erroneous assumption of similarity to some robust and widely known forms like *Rhizopus nigricans* Ehrenb. that in truth reveal such a habit very clearly even on opaque substrata. If finally the clusters figured by Corda exceed those of the present fungus in number of conidia, they seem hardly less clearly to exceed also the spatial capacity of the nodes as illustrated in their denuded state—a circumstance suggesting that the distinguished iconographer may have chosen here to err on the side of generosity.

In his brief but fairly unambiguous description of *Arthrobotrys oligospora,* Fresenius properly recognized the larger dimensions and unequal partitioning of the piriform conidium of his fungus as representing marked departures from the morphology ascribed to *A. superba.* Somewhat unfortunately, in view of subsequent developments, he mentioned a less profuse production of conidial heads as an important character whereby his fungus was distinguished from Corda's species; and brought this presumed diagnostic feature more prominently into relief in his choice of a name that anyone who has seen the fungus to which it was applied growing in pure culture on a favorable substratum, cannot fail to consider a singularly unhappy one. In spite of these differences, actual and supposed, Fresenius confessed to having harbored misgivings that his fungus might after all be identical with *A. superba,* adding with a hint of suspicion, that in such event it would need to be assumed that Corda's description had in excessive measure sacrificed accuracy to artistic effect.

Coemans (8) after studying some material of *Arthrobotrys* concluded that Corda had been inexact in representing the conidia of his fungus as consisting of two equal cells. He recognized *A. oligospora* as merely a somewhat depauperate form of *A. superba* bearing not more than three verticillate clusters, with few conidia in a cluster. It remains uncertain with which or with how many species of *Arthrobotrys* this investigator may have been dealing. His reference to a variation wherein 2-celled, somewhat elongated, small conidia (12 to 15 μ in length) originated from mycelial filaments, may well have been based on some admixture of material with anastomosing germ tubes, referable either to the species under consideration or to *A. cladodes;* though the possibility that very small spores of one of the larger species may have been concerned, is not to be excluded. Rather curiously, Coemans figured a group of conidia having their two component cells no less equal to one another than those shown in the illustrations of Corda denounced by him. Nevertheless, his strong approval of Fresenius' illustrations indicates that probably for the most part he was dealing with the species described by the German mycologist; the range in spore lengths reported by him, 30 to 40 μ, corroborating in a puzzling manner the decidedly high value, $\frac{1}{28}$ mm., or 35.7 μ, assigned to this dimension in the original description of *A. oligospora*. Coemans' larger illustrations of "spores didymes de l'*Arthrobotrys superba*," though not noticeably impaired by any artistic virtues, show in each of the three specimens figured such deep constriction at the septum, which is placed slightly below the middle, that identification with one or another of the predacious fungi herein discussed is hardly to be attempted.

The nomenclatorial confusion of *Arthrobotrys superba* with *A. oligospora* thus initiated, was later promoted effectively through the meritorious researches of Matruchot (**47**). This author apparently recognized the number of successive conidial clusters as the sole difference between the two species as they occur on natural substrata. He succeeded several times in isolating typical *A. oligospora*, and observed that the fungus which on the original substratum had normally shown two or three spore clusters developed as many as 16 superimposed heads when grown in pure culture on moist slices of carrot. Thus misled by the similarity in asexual reproductive development of the two species, and apparently having neither seen plants with generally smaller conidia divided into approximately equal segments, nor considered the likelihood of such plants being existant, he reduced *A. oligospora* to the status of a cultural form of the earlier described *A. superba*. While this disposition conserved Corda's binomial, it transferred to his species the morphological characterization of an entirely separate congeneric fungus. The application of *A. superba* inaugurated by Coemans and adopted by Matruchot was given wider currency on being incorporated in the works of Saccardo (**61**), Massee and Salmon (**46**) and Lindau (**38**); and has evidently in large part at least governed such scattered usage as has subsequently been accorded to the binomial. Thus, in the absence of morphological comment, it appears probable that citations of *A. superba* found in such floristic contributions as those of Eisenach (**21**), Smith and Rea (**66**), Rea (**57**), Schmidt (**63**), and Girzitska (**25**) were based on specimens of *A. oligospora*. Lind's (**37**) separate enumeration of *A. superba* and *A. oligospora* furnishes evidence that this author regarded the two species as being distinct, without however indicating on what grounds the distinction was acknowledged. On the other hand, Mahju's (43) description of *A. superba*, based on material from rabbit dung in India, shows such close agreement in morphological detail with the nematode-capturing fungi to which I am applying Corda's binomial that its identity with the latter appears altogether probable. The approximately equal partitioning of the conidia and the slight inflation of the sporiferous nodes shown in Berlese's (3) figures of *A. arthrobotryoides* (Berl.) Lindau (= *Trichothecium roseum* var. *arthrobotryoides* Berl.), together with the dimensions, 20–22 × 9–10 μ, attributed to the conidia, suggest the possibility that the Italian author likewise was dealing with Corda's fungus.

Chlamydospores of the type formed by *Arthrobotrys oligospora, A. conoides, A. musiformis* and *Dactylaria thaumasia* have never been observed either in pure or in nematode-infested cultures of *A. superba*.

Shortly after the present studies were begun, there were found developing in a wormy agar plate culture of *Arthrobotrys superba* about a score of flesh-colored disciform apothecia mostly between .5 and .8 mm. in diameter. Viewed from above these apothecia showed individually a central, perceptibly upcurved hymenial region, and surrounding it a slightly prominent circular border (FIG. 18, *R, a*). Except for its somewhat slender central stalk, each fruiting body rested with its under side flush on the substratum. In sections of the hymenium the most nearly mature of the cylindrical asci, measuring 29 to 32 μ in length and 3.1 to 3.4 μ in width, revealed 8 colorless hyaline tear-shaped ascospores about 5 μ long and 1.3 μ wide, the widened ends of the upper spores being directed toward the apex, those of the lower spores toward the base (FIG. 18, *R, b–d*).

As most of the apothecia were slow in maturing, the culture was bathed in water for a time in the hope that accumulated staling products might thereby be partially removed. This treatment, which had previously been found beneficial for the maturation of some much hardier Sphaeriaceae, unfortunately resulted in a thoroughgoing degeneration of every one of the apothecia, making it then impossible to determine the presence or absence of a pleomorphic connection with the predacious conidial form. The discomycete has not been seen again, in spite of several attempts to recover it by employing various substrata, and by planting different strains of *Arthrobotrys superba* together on the same plate culture. At first thought the small size of the ascospores would seem to preclude definitely any pleomorphic connection with a fungus dependent for its nourishment on capture of nematodes, since such capture requires in the very beginning a substantial outlay of material for the development of predacious apparatus that needs to be sturdy as well as of some extent. However, the similarity in shape of the ascospores to the endogenous spores of *Protascus subuliformis* Dang. (**11**) suggests that possibly the sexual spores of the predacious Hyphomycetes might begin development in the manner usual among parasites, that is, by adhering to the animal, penetrating the integument and extending a mycelium through the fleshy interior.

ARTHROBOTRYS CLADODES

A fungus so similar to *Arthrobotrys superba* that I first mistook it for that species, was repeatedly obtained in nematode-infested agar plate cultures to which pinches of leaf mold from deciduous woods in Virginia and Maryland had been added. In its vegetative stage there is little to distinguish it from Corda's species, or for that matter, from *A. oligospora* and *A. conoides;* a general family resemblance to those congeneric forms being evident not only in the undifferentiated mycelial hyphae and in the greatly enlarged storage filaments often developing tardily (FIG. 2, *A*), but also in the predacious apparatus. For this apparatus consists likewise of fused hyphal bails or loops that at the beginning are formed singly here and there on the mycelial filaments, but usually soon become compounded into more or less extensive anastomosing reticular systems (FIG. 2, *B*, *C*). Nematodes are captured often through mere adhesion to the outer surface of these specialized structures (FIG. 2, *E*), or through adhesion combined with physical enmeshment (FIG. 2, *D*).

To extend the resemblance, the sparsely scattered conidiophores arising from the substratum in nematode-infected cultures present much the same appearance as the usually monocephalous conidiophores produced by *Arthrobotrys superba* under similar conditions. Unlike that species, however, when the fungus is brought into pure culture on a favorable medium, as, for example, maizemeal agar, it is slow in giving rise to conidiophores. Often no fertile hyphae are formed until two or three weeks after the culture was planted—at a time, therefore, when in contemporary cultures of *A. superba* conidial production has usually come to an end, and degeneration is well under way. The acme of reproductive development is ordinarily not reached until four weeks after planting; examination of the conidiophorous turf under low magnification then revealing an innumerable array of handsome spore clusters, all in prime condition like the hyphae supporting them, and offering accordingly a very marked contrast to the advanced debilitation evident in cultures of *A. superba* started at the same time.

Axial elongation of the conidiophores with development of successive spore clusters takes place only rather infrequently; increase in number of heads being made possible, instead, through the production of one (FIG. 2, *F*) or more (FIG. 2, *G*, *a*, *c*) branches from the primary axis. Each of the branches, after giving rise to a terminal cluster of conidia, may in turn supply a number of fertile elements. Lateral branching, combined often with crowded arrangement of the conidiophores on the parent filament (FIG. 2, *F*, *H*), thus accomplishes here, in part at least, the purpose accomplished in *Arthrobotrys superba* through repeated elongation. Besides, the individual heads contain a larger number of spores than are ordinarily found at separate nodes in Corda's species; the considerably greater spatial requirements being provided for through marked inflation of the sporiferous tips (FIG. 2, *H*, *I*, *a–g*), which in the more extreme instances often come to appear as lobulate or coralloid enlargements (FIG. 2, *H*, *a*; *I*, *a*, *b*, *e*). A denser capitate arrangement is made possible by noticeable tapering in the proximal portion of many conidia (FIG. 2, *J*, *a–z*). If the two cells composing the more tapering specimens (FIG. 2, *J*, *d*, *e*, *h*, *i*, *o*, *y*, *z*) are often perceptibly unequal, the conidia on the whole yet show both in shape and partitioning as also in size much more similarity to *A. superba* than to *A. oligospora*. Variations in the conidial dimensions would seem somewhat less pronounced than in some other nematode-capturing Hyphomycetes. The 200 spore meas-

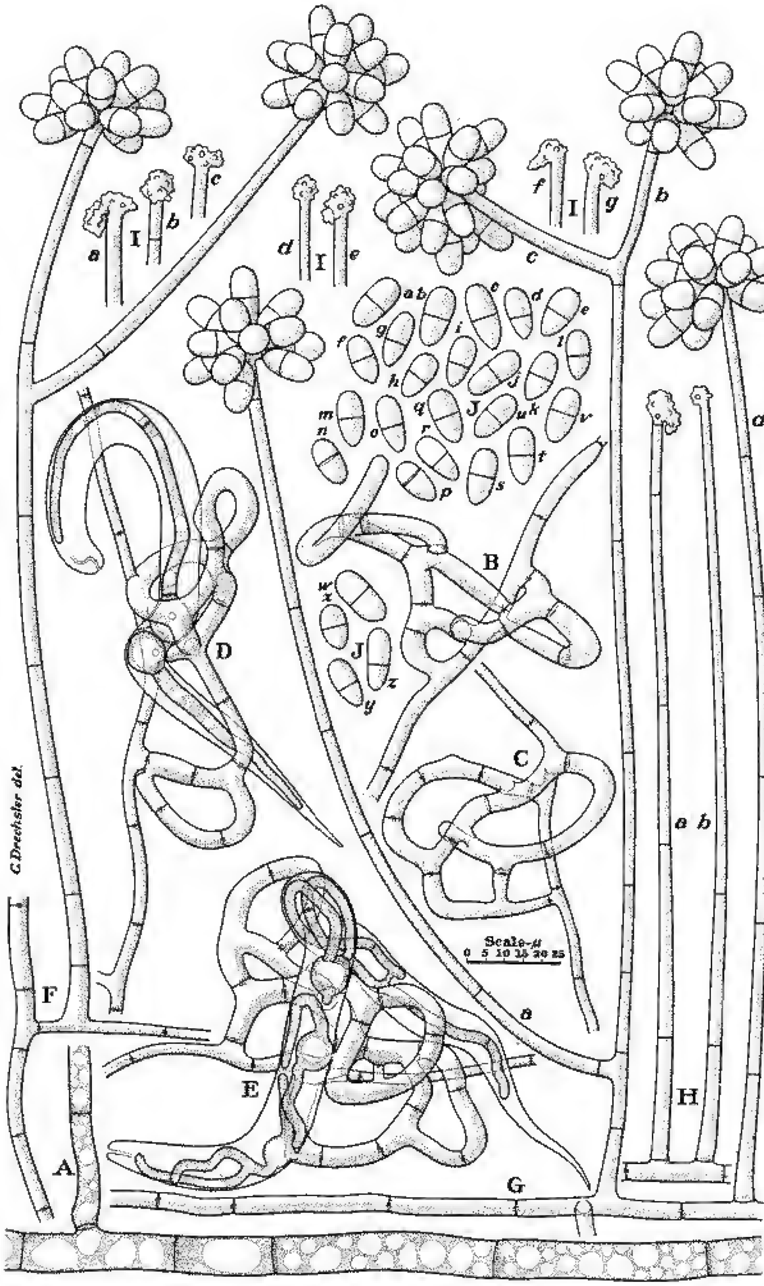

FIG. 2. *Arthrobotrys cladodes.*

urements from which were obtained the relevant dimensional ranges and computed averages submitted in the diagnosis—measurements made on specimens taken at random in equal numbers from four different strains growing in pure culture on maizemeal agar in Petri dishes—gave a distribution of values for length expressed to the nearest micron as follows: 11 μ, 2; 12 μ, 3; 13 μ, 20; 14 μ, 55; 15 μ, 71; 16 μ, 42; 17 μ, 6; 18 μ, 1; and a distribution of values for width as follows: 6 μ, 2: 7 μ, 120; 8 μ, 77; 9 μ, 1.

As has been intimated, the fungus, even when producing conidia very profusely, only occasionally shows a succession of clusters on a repeatedly elongated conidiophore. Its eligibility for inclusion in *Arthrobotrys* might therefore be questioned as Corda in his definition of the genus specified nodulose " flocci " presumably of the type found in *A. superba.* The requirement thus introduced was retained in the generic diagnosis published by Saccardo, according to whose system the corresponding monocephalous forms would need to be referred to *Cephalothecium.* In defining the genus *Arthrobotrys,* Lindau likewise mentioned the presence of nodose swellings with conidium-bearing protuberances among the characteristics pertaining to the conidiophore. Except for the additional attribute of repeated elongation and repeated sporulation, he regarded *Arthrobotrys* as virtually identical with *Trichothecium,* to which genus he assimilated *Cephalothecium* and with it presumably all monocephalous fungi like the one under consideration.

The misunderstanding underlying the slightly variant dispositions favored by Saccardo and by Lindau will receive attention more appropriately in the discussion of *Arthrobotrys oligospora.* It can hardly be a matter of astonishment if these distinguished compilers, perhaps neither of whom had ever had occasion to become very familiar with any species of either *Arthrobotrys* or *Trichothecium,* should have been somewhat misled by the flow of wrong opinion issuing persistently from investigators who had studied material of one genus and held it representative of both.

The predacious fungus illustrated in figure 2 is beyond any doubt closely related to *Arthrobotrys superba;* and no less certainly is wholly lacking in intimate relationship to *Trichothecium roseum* Link (= *Cephalothecium roseum* Corda). It is assigned, therefore, to the genus typified by the former species, in the hope that the slight adjustment in prevailing concept will commend itself to students of the group. A term having reference to the branching habit of its conidiophores is proposed as specific name.

Arthrobotrys cladodes sp. nov.

Mycelium effusum; hyphis hyalinis septatis, plerumque 2–7 μ crassis, subinde usque 11 μ crassis protoplasmatis confertim repletis, laqueos tenaces arcuatos vel circulares in reticula saepe conjunctos evolventibus; his laqueis vermiculos nematodeos illaqueantibus, deinde tum integumentum perforantibus, tuber mortiferum intrudentibus, hyphas intus evolventibus quae carnem exhauriunt. Hyphae fertiles hyalinae, erectae, septatae, ramosae, 200–400 μ altae, basi 4–7 μ crassae, sursum paulo fastigatae, subter apicem 2.5–4 μ crassae, apice verrucosae irregulariter dilatatae modo globosae modo coralloideae 5–30 conidia in capitulum confertum aggregata ferentes. Conidia hyalina, ellipsoidea vel elongato-obovoidea, ad septum subinde paulo constricta, 11–18 μ (saepe circa 14.7 μ) longa, 6.2–8.8 μ (saepe circa 7.3 μ) lata, loculis duobus inter se nunc aequalibus nunc inaequalibus, loculo superiore interdum majore rarius minore quam loculo inferiore. Chlamydosporae ignotae.

Vermiculos nematodeos diversos vulgo usque .5 mm. longos laqueans consumensque habitat in humo silvestri, in Arlington, Virginia, atque prope Beltsville et Cumberland, Maryland.

Mycelium spreading; vegetative hyphae hyaline, septate, except for occasional storage filaments that are densely filled with protoplasm and up to 11 μ wide measuring mostly 2 to 7 μ in diameter, often especially in the presence of nematodes giving rise to hyphal bails and loops, which, though at first discrete, are later frequently compounded into more or less extensive networks; the bails and networks capturing nematodes through adhesion and entanglement, perforating the integument of each animal and intruding one or more globose mortiferous excrescences from which are extended assimilative hyphae to appropriate the fleshy contents. Conidiophores hyaline, erect, septate, frequently more or less branched, 200 to 400 μ high, 4 to 7 μ wide at the base, tapering gradually upward to a width of 2.5 to 4 μ below the irregularly expanded, globose or somewhat coralloid tip whereon are borne 5 to 30 conidia in usually dense capitate arrangement. Conidia hyaline, ellipsoid or elongate obovoid, mostly 11 to 18 μ (average 14.7 μ) long, 6.2 to 8.8 μ (average 7.3 μ) wide, uniseptate, the upper cell often approximately of the same size as the lower or slightly larger, but occasionally somewhat smaller. Chlamydospores not known.

Capturing and consuming nematodes commonly measuring up to .5 mm. in length and mostly referable to the genera *Acrobeles,* *Acrobeloides, Cephalobus, Diplogaster, Diploscapter, Plectus* and *Rhabditis,* it occurs in leaf mold near Beltsville, Md., near Cumberland, Md., and in Arlington, Va.

ARTHROBOTRYS OLIGOSPORA Fres.

Of all predacious fungi *Arthrobotrys oligospora* is undoubtedly by far the most widely known among mycologists. Its ready appearance on a wide variety of decaying vegetable materials as well as on the dung of many wild and domestic animals, following incubation in a damp chamber, has made it a familiar object to the numerous investigators who have devoted attention to the saprophytic, and often more particularly to the coprophilous flora of their respective localities. After addition of small masses of decomposing refuse to nematode-infested agar plate cultures, it makes its appearance not only more frequently than any other of the related predacious forms, but perhaps in larger quantity than all the other predacious forms taken together. Indeed, its prompt and rapid development in such cultures, by bringing about an early and usually tremendous reduction in the supply of eelworms available for slower-growing forms, often operates in an annoying manner to conceal the true content of nematode-destroying microorganisms present in materials under study.

The vegetative filaments of the fungus show the disposition usual for members of the series: being arranged somewhat radially in a fairly compact mycelium when developing in pure culture on agar media; but in nematode-infested cultures only sparsely permeating the substratum and bearing predacious apparatus in seemingly haphazard distribution. This apparatus, consisting of hyphal bails that are first discrete but later usually are compounded into more or less extensive networks (FIG. 3, *A–D*), closely resembles that produced under similar conditions by *Arthrobotrys superba* and *A. cladodes,* except that in the present species the bail-like elements often appear a little rangier and the meshes correspondingly a little wider. Woronin (**71**) first gave a descriptive account of the hyphal bails and networks, without, however, offering any explanation as to their use. Their special function in the capture of nematodes was later capably set forth by Zopf in the classical

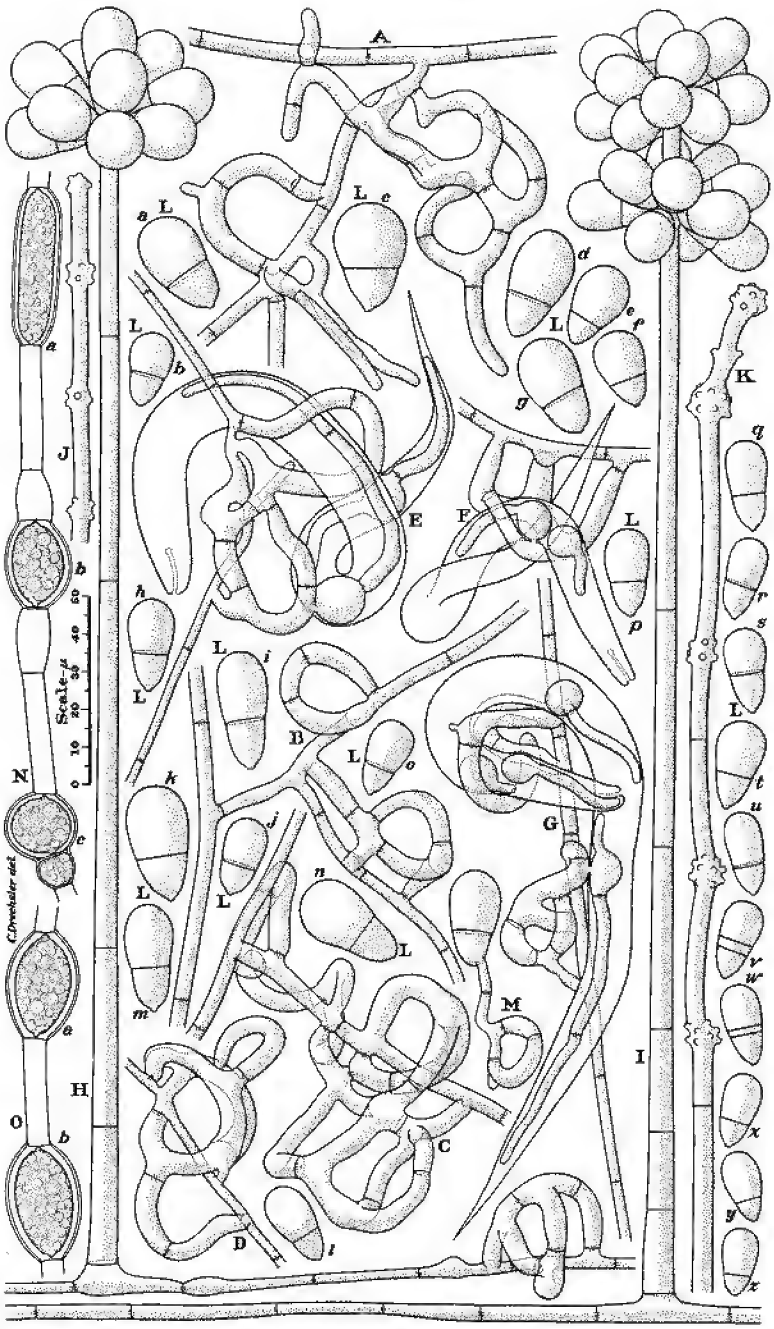

FIG. 3. *Arthrobotrys oligospora.*

memoir wherein also, though less plausibly, was given an intimation of similar utility in the "conidia" of his *Monosporidium repens*. Despite the unescapable suggestion in the operation of the supposed conidia of some other mode of prehension, the efficacy of the predacious organs formed by *A. oligospora* was imputed entirely to physical entanglement. Actually, of course, in this as in other retiary species, the secretion of an adhesive substance is exceedingly important in the capture of nematodes. Soon after capture is effected the animal's integument is perforated, and one or more mortiferous bodies are intruded, from which assimilative hyphae are extended through the fleshy interior (FIG. 3, *E, F, G*).

Though Zopf included an adequate account of the remarkable biological relationships of *Arthrobotrys oligospora* in his general treatise on fungi (**73**), his discoveries evoked surprisingly little response at the time. Matruchot somewhat casually referred to Zopf's fungus as a strain of *A. oligospora* living parasitically on a species of nematode, without betraying any hint of recognition that the parasitism in question was anything but commonplace. Possibly, indeed, the true distinctiveness of the biological relationship represented here could not be fully appreciated until an analogous instance was brought to light in the discovery by Sommerstorff more than two decades later of his *Zoöphagus insidians*, an aquatic phycomycete subsisting through the capture of rotifers. Both in the excellent original descriptive account (**67**) of this fungus and in a shorter interpretative communication (**68**), Sommerstorff appropriately recalled *A. oligospora*, as did also Mirande (**48**) and Gicklhorn (**24**) in later publications on *Z. insidians*. A continuing interest in carnivorous and predacious fungi subsequently inspired a review-article by Kostka (**36**) wherein Zopf's observations on *A. oligospora* were rather fully set forth, together with relevant speculations that appear of moment more particularly from a discerning prediction that further research might show adhesive material operative in the capture of prey. Brief statements at second hand, concerning the predacious action of the same fungus were given in recent years by Goffart (**26**) and Stehli (**69**). In the meantime a serious lack of corroborative testimony had been corrected when from observations at first hand Rahm (**56**) noted that moss-inhabiting eelworms belonging to species of *Tylenchus* and of *Mononchus* became abundantly entangled in hyphal bails of the fungus; entanglement being followed by invasion of the captives, fatty degeneration of their soft structures, and death. Additional records of *A. oligospora* in predacious relationship have since been supplied by Sherbakoff (64) and Linford (40). Of kindred interest is Korab's (35) inclusion of the fungus among the parasites destructive to cysts of the sugar beet nematode, *Heterodera Schachtii* Schm., in Russia.

After its predacious apparatus has for some time been operative in nematode-infested maizemeal agar-plate cultures, *Arthrobotrys oligospora* gives rise to sporophores that in the aggregate often become visible to the naked eye as a sparse downy turf. Individually these are sturdy structures, often divided by 3 to 8 cross-walls, measuring mostly 7 to 10 μ at the base and tapering gradually upward to a diameter of 4 to 6.5 μ below the first head of conidia, which is commonly formed at a height of 350 to 450 μ, though instances of heads formed at lesser heights are to be found (FIG. 3, *H, I*). Development may cease with the production of one head, or through repeated elongation of the axis several more heads may be added successively; conidiophores with four or a greater number of clusters being, however, not frequent in such material. The conidia thus produced (FIG. 3, *L, a, c, d, g, i, k, m, n*) are plump, obovoid bodies, mostly 22 to 32 μ long and 12 to 20 μ wide, measurements of 100 specimens taken at random giving values of 26.6 μ and 15.8 μ for average length and average width respectively.

In pure culture on suitable media, as, for example, maizemeal agar, sporulation is much more profuse. If care is taken to reduce normal evaporation the individual conidiophores continue to develop successive conidial heads, so that in six weeks fertile hyphae weighted down horizontally with 20 to 30 spore clusters are piled on one another to form a loosely matted aerial tangle. Usually the conidiophores here are somewhat less stout than when arising from wormy substrata, measuring mostly 6 to 8 μ in width at the base, and diminishing to a width of 4 to 5.5 μ in the sporiferous portion (FIG. 3, *J, K*). The conidia, too, are smaller than those produced on nematode-infested media, measurements of 100 specimens taken at random showing a range in length of from 18 to 30 μ, and a range in width of from 10 to 15 μ, and yielding computed averages of 23.3 μ and 12.6 μ for these dimensions respectively. When agar plate cultures are exposed in a manner to permit free evaporation, the increasingly dry conditions that then come about are reflected in progressive reduction in size of the conidia produced as sporulation gradually comes to an end.

The differences in reproductive habit and conidial dimensions associated with development on wormy agar media as compared with reproductive habit and dimensions associated with development in pure culture, represent approximately the morphological differences indicated as separating *Arthrobotrys superba* var. *oligospora* from typical *A. superba* by those authors who identified the present fungus with Corda's species, and accordingly subsumed material with few heads as a variety thereof. Among these authors, Saccardo (**61**) indicated for the conidia of *A. superba* a length of 20 to 26 μ, and a width of 12 to 15 μ; whereas the corresponding dimensions of *A. superba* var. *oligospora* were given as being 23 to 27 μ and 14 to 17 μ respectively. Again, Lindau indicated for the conidia of *A. superba* a length of 20 to 26 μ and a width of 13 to 15 μ; for those of *A. superba* var. *oligospora* a length of 23 to 28 μ and a width of 14 to 19 μ. It is not surprising that development on wormy agar should be much the same as on dung or on decaying plant remains, since on any of these substrata the fungus must live exclusively on the nematodes infesting them —a food supply often very abundant for a time but locally subject to serious reduction, or even to virtual depletion, after a relatively short period of exploitation. In any case, if the values given by Loew (**42**) for conidial dimensions, 25 to 30 μ for length and 14 to 18 μ for width, or those given by Oudemans (**52**), 28 μ for length and 16 to 19 μ for width, or those given by Grove (**29**), 30 μ for length and 15 μ for width, appear considerably larger than the corresponding values, 20 μ and 15 μ respectively, mentioned by Matruchot, an explanation for the difference may be found in the circumstance that Loew and Oudemans like Grove used natural substrata, whereas Matruchot studied the fungus in pure culture on sliced carrots. On the other hand, the value for length of conidium, $\frac{1}{28}$ mm. or 35.7 μ, given by Fresenius, and also the range for this dimension, 30 to 40 μ, submitted by Coemans, would seem somewhat higher than might be expected even in material from natural substrata such as these writers studied.

From *Arthrobotrys superba* and *A. cladodes,* the two species previously discussed, *A. oligospora* is distinguished not alone by generally greater conidial dimensions, but also, and perhaps more especially by the inequality in size of the two segments into which its conidium is typically divided. The cross-wall delimiting the segments is placed at a distance from the base varying mostly from one-third to two-fifths of the length of the spore. As the distal cell is therefore longer than the basal cell, besides being wider because of the obovoid shape of the spore, its volume may well be 1.5 to 3 or occasionally even 4 times that of the proximal segment. In Massee's (**45**) figures of his *A. rosea* similar proportions between basal and distal cells are revealed. Indeed, except for the acutely pointed shape of the "minute spicules arranged in a spiral, to which the conidia are attached," Massee's description fits *A. oligospora* so well that few would disagree with Matruchot in considering *A. rosea* identical with the older species of Fresenius. Apparently the description was written without any knowledge of Fresenius' publication, yet is deserving of commendation in distinguishing the fungus under consideration from *A. superba* on the proper ground that the latter has "oblong conidia divided into equal parts by the septum." Possibly another and much more questionable synonomy might be inferred from Preuss' description (**54**) of the spores of his *A. recta* as being obovoid—the remainder of the diagnosis, which antedates that of Fresenius, being, however, so lacking in specific characterization that positive reference to any particular fungus seems definitely out of the question.

A troublesome misconception, referred to previously, concerning the relationship of the genus *Arthrobotrys* to *Trichothecium* (including *Cephalothecium*) has long persisted through an obstinate confusion of *A. oligospora* with *T. roseum* Link. Rather curiously the confusion was initiated after the morphological characteristics distinguishing the two genera had been adequately set forth. After Corda in 1839 had described the arrangement of conidia on the conidiophore in *A. superba* very graphically and with regard to the more essential points, quite correctly, Fresenius made known a similar arrangement and development in *A. oligospora.*

Hoffmann (32) in 1854 described sporulation in *T. roseum* to proceed, following delimitation of a first terminal spore, by production of lateral outgrowths from successively lower portions of the fertile hypha, each outgrowth and associated axial portion being in turn converted into a conidium. The next year Bail (1) confirmed Hoffmann's description, characterizing the arrangement of the spores in *T. roseum* as an alternately spicate one which on casual examination simulates a verticillate arrangement. Then in 1866 Münter (49) published an account of a Hyphomycete that gave rise to heads of conidia approximately after the manner described by Hoffmann; but apparently not being aware of either Hoffmann's or Bail's contribution, he insisted on identifying his fungus with *A. oligospora*. The morphological departures from the description of the latter species Münter held attributable to faulty observation on the part of Fresenius! Corroboration of Münter's findings soon appeared in a paper by Loew (41), which represented spore development like that set forth by Hoffmann taking place in a fungus recognized as entirely similar to Münter's, and likewise referred, though with expressed misgivings, to *A. oligospora*. De Bary (2) thereupon pointed out that the studies reported by Münter and Loew had not been carried out on *A. oligospora*, nor indeed, on any species of *Arthrobotrys* at all, but on the widely distributed *T. roseum*. With this altogether sufficient explanation Karsten (34) promptly took issue, asserting that the fungus growing out of material received from Münter showed under appropriate cultivation a succession of spore clusters and development of spore pedicels just as had been described by Fresenius. He concluded therefore that Münter's fungus was identical with *A. oligospora;* which species, however, he considered as representing not a member of the genus *Arthrobotrys*, but a variety of *T. roseum*. In 1870 Woronin again presented De Bary's arguments to the effect that Loew's as well as Münter's conclusions were wrong, being based on *T. roseum* rather than on true *A. oligospora*. Nevertheless Harz (30) a year later came forward with a view not dissimilar from Karsten's, holding that Fresenius had erroneously assigned a luxuriant form of *T. roseum* with repeated spore clusters to *Arthrobotrys;* and accordingly cited *T.*

roseum together with *A. oligospora* and *A. superba β oligospora* in an impressively copious synonomy.

It remains to Loew's credit that after his earlier contribution had thus been given confirmation of a sort, he (**42**) emended his position as a result of studies on material of true *Arthrobotrys oligospora* which he had in the meantime acquired. He now quite understandably agreed with the views of De Bary and of Woronin bearing on the identity of the fungus previously studied by himself and Münter, and on the separateness of that fungus from *A. oligospora.* The repeated conidial heads and the sterigmata reported by Karsten he explained through the presumption that this author had dealt with a mixture of *A. oligospora* and *T. roseum.*

Constantin (**9**) in 1888 confirmed from personal observation the distinction drawn by De Bary, by Woronin and by Loew between *Arthrobotrys oligospora* and *Trichothecium roseum.* Yet even during the same year the two genera typified in these species were again confused when Berlese (**3**) described under the name *T. roseum* var. *arthrobotryoides* a fungus that obviously was a true *Arthrobotrys* whether referable to *A. oligospora* as Matruchot considered certain, or to *A. superba* as appears to me about equally possible. Though Matruchot's memoir, which appeared four years later and was based on extensive comparative studies wherein pure cultures were employed, may have been mischievous in erroneously assimilating *A. oligospora* to *A. superba,* it nevertheless should have laid any lingering doubt concerning the wide difference in morphology of conidial apparatus between the former species and *T. roseum.* Still, two decades later, Grove (**29**) mentioned *A. oligospora* and *T. roseum* in a list of probable synonyms that included notably also *T. obovatum* Sacc. and *A. superba;* holding that nothing but cultures under diverse conditions could decide whether the names cited apply to different species or to varying states of one species. In 1918 Elliott (**22**), apparently not cognizant of similar earlier studies, described anew from observations at first hand the course of conidial development in *T. roseum.* Again, in more recent times, Reinhardt (**58**), though fully informed of earlier contributions on the subject, considered it far from superfluous to submit an illustrated account of spore formation in the same fungus, contrasting its successive basipetal course with the truly capitate development in *A. oligospora*.

In view more particularly of the suggestion made by Grove, I took occasion to grow in pure culture on several artificial media two strains of *T. roseum* originally isolated from apple fruits affected with pink rot. The cultures prepared in this way showed only the most superficial outward similarity to parallel cultures of *Arthrobotrys oligospora*. Microscopic inspection revealed the characteristic development of conidia repeatedly described in the literature. Conidial apparatus and vegetative mycelium were equally lacking in the intimate family resemblance to *A. oligospora* that unmistakably comes to light in members of the predacious series, often despite pronounced differences in reproductive habit. When large pieces cut from agar plate cultures of *T. roseum* were placed on agar cultures abundantly infested with nematodes, *Amoebae* and shelled rhizopods, no predacious qualities of any kind were ever manifested. In fine, a clear impression was left that *T. roseum* is not only distinct from *A. oligospora* as a species, but is alien to the series, and therefore definitely more remote than are, for example, the fungi I described earlier as *Pedilospora dactylopaga* (**16**) and *Dactylella passalopaga* (**20**). And assuredly, Vanha's (**70**) citation of *Trichothecium* as a fungus capturing nematodes in the soil must have been based on some species other than *T. roseum*.

Chlamydospores, first reported in the fungus, though apparently in somewhat immature condition, by Woronin, and later fully described by Zopf (**72**), regularly make their appearance in old cultures, whether these be pure or infested with nematodes. When mature they have usually a distinctly yellow color. They show considerable variety in shape, some being mostly cylindrical (FIG. 3, *N, a*), others subspherical (FIG. 3, *N, c*) and still others ellipsoid (FIG. 3, *N, b; O, a, b*). The enveloping wall usually shows two layers, a thin outer layer presumably consisting of the original hyphal membrane, and rather closely adnate to it, a thick inner layer marked with a deep central pit at each of the ends.

ARTHROBOTRYS CONOIDES

Of the several congeneric forms dealt with herein, the one morphologically most similar to *Arthrobotrys oligospora* was referred to and figured in an earlier summary (12: p. 138, lines 31–34; p. 139, fig. 3, A–C) as bearing longer conidia with characteristically tapering basal cells. It has been found especially frequently in decaying plant refuse from greenhouses, as also in débris of similar nature accumulating in meager quantity under potted house plants. Though apparently of somewhat less abundant occurrence out of doors, it has yet developed in many nematode-infested plate cultures to which had been added pieces of decaying roots of herbaceous field plants or pinches of leaf mold from deciduous woods.

The mycelium of the fungus has much the same appearance as that of *Arthrobotrys oligospora*. In nematode-infested agar plate cultures the vegetative filaments are sparsely extended to produce here and there hyphal bails that often become compounded into more or less rangy networks (FIG. 4, *A*, *B*). Under moist conditions the animals are held, sometimes in enormous numbers, largely through adhesion to the anastomosing elements (FIG. 4, *C*); entanglement becoming necessary to effect capture, at least of the larger and more vigorous prey, under drier conditions (FIG. 4, *D*). The killing of the eelworms by intrusion of globose structures, and appropriation of their fleshy substance by assimilative hyphae arising from the globose bodies, ensues as in the forms already discussed.

Tall conidiophores are produced on wormy agar media, occasionally in such numbers as to become visible to the naked eye as a fine downy growth. They usually conclude their development with the production of a single terminal conidial head, often containing 20 to 30 spores in compact arrangement (FIG. 4, *E*). In pure culture on maizemeal agar, with evaporation reduced to prevent early drying out of the substratum, the conidiophores continue development by repeated elongation and successive production of 5 to 10 additional spore clusters. The individual clusters in series thus produced ordinarily consist of fewer conidia than the single heads on fertile hyphae arising from wormy substrata; the capitate arrangement being, of course, correspondingly looser (FIG. 4, *F*). Denuded conidiophores show modification of the sporiferous parts, whether terminal or intercalary, commensurate with the number of spores that had been formed thereon (FIG. 4, *G*, *H*).

Arrangement of the conidia in compact heads is facilitated by their distinctive conformation. Comparison of the values pertaining to conidial dimensions in the diagnosis below, which were derived from measurements of 200 specimens taken at random, with the homologous values for *Arthrobotrys oligospora*, shows considerably greater length and appreciably lesser width in the conidia of the present species (FIG. 4, *I*, *a–z*). Associated with these differences is a pronounced tapering toward the base, whereby the conidium is given on obconical shape, modified, to be sure, by the broad rotundity of the apex and a noticeable constriction at the septum.

Like other retiary species of *Arthrobotrys*, the fungus in aging cultures often gives rise to some greatly distended storage hyphae. These hyphae may remain filled with protoplasm long after other filaments have lost their contents (FIG. 4, *J*). In older cultures, too, chlamydospores not differing much in coloration, shape and size from the corresponding bodies of *A. oligospora*, are often formed. For the most part well scattered through the substratum (FIG. 4, *K–O*), they sometimes appear crowded here and there, then collectively becoming visible to the naked eye as minute yellow masses.

Though of less frequent occurrence than *Arthrobotrys oligospora* the fungus can hardly have escaped observation by all of the many mycologists that have studied the microscopic flora of decaying vegetable materials. When encountered it must in all probability have been identified usually with Fresenius' species. Indeed, the possibility even suggests itself that the value for length of conidium given by Fresenius may have been derived from an admixture of the present species with the one which unmistakably he illustrated. Rostrup (**60**) recently listed under the binomial *A. longispora* Preuss a species with conidia 27 to 32 μ in length and 7 to 11 μ in width; the ratio of these dimensions, 3.3, being held, justifiably enough, to distinguish the species from the supposedly similar *A. superba*, to which a corresponding ratio of 1.5

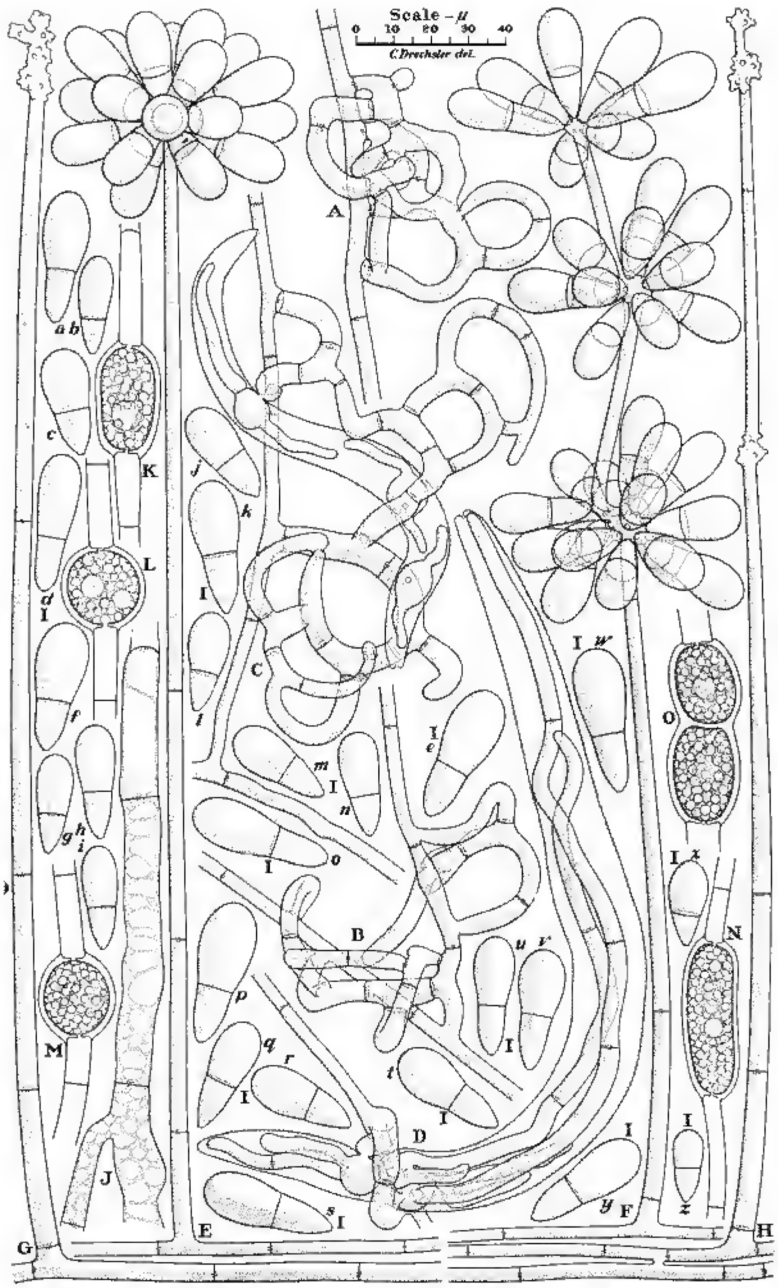

FIG. 4. *Arthrobotrys conoides.*

was attributed. My fungus, while agreeing well with Rostrup's in length of conidium, exceeds it rather markedly in width of conidium; wherefore the ratio between the averages of the two dimensions, 2.5, naturally falls below that given by the Danish mycologist. In any case the original diagnosis of *A. longispora* given by Preuss (**55**) would seem, like his diagnosis of *A. recta,* too deficient in specific characterization to permit application of the binomial to any particular species; and certainly, " floccis subramosis " and " sporis oblongis " provide little encouragement for its application to the species under consideration.

The fungus as developing in nematode-infested agar cultures has on many occasions been compared side by side with similar material of *Arthrobotrys oligospora.* Further, as opportunity offered during four years, more than a dozen strains of the two species, each strain isolated from a separate lot of vegetable refuse or of leaf mold, have been grown side by side in pure culture on several kinds of artificial media. Numerous variations in morphological expression, some evidently of a genetic nature, others manifestly of cultural origin, were noted. Yet in all its strains the fungus with the more slender, obconical conidia and the somewhat slower rate of mycelial extension at a temperature of 25° C., was always readily distinguishable from the faster growing fungus with the broader obovoid conidia. It is accordingly described as a new species under a name intended to be descriptive of its characteristic conidia.

Arthrobotrys conoides sp. nov.

Mycelium effusum; hyphis hyalinis, septatis, plerumque 2–8 μ crassis, subinde usque 12 μ crassis protoplasmatis confertim repletis, laqueos tenaces arcuatos vel circulares in reticula saepe conjunctos evolventibus; his laqueis vermiculos nematodeos illaqueantibus, deinde tum integumentum perforantibus, tuber mortiferum intrudentibus, hyphas intus evolventibus quae carnem exhauriunt. Hyphae fertiles hyalinae, septatae, erectae, simplices, primo 150–400 μ altae, basi 4–8 μ crassae, sursum paulo fastigatae, subter apicem 2.5–5 μ crassae, apice verrucosae, irregulariter dialatatae, modo globosae modo coralloidae, usque 30 conidia in capitulum confertum aggregata ferentes, deinde identidem recrescentes alia similia vel laxiora capitula singulatim deinceps gerentes. Conidia hyalina, obconica, basi truncata, apice rotundata, ad septum paulo constricta, 19–42 μ (saepe circa 30 μ) longa, 8–15 μ (saepe circa 12 μ) lata, loculo inferiore 8–17 μ (saepe circa 12.5 μ) longa. Chlamydosporae flavidae, globosae vel ellipsoideae, 18–25 μ diametro, subinde angustiores, oblongo-clindraceae, 30–50 μ longae, circa 15 μ crassae.

Vermiculos nematodeos multarum specierum vulgo usque .6 mm. longos laqueans consumensque habitat in materiis plantarum putrescentibus vel in humo silvestri foris vel praecipue abunde in viridario, in Arlington, Virginia, atque prope Beltsville, Maryland.

Mycelium spreading; the vegetative hyphae hyaline, septate, except for occasional storage filaments that are densely filled with protoplasm and up to 12 μ wide, measuring mostly 2 to 8 μ in diameter, often, especially in the presence of nematodes, giving rise to hyphal bails and loops, which though at first discrete are later frequently compounded into more or less extensive networks; the bails and networks capturing nematodes through adhesion and entanglement, perforating the integument of each animal and intruding one or more globose mortiferous excrescences from which are extended assimilative hyphae to appropriate the fleshy contents. Conidiophores hyaline, erect, septate, usually not branched, mostly 4 to 8 μ wide at the base, tapering gradually to a width of 2.5 to 5 μ in attaining a height of 150 to 400 μ before bearing on a globose or more irregularly expanded tip as many as 30 conidia in dense capitate arrangement; subsequently often, following repeated elongation, giving rise successively to additional clusters of conidia. Conidia hyaline, obconical, somewhat flattened at the base, broadly rounded at the tip, usually perceptibly constricted at the septum, 19 to 42 μ (average 30 μ) long, 8 to 15 μ (average 12 μ) wide, the lower cell measuring 8 to 17 μ (average 12.5 μ) in length. Chlamydospores yellowish, globose or prolate ellipsoidal, 18 to 25 μ in diameter, or sometimes narrower, oblong-cylindrical, 30 to 50 μ long and approximately 15 μ wide.

Capturing and consuming nematodes measuring up to .6 mm. in length, referable to the genera *Acrobeles*, *Acrobeloides*, *Cephalobus*, *Diplogaster*, *Diploscapter*, *Plectus* and *Rhabditis*, it occurs in decaying plant remains and in leaf mold, often outdoors but especially abundantly in greenhouses, near Beltsville, Md., and in Arlington, Va.

ARTHROBOTRYS MUSIFORMIS

Among the predacious fungi closely similar to *Arthrobotrys oligospora* that were referred to in an earlier summary was one characterized (**12**: p. 138, lines 34–36; p. 139, fig. 4, A) in part as having " straight or slightly curved elongated ellipsoidal conidia borne in looser capitate arrangement on a terminal head of stubby branches." It was first observed in isolation plate cultures planted with pieces of decaying spinach (*Spinacea oleracea* L.) roots collected near Norfolk, Va.; and has later been obtained in quantity also from samples of potting soil received from Florida, as well as from several lots of leaf mold collected in deciduous woods in Virginia. Recently Linford recorded it among various nematode-capturing fungi found in Hawaii.

In nematode-infested agar plate cultures the mycelium permeates the substratum rapidly though rather sparsely. Predacious apparatus is soon produced at irregular intervals on the individual filaments. Though of the same general type as that of the four species of *Arthrobotrys* already discussed, it is sufficiently distinctive to permit recognition of the fungus even in the absence of reproductive structures. The recurved hyphal element here usually anastomoses closer to its origin than in other retiary species, and often, indeed, the tip is united with a proximal part of the element itself (FIG. 5, *A*, *a*, *b*; *B*, *a*). Thus instead of bail-like arches, horseshoe-like arches and annular loops are formed, the latter sometimes slightly resembling the constricting rings found in some nematode-capturing fungi. Through the compounding of these elements, networks are produced (FIG. 5, *A*, *c*; *F*, *a*), which in the present species, however, ordinarily fail to attain the extent and intricacy known elsewhere.

Capture of nematodes, sometimes in enormous numbers, is accomplished, especially under dry conditions, combinedly through adhesion and entanglement in the anastomosed elements (FIG. 5, *B*, *b*); under moist conditions, and more particularly with small animals, often through adhesion alone (FIG. 5, *C*). In either case, after the integument has been narrowly penetrated, one or more globose bodies are intruded into the captive, which is thereby soon rendered incapable of further struggle. Assimilative hyphae are then extended from the globose bodies lengthwise through the interior of the animal, to appropriate the materials resulting from fatty degeneration of its organs and musculature.

The fungus is very readily isolated, and grows rapidly in pure culture on maizemeal agar, producing a fairly dense mycelium, and strongly giving off the peculiar, somewhat sickeningly sweetish odor characteristic of the predacious series generally. As also on

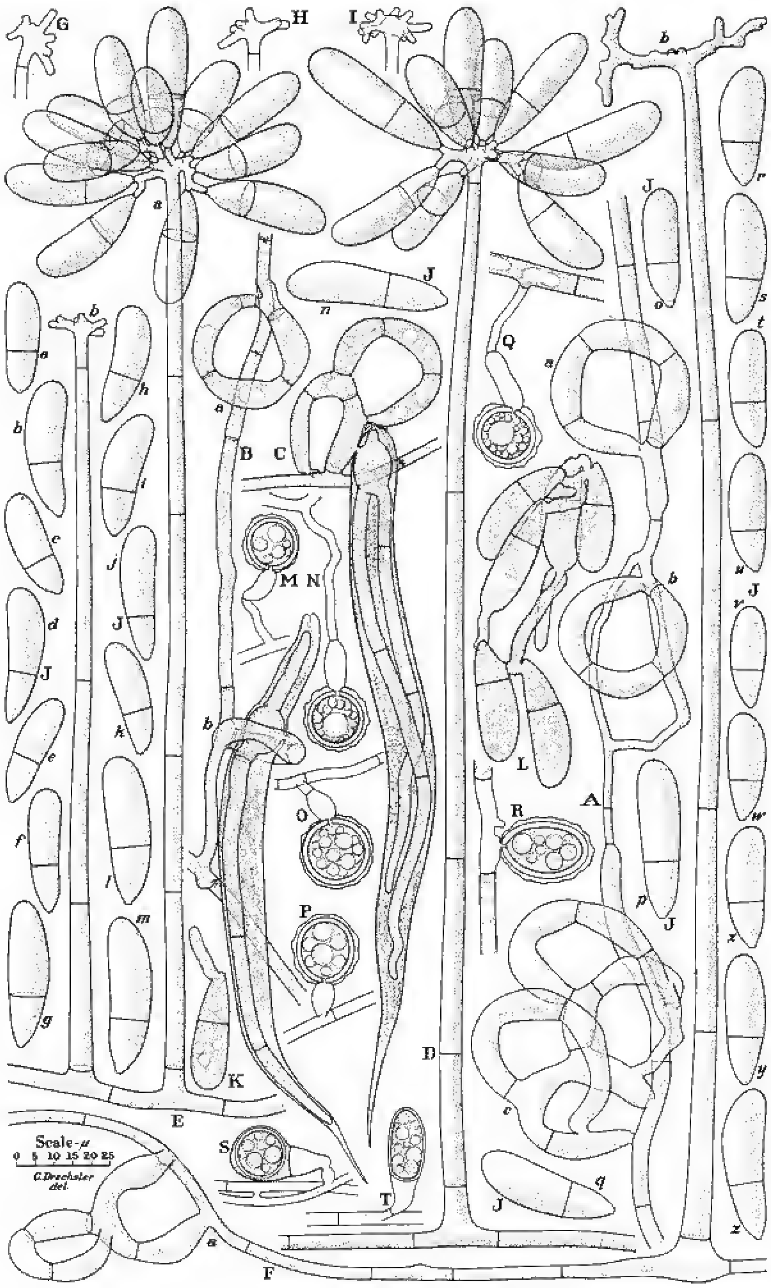

FIG. 5. *Arthrobotrys musiformis.*

nematode-infested substrata, conidial apparatus is soon developed, usually in sufficient quantity to form a downy turf readily visible to the naked eye. In stature the individual conidiophores resemble those of *Arthrobotrys oligospora* and *A. conoides*. However, a very distinctive appearance results from the arrangement of the conidia in a loose terminal head (FIG. 5, *D; E, a*); the spores here being borne on stubby sterigmata of appreciable length that diverge in various directions from the tip of the axial stalk (FIG. 5, *E, b; F, b; G; H; I*). Production of more than a single conidial cluster on one axis has never been observed.

The conidia (FIG. 5, *J, a-z*) are of a shape not greatly unlike that of the plump asexual spores often produced on artificial media by the widely familiar *Helminthosporium sativum* P. B. & K.; though a noticeable protrusion of the base, not usual in the grass parasite, gives them a profile reminiscent rather of banana (*Musa sapientum* L.) fruit, thereby suggesting the name proposed for the species. Their dimensional variations would seem, for the most part, more moderate than might be inferred especially from the wide range in length indicated in the diagnosis. The 200 spore measurements from which were obtained all the relevant metrical data there presented—measurements made on specimens taken at random in equal numbers from four different strains growing in nematode-infested maizemeal agar cultures—gave a distribution of values for length expressed to the nearest micron as follows: 22 μ, 1; 25 μ, 1; 26 μ, 1; 27 μ, 2; 28 μ, 3; 29 μ, 10; 30 μ, 9; 31 μ, 19; 32 μ, 20; 33 μ, 26; 34 μ, 25; 35 μ, 13; 36 μ, 20; 37 μ, 18; 38 μ, 14; 39 μ, 7; 40 μ, 4; 41 μ, 2; 42 μ, 3; 43 μ, 1; 44 μ, 1; a distribution of values for width as follows: 8 μ, 4; 9 μ, 18; 10 μ, 77; 11 μ, 79; 12 μ, 21; 13 μ, 1; and a distribution of values for length of the proximal cell as follows: 8 μ, 1; 9 μ, 4; 10 μ, 26; 11 μ, 54; 12 μ, 62; 13 μ, 31; 14 μ, 12; 15 μ, 9; 16 μ, 1. It is evident that on the whole the conidial measurements here appreciably exceed those submitted by Rostrup (60) for his *Arthrobotrys longispora;* though the ratio of length to width, using the averages computed for these dimensions, agrees well with the corresponding ratio given for the Danish fungus. In any case the present species is so conspicuously different from *A. superba* in the general appearance of its conidial apparatus, that it hardly could have been the form with which Rostrup was concerned.

Germination takes place whenever conidia come in contact with a moist substratum (FIG. 5, *K*), and is often followed by anastomosis with sporophores, mycelial filaments, other germ tubes, or other conidia (FIG. 5, *L*). In old cultures, after such vegetative union, a conidium sometimes gives rise to a yellowish chlamydospore within its distal segment (FIG. 5, *S*, *T*). Chlamydospores produced within conidia are generally smaller than those formed on lateral branches arising from vegetative filaments in the substratum (FIG. 5, *M-R*); these being remarkable, besides, in the wide separation of the enveloping wall into a somewhat folded, thin, outer layer and a thick, smooth, spherical inner layer. This separation, together with the inflated condition of the adjacent cell, makes for an appearance more than a little suggestive of the sexual apparatus of some oömycetes.

Arthrobotrys musiformis sp. nov.

Mycelium effusum; hyphis hyalinis, septatis, plerumque 2–9 μ crassis, laqueos tenaces arcuatos vel circulares in reticula interdum conjunctos evolventibus; his laqueis reticulisque vermiculos nematodeos illaqueantibus, deinde tum integumentum perforantibus, tuber mortiferum intrudentibus, hyphas intus evolventibus quae carnem exhauriunt. Hyphae fertiles hyalinae, septatae, erectae, simplices, 200–500 μ altae, basi 5–9 μ crassae, sursum paulo fastigatae, subter apicem 2.5–4 μ crassae, apice brevi-ramosae, 5–15 conidia in capitulum laxum ferentes. Conidia hyalina, ellipsoidea, ad basin versus paulo attenuata, recta vel leviter curvata, 22–44 μ (saepe circa 33.9 μ) longa, 7.5–12.7 μ (saepe circa 10.4 μ) lata, loculo inferiore 8–16.4 μ (saepe circa 11.7 μ) longo. Chlamydosporae flavidae, globosae vel interdum ellipsoideae, 14–22 μ (saepe circa 17.5 μ) diametro.

Vermiculos nematodeos multarum specierum vulgo usque .6 mm. longos laqueans consumensque habitat in radicibus putrescentibus *Spinaciae oleraceae* prope Norfolk, Virginia, in humo pingui prope Coconut Grove, Florida, in humo silvestri prope Beltsville, Maryland, atque in Arlington, Virginia.

Mycelium spreading; the vegetative hyphae hyaline, septate, mostly 2 to 9 μ wide, often, especially in the presence of nematodes, giving rise to horseshoe-like hyphal arches and loops that may remain discrete, or in numbers not usually exceeding 6 may be compounded into networks—the individual circular loops mostly composed of 3 to 5 arcuate cells surrounding an aperture 15 to 25 μ wide; the loops and networks capturing nematodes through adhesion and entanglement, perforating the integument of each animal and intruding one or more globose mortiferous excrescences from which are extended assimilative hyphae to appropriate the fleshy contents. Conidiophores hyaline, septate, erect, not branched below, 200 to 500 μ high, 5 to 9 μ wide at the base, tapering upward gradually to a width of 2.5 to 4 μ near the tip, where are borne on divergent, slightly tapering, simple or branched sterigmata, mostly 2 to 3 μ wide and 3 to 10 μ long, usually 5 to 15 conidia in loose capitate arrangement. Conidia hyaline, ellipsoid, straight or slightly curved, broadly rounded at the wider distal end, tapering noticeably toward the slightly protruded base, 22 to 44 μ (average 33.9 μ) long, 7.5 to 12.7 μ (average 10.4 μ) wide, the lower and smaller cell 8 to 16.4 μ (average 11.7 μ) long. Chlamydospores yellow, globose or less frequently ellipsoidal, mostly 14 to 22 μ (average about 17.5 μ) in diameter.

Capturing and consuming nematodes measuring up to .6 mm. in length, referable to the genera *Acrobeles, Acrobeloides, Cephalobus, Diplogaster, Diploscapter, Plectus* and *Rhabditis,* it occurs in decaying spinach roots near Norfolk, Va., in potting soil near Coconut Grove, Fla., and in leaf mold near Beltsville, Md., and in Arlington, Va.

ARTHROBOTRYS DACTYLOIDES

The strangling predacious fungus set forth synoptically (**13**: p. 268, lines 25–32; p. 269, fig. 13, A–C) as bearing elongated uniseptate conidia in open capitate arrangement, makes its appearance now and then in nematode-infested agar-plate cultures to which have been added small quantities of leaf mold or of other decaying vegetable materials. Its development is conditioned by a consistency of the substratum soft enough to permit nematodes to move freely through it, rather than only on the surface of it. For apparently the organs of capture, though sometimes jostled to the surface by large nematodes and earthworms, often, indeed, into angular positions conveniently exposing their remarkably uniform make-up (FIG. 6, *A, B*), are regularly produced in the subtratum beneath and a little to one side of the parent filaments, which, as in other predacious forms, are sparsely distributed and follow somewhat straightforward courses (FIG. 6, *C, a–c*). These organs originally consist of rings formed separately in planes approximately at right angles with the parent hypha, to which they are attached at intervals rarely less than 50 μ by short, stout, two-celled

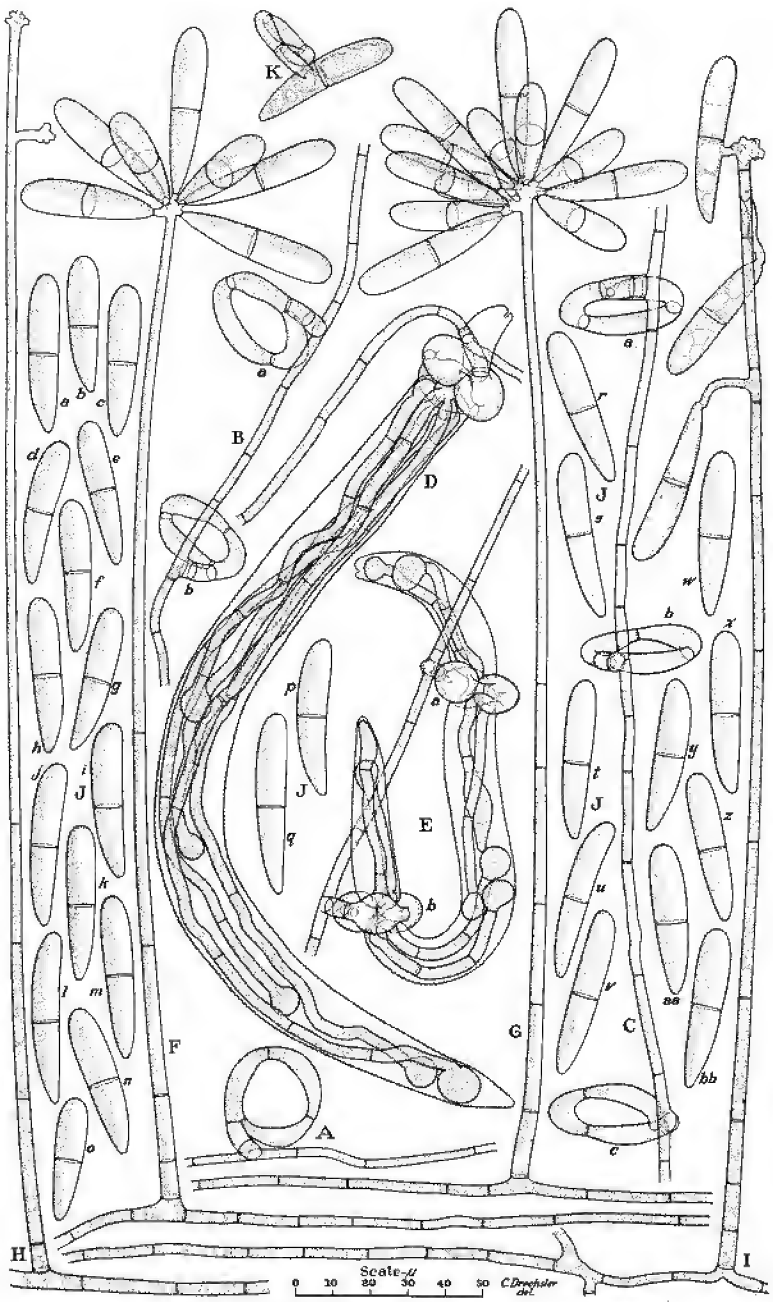

FIG. 6. *Arthrobotrys dactyloides.*

stalks. Unlike the hyphal bails and loops of the five retiary species already discussed, which, apart from entanglement and adhesion exert no violence externally on ensnared nematodes, the stalked ring of the form under discussion constricts its captive through extraordinary swelling and contraction of its three component cells, until musculature and organs are virtually, if not wholly, severed within the strangulated integument. The constricting action here, proceeding with gradual reduction and eventual cessation of the captive's violent struggles, is probably without parallel among carnivorous plants for outward appearance of implacableness and malignancy. It accomplishes in a much different manner what is accomplished in retiary and knobbed species through intrusion of a globose body—that is, virtual severance and paralysis of the animal, making possible the extension of assimilative hyphae through the fleshy interior (FIG. 6, *D, E*). In the present species these hyphae regularly terminate in a bulbous enlargement—a curious modification, the utility of which is not yet apparent.

Despite the astonishing manner of bringing about the death of nematodes ensnared in its constricting rings, the number of animals destroyed by the fungus is usually moderate in comparison to those consumed under favorable conditions by allied retiary species. As a result, conidial apparatus is produced rather sparsely. The fertile hyphae resemble the corresponding elements of *Arthrobotrys musiformis* in general stature, even if, perhaps, on the whole a little shorter and slightly less sturdy. At the tip, moreover, they terminate in perceptibly shorter sterigmata, so that the conidial heads borne on them show a slightly more compact central arrangement (FIG. 6, *F, G*). To be sure, the sterigmata are not always collected in a single terminal group, some occasionally being found on a lateral spur a short distance from the apex (FIG. 6, *H*), there bearing conidia in a recognizably separate subsidiary cluster.

In most cultures the conidia (FIG. 6, *I, a-z, aa, bb*) are uniformly uniseptate and of an elongated shape only rather poorly described in the epithet that for lack of a classical term equivalent to "cigar-shaped" is proposed for the fungus. Occasionally, however, material is found showing an admixture of conidia (FIG.

18, *K*, *a-p*) shortened and widened in varying degree. The more pronouncedly modified specimens approach an ovoid shape, and frequently contain two septa placed so as to delimit a large swollen dolioform middle segment from the two smaller conoidal end segments (FIG. 18, *K*, *d*, *e*, *f*, *i*, *j*, *l*, *m*, *n*, *p*). This variation in conidial morphology appeared so much in excess of the variation usual in members of the predacious series that it was earlier held as possibly indicative of a separate species (**14**: p. 356, lines 31–37; p. 357, lines 1–3, 19–25, fig. 18, A, B). However, pure cultures made from the swollen biseptate conidia showed no important difference from cultures started with the slender uniseptate spores. Further evidence of identity is provided in the vegetative fusion of germ tubes from both types of spores with one and the same hypha (FIG. 18, *I*, *J*); anastomoses with slender and with swollen spores taking place indiscriminately, and in no wise less freely than when slender conidia alone are present (FIG. 6, *I*).

Sometimes conidia in germinating give rise individually to a predacious ring (FIG. 6, *K*) of slightly smaller dimensions than the similar organs formed on mycelial hyphae. A nematode ensnared in such a ring is, of course, not held in place, but with the conidium clamped to its body continues for a few hours to move about, at first frantically, then more feebly, offering a ludicrous yet pitiful sight. The increasing constriction finally brings about a cessation of movement, whereupon, if not before, penetration is effected, followed by intrusion of assimilative hyphae and appropriation of the fleshy contents. An altogether similar ectoparasitic relationship occasionally replaces the more usual predacious relationship when large vigorous nematodes belonging often to species of *Rhabditis* and of *Mononchus*, tear rings wherein they have become ensnared from their attachments on the mycelial hyphae, and then continue to move about until overtaken by paralysis.

As might be inferred from previous remarks, the fungus produces uniseptate conidia so often to the exclusion of biseptate specimens that mycologists encountering its reproductive apparatus in the course of routine examinations would hardly ever have reason to suspect any possible eligibility for inclusion in *Dactylaria*. It is accordingly referred, though not without reluctance, to the genus *Arthrobotrys*. Of the five other species of *Arthrobotrys* herein discussed, it would seem most closely related to *A. musiformis,* whose frequently discrete circular loops bear a resemblance to the stalked constricting nooses of the present form not shared by the hyphal bails and reticula of the other retiary congeners. However, its most intimate kinship is very probably with the fungus to be described as *Dactylaria brochopaga.* This fungus it resembles closely not only in outward habit and in design of predacious organs, but also in producing on maizemeal agar-plate cultures a somewhat lustrous radiating mycelium whose hyphae under the microscope appear disposed in nearly parallel arrangement.

Arthrobotrys dactyloides sp. nov.

Mycelium effusum; hyphis hyalinis, septatis, plerumque 2–5 μ crassis, laqueos circulares 20–32 μ latos in 3 cellulis arcuatis 12–28 μ longis medio 4.5–7 μ extremo 2.5–6 μ crassis consistentes ex ramulo biloculari circa 7–14 μ longo 4–5 μ crasso proferentibus; his laqueis vermiculos nematoideos illaqueantibus, deinde tum per contractionem inflationemque trium cellularum animal magnopere comprimentibus, ita hoc trucidentibus, statim integumentum perforantibus, hyphas intus evolventibus quae carnem exhauriunt. Hyphae fertiles hyalinae, septatae, erectae, plerumque 200–400 μ altae, basi 4–6 μ crassae, sursum leviter fastigatae, apice 2.5–3.5 μ crassae, 4–13 conidia in capitulum laxum subinde in duo capitula distincta aggregata ferentes. Conidia hyalina, elongata-ellipsoidea, aliquantulum digitiformia, recta vel leviter curvata, apice late rotundata, deorsum aliquantum attentuata, basi truncata, 32–48 μ (saepe circa 41.6 μ) longa, 7–9.5 μ (saepe circa 8.4 μ) lata, loculo inferiore 16–23 μ (saepe circa 20.5 μ) longo; sed quandoque incrassata, abbreviata, usque 18 μ lata, tum saepe 2-septata, loculo medio majore quam alteriis.

Vermiculos nematodeos multarum specierum vulgo usque .6 mm. longos laqueans consumensque habitat in foliis et radicibus plantarum putrescentibus prope Beltsville, Maryland, atque in humo silvestri in Arlington, Virginia.

Mycelium spreading; the vegetative hyphae hyaline, septate, mostly 2 to 5 μ wide, often, especially in the presence of nematodes, producing underneath and at right angles to their respective axes approximately circular rings, 20 to 32 μ in diameter, composed individually of 3 arcuate cells, 12 to 28 μ long, 4.5 to 7 μ wide in the middle and 2.5 to 6 μ wide at the ends—the first and third of the cells being united to one another as well as to the distal part of a somewhat curved sturdy supporting branch 7 to 14 μ long, 4 to 5 μ wide, and consisting usually of 2 cells whereof the proximal one is generally the shorter; 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 giving rise to assimilative hyphae that appropriate the fleshy contents. Conidiophores hyaline, septate, erect, mostly 200 to 400 μ high, 4 to 6 μ wide at the base, tapering gradually upward to a width of 2.5 to 3.5 μ at the tip, there bearing on sterigmata 1 to 5 μ long and 2 to 3 μ wide, from 4 to 13 conidia usually in a single loose head, more rarely in two somewhat distinct clusters. Conidia hyaline, usually elongate ellipsoidal or somewhat digitiform, straight or slightly curved, tapering noticeably from the broadly rounded wider distal end toward the narrower truncate basal end, 32 to 48 μ (average 41.6 μ) long, 7 to 9.5 μ (average 8.4 μ) wide, with the single septum 16 to 23 μ (average 20.5 μ) from the base; but occasionally becoming wider and shorter, measuring as much as 18 μ in width and as little as 25 μ in length, then often 2-septate, with the inflated middle cell greatly exceeding the end cells in size.

Capturing and consuming nematodes measuring up to .6 mm. in length, referable to the genera *Acrobeles*, *Acrobeloides*, *Cephalobus*, *Diplogaster*, *Diploscapter*, *Plectus*, *Rhabditis* and *Mononchus*, it occurs in decaying leaves and roots of many plants near Beltsville, Md., and also in leaf mold in deciduous woods in Arlington, Va.

DACTYLELLA BEMBICODES

A fungus obtained occasionally in nematode-infested agar-plate cultures following the addition of small quantities of miscellaneous leaf mold, and much more frequently following addition of the dark friable material from the interior of decaying acorns, produces rings very similar to those of *Arthrobotrys dactyloides* both in cellular make-up and in positional relationship to parent hypha and substratum (FIG. 7, *A-H*). Sometimes the predacious organs here have given slightly larger measurements than in the species already described, yet for the most part differences between the two forms with respect to the robustness of these structures are not readily apparent. Capture (FIG. 7, *I*) and invasion (FIG. 7, *J, K, L*) of prey likewise proceeds as in *A. dactyloides*, except that here the assimilative hyphae generally terminate after the usual manner of mycelial filaments rather than in bulbous enlargements. Though the constricting ring would seem designed especially for the capture of nematodes, specimens of rotifers have occasionally been found squeezed to death in agar cultures moist enough to encourage multiplication of these animals (FIG. 18, *N*).

The conidiophores produced by the fungus on nematode-infested agar cultures are usually too sparsely distributed on the substratum to make up a stand at all easily discernible with the naked eye. On microscopic inspection, however, they appear as tall, erect, sturdy hyphae, which, individually, for some time after attaining definite height are continuous with the swollen tip (FIG. 7, *M*) that gradually develops into the terminal conidium (FIG. 7, *N*). Somewhat rarely a second conidium may be formed following elongation of the hypha from below the attachment of the first. As a conidiophore approaches or attains maturity it frequently puts out a lateral branch some short distance, usually about 50 μ, above the base (FIG. 7, *N, d*). This branch grows into a second conidiophore (FIG. 7, *M, b*), gradually assuming an erect position as the parent hypha (FIG. 7, *M, a*) declines toward the substratum. Where no such secondary development ensues a conidiophore may retain its upright posture for a considerable period after the spore has fallen off (FIG. 7, *O*).

The fungus, though readily isolated, grows very slowly in pure culture. On maizemeal agar white aerial mycelium is produced without, however, any vestige of conidial apparatus. Nor has such apparatus been seen in pure culture on other media.

After its principal morphological features had been briefly set forth (**14**: p. 356, lines 5–26; p. 357, lines 15–18, fig. 17, A, B, C), the fungus was referred to incidentally (**17**, **18**) as probably being identical with *Monacrosporium elegans*. The likelihood of such identity was suggested by a general resemblance of the conidia (FIG. 7, *P, a–z*) to those described and figured in the original account of Oudemans' species. Closer comparison has, however, always revealed serious differences in detail. Conidiophores so short as not to exceed the length indicated in Oudemans' diagnosis, 250 μ, have been seen only rarely in my material, and then mostly after special search. Measurements of the largest conidia in cultures started with materials collected in more than a dozen different places have failed to disclose even a single specimen having a length of 50 μ, the lower limit of the range given for this dimension in the description of *M. elegans*. The discrepancy can not

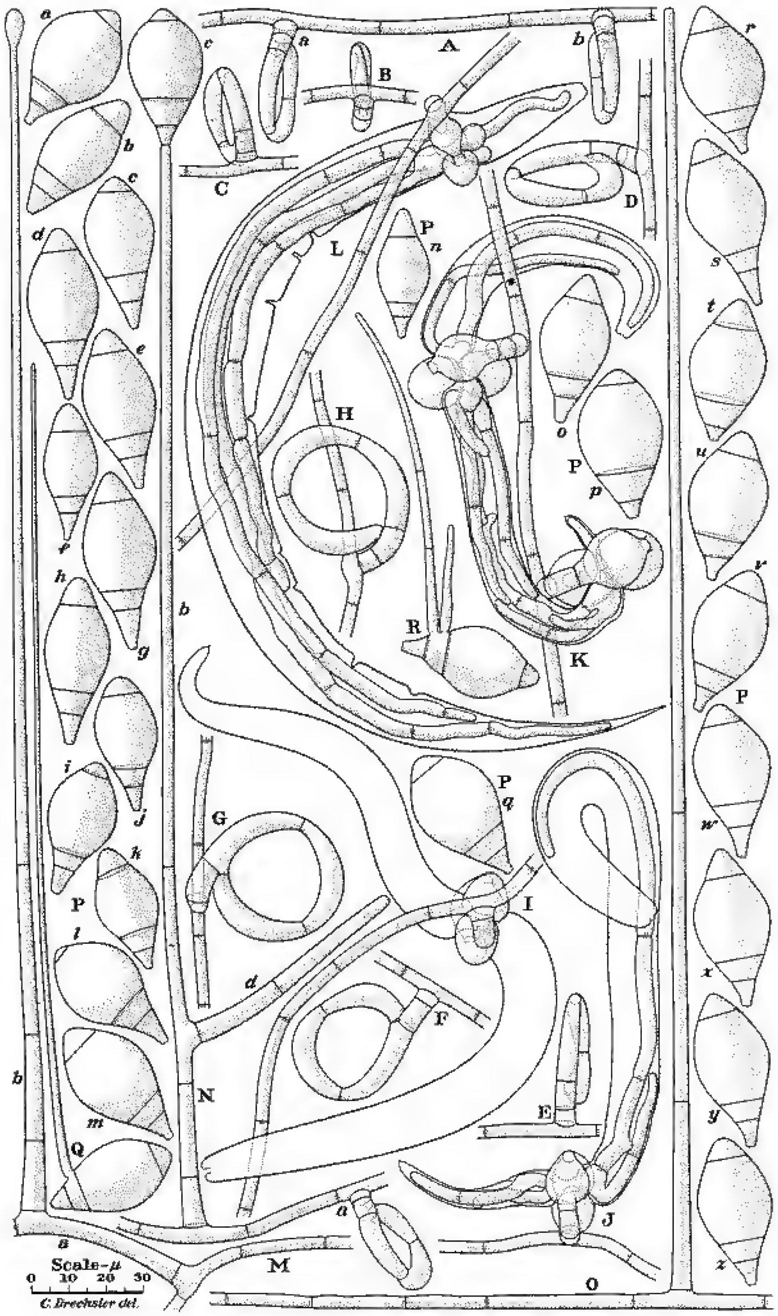

FIG. 7. *Dactylella bembicodes.*

well be explained away as resulting from wide variability, since the present fungus, unlike many other members of the predacious series, has consistently shown only rather moderate variations in conidial dimensions, always over approximately the same range. Thus, the 100 spore measurements from which were obtained the relevant metric data presented in the accompanying diagnosis—measurements made on specimens taken at random in equal numbers from four different strains growing in nematode-infested maizemeal agar plate cultures—gave a distribution of values for length expressed to the nearest micron as follows: 34 μ, 2; 36 μ, 2; 37 μ, 2; 38 μ, 2; 39 μ, 5; 40 μ, 10; 41 μ, 18; 42 μ, 14; 43 μ, 20; 44 μ, 12; 45 μ, 5; 46 μ, 4; 47 μ, 3; 48 μ, 1; and a distribution of values for width as follows: 14 μ, 1; 15 μ, 1; 16 μ, 1; 17 μ, 3; 18 μ, 6; 19 μ, 18; 20 μ, 29; 21 μ, 27; 22 μ, 12; 23 μ, 2.

It is true that more pronounced differences than those just noted have not always been deemed sufficient to separate from *Monacrosporium elegans* fungi having conidia of somewhat similar ventricose shape. Marchal (44), for example, assigned to Oudemans' species a form with spores only 20 to 40 μ long and 15 to 18 μ wide. This form, no less than *M. ovatum* later described by Petch (53) as having conidia 26 to 36 μ long and 12 to 16 μ wide, would seem, however, definitely too small to be identified with *M. elegans*, or, for that matter, with the predacious fungus under discussion. Again, Rostrup (59) listed as *M. elegans* a plant whose symmetrically and broadly spindle-shaped 4-septate conidia show far better agreement with those of the species to be subsequently treated under the binomial *Dactylella ellipsospora*. It must be apparent from a consideration of the several distinct nematode-capturing forms with ventricose conidia presented herein, that such swollen spores, however infrequent elsewhere, are far from unusual in the predacious series of which *M. elegans* most probably is a member. Certainly the conidia of the present form correspond more closely to the 3-septate spores usual in *Dactylaria thaumasia* and frequent in *Dactylella gephyropaga* than they correspond to the spores described in the original account of *M. elegans*. The fungus evidently represents a new species, for which an epithet meaning "top-shaped," suggested by its characteristically turbinate conidia, may not be inappropriate.

Dactylella bembicodes sp. nov.

Mycelium effusum; hyphis hyalinis, septatis, plerumque 2–5 μ crassis, laqueos circulares 22–37 μ latos in 3 cellulis arcuatis 14–30 μ longis medio 4.5–7 μ extremo 3–6 μ crassis consistentes ex ramulo biloculari circa 7–14 μ longo, 4.5–6 μ crasso proferentibus; his laqueis vermiculos nematodeos illaqueantibus, deinde tum per contractionem inflationemque trium cellularum animalia magnopere comprimentibus, ita haec trucidentibus, statim integumentum perforantibus, hyphas intus evolventibus quae carnem exhauriunt. Hyphae fertiles hyalinae, erectae, septatae, 250–500 μ altae, basi 5–7.5 μ crassae, sursum leviter fastigatae, apice 2–3.2 μ crassae, ibi unicum conidium ferentes. Conidia hyalina, speciose turbinea, 34–48 μ (saepe circa 42 μ) longa, 16–23 μ (saepe circa 20 μ) lata, vulgo 3-septata: loculo infimo obconico, saepe circa 7.6 longo; loculo antepaenultimo disciformi, saepe circa 5.7 longo; loculo paenultimo dolioformi, ventricoso, saepe circa 22.5 μ longo; loculo summo apice rotundato, saepe circa 6.2 μ longo.

Vermiculos nematodeos multarum specierum etiam rarissime rotifera laqueans consumensque habitat exigue in humo silvestri sed abunde praecipue in glandibus quernis *Querci Prini* putrescentibus prope Beltsville, Maryland, et in Arlington, Virginia.

Mycelium spreading; vegetative hyphae hyaline, septate, mostly 2 to 5 μ wide, often, especially in the presence of nematodes, producing underneath and at right angles to their axes approximately circular rings 22 to 37 μ in outside diameter, composed individually of 3 arcuate cells 14 to 30 μ long, 4.5 to 7 μ wide at the middle and 3 to 6 μ wide at the ends—the first and third of the cells being united usually to one another as well as to the distal end of the sturdy, somewhat curved or straight supporting branch 7 to 14 μ long, 4.5 to 6 μ thick, and consisting usually of 2 cells, whereof the proximal one is generally the shorter; 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 throughout the body assimilative hyphae that appropriate the fleshy contents. Conidiophores hyaline, erect, septate, 250 to 500 μ, mostly 300 to 450 μ high, 5 to 7.5 μ wide at the base, tapering gradually upward to a diameter of 2 to 3.2 μ at the tip, whereon is borne usually a single conidium. Conidia hyaline, handsomely top-shaped, broadly rounded at the apex, tapering toward the slightly protruding truncate base, 34 to 48 μ (average 42 μ) long, 16 to 23 μ (average 20 μ) wide, regularly divided by 3 septa into 4 cells: the basal cell obconical, with an average length of 7.6 μ; the antepenultimate cell disciform, with an average length of 5.7 μ; the penultimate cell ventricose or inflated barrel-shaped, with an average length of 22.5 μ; the apical cell conico-hemispherical, with an average length of 6.2 μ.

Capturing and consuming nematodes measuring up to .6 mm. in length, referable to the genera *Acrobeles, Acrobeloides, Cephalobus, Diplogaster, Diploscapter, Plectus, Rhabditis* and *Mononchus*, and very rarely also rotifers, it occurs rather sparingly in leaf mold generally, but more abundantly especially within decaying acorns (*Quercus Prinus* L.), near Beltsville, Md., and in Arlington, Va.

DACTYLELLA ELLIPSOSPORA Grove

Though in recent times Zopf's discoveries relative to the capture of nematodes by *Arthrobotrys oligospora* appear finally to have become widely recognized, it is less generally known that in the same paper in which these discoveries were published he set forth also, even if somewhat briefly, the destruction of nematodes by another predacious fungus referred to under the name *Monosporidium repens*. The latter species was described as forming on the surface of its substratum a delicate white coating composed of narrow septate filaments from which arise simple, relatively short conidiophores individually bearing at their tips a solitary, nonseptate, colorless conidium, globose or pyriform in shape, and measuring 8 to 10 μ along its longest axis. The strange thing, according to the account, is that infection proceeds always from the conidium; this structure applying itself to the nematode, mostly at the forward end, and then intruding into the body a short, stout infection-vesicle from which two or three filaments are extended through the interior of the animal to the caudal end. Further development was reported to take place by the production from the endozoic hyphae of lateral branches that after perforating the animal's integument form new conidia outside to repeat the cycle.

In one of my summaries (**12**: p. 139, lines 24–26, fig. 7, A, B, C; p. 140, lines 1–7), and again somewhat more fully in a later paper (**15**: p. 138–139), the structures taken by Zopf for conidia were presented as specialized predacious organs owing their functional efficacy to adhesive material secreted by them. At all events adhesive organs corresponding well to Zopf's supposed conidia have been seen frequently in nematode-infested agar-plate cultures following the addition of leaf mold, or of bits of decaying wood. Sometimes nearly spherical but more often perceptibly prolate,

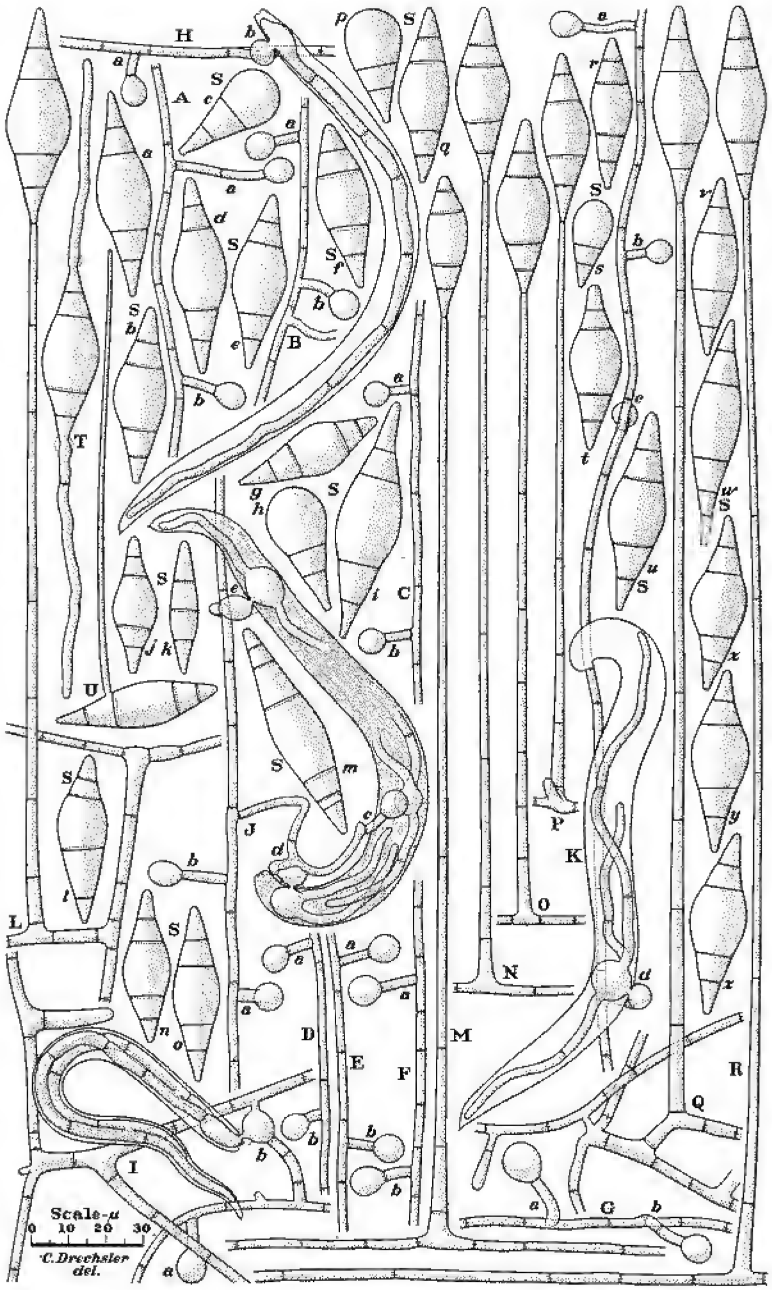

FIG. 8. *Dactylella ellipsospora.*

they vary in length from 7 to 11.5 μ, and in width from 6.5 to 10 μ (FIG. 8, *A–G: a–b; H, a; I, a; J, a, b; K, a–c*). The stalks bearing them are mostly unicellular, 2.4 to 3 μ wide and 5 to 10 μ long, though examples may be found as little as 3 μ (FIG. 8, *D, b*) or as much as 25 μ (FIG. 8, *A, a*) in length; the longer specimens often consisting of two or more cells (FIG. 8, *A, a; I, b*). Generally the stalks arise at nearly right angles from the rather straightforward, septate hyphae, mostly 2 to 3 μ wide, that make up the sparse mycelium. Capture of nematodes is effected through adhesion on the globose cells, the adhesive material here, as in retiary species, becoming visible as a sizable deposit after the struggles of the animal have stimulated its secretion for some time (FIG. 8, *H–K*). In the absence of all structural ensnarement, only somewhat small animals are usually held, though larger prey may be taken when because of moist conditions the mechanical leverage of struggling captives has been reduced. Penetration of the integument, intrusion of a bulbous outgrowth, extension therefrom of assimilative hyphae through the paralyzed body, and appropriation of the degenerating fleshy contents, follow in their familiar sequence.

From the prostrate superficial mycelial filaments are put forth erect, septate conidiophores (FIG. 8, *L–R*) 150 to 300 μ high, 3.2 to 5 μ wide at the base, tapering upward to a width of 1.5 to 2.5 μ at the tip, whereon is borne a solitary conidium. Occasionally a second spore is formed, following elongation of the fertile hypha. More frequently a branch from the basal portion of an aging conidiophore grows into a new conidiophore, assuming an erect position as the old one declines to the substratum. The conidia thus produced (FIG. 8, *S, a–z*) are for the most part broadly spindle-shaped, rounded at the ends, and divided by four septa into five cells, of which the middle, barrel-shaped one is usually by far the largest. They vary in length between observed extremes of 24 μ and 65 μ, and in width between observed extremes of 7.5 μ and 19 μ; some of the longer specimens containing as many as six cross-walls (FIG. 8, *S, m*), while most of the shortest specimens are of atypical obconical shape (FIG. 8, *S, c, h, p, s*) with only two septa—these corresponding evidently to the two proximal partitions of the four more commonly present. Germination takes place by the production frequently of two polar germ tubes (FIG.

8, *T*); but on relatively dry substrata a delicate conidiophore (FIG. 8, *U*) is often thrust up to bear a secondary conidium, which is regularly somewhat smaller than the primary one from which it originated.

The conidial apparatus in question shows fairly satisfactory agreement with Grove's (**28**) description of his *Dactylella ellipsospora.* The range for length of conidium indicated in that description, 40 to 50 μ, coincides with the usual range for this dimension in my material; while the range indicated by Grove for width of conidium, 16 to 18 μ, if somewhat higher than would seem representative of my fungus, is yet exceeded by the maximum value for this dimension given in the preceding paragraph. Equally good, or perhaps even better agreement is found when comparison is extended to *Monacrosporium leporinum,* described by Bubák (**6**) as having conidiophores 180 to 300 μ long together with conidia 42 to 53 μ long, 13 to 18.5 μ wide, and composed of five cells, the median one exceeding the others in size.

The nematode-capturing fungus whose predacious apparatus is evidently identical with the supposed conidia discussed by Zopf in 1888, must on grounds of priority be referred to *D. ellipsospora* described two years earlier from true reproductive structures. With this species *M. leporinum* described two decades later from reproductive structures of very similar morphology appears to be synonymous, as would seem to be, also, though somewhat more doubtfully, the *M. elegans* of Rostrup. On the other hand, the *D. ellipsospora* of Smith (**65**), with spores measuring 40 μ in length and 10 to 12 μ in width, may with equal or perhaps greater probability, have been identical with the species herein to be described as *D. lysipaga.*

In pure culture on maizemeal agar the fungus grows well, giving rise to a moderately dense submerged mycelium of somewhat radiating aspect. Sporulation is frequently wholly absent, but can often be brought on by exposure to direct sunlight for brief periods. Reproductive apparatus obtained through such exposure is, however, mostly so variable that despite the generally more robust conidiophores and larger conidia characteristic of the species, separation from *Dactylella lysipaga* in similarly treated cultures is usually not easy. For definite identification, therefore, the fungus should preferably be viewed also in nematode-infested cultures, where its predacious organs distinguish it very readily from any other known species with typically 4-septate conidia.

DACTYLELLA ASTHENOPAGA

A fungus with predacious knobs (FIG. 9, *A, B*) perceptibly smaller than those formed by *Dactylella ellipsospora* often makes its appearance in maizemeal agar cultures following the addition of small quantities of the black friable material from the interior of decaying acorns; and much less frequently following the addition of miscellaneous leaf mold. The knobs in the present species ordinarily appear operative only in the capture of nematodes belonging to the genus *Bunonema*—phlegmatic animals that after being introduced with the decaying forest refuse multiply slowly in the cultures to attain respectable numbers in two or three weeks. On especially moist agar culture media small individuals of more energetic genera have been seen captured, indicating that the selection usually evident results from the inability of the adhesive organs to hold the more active eelworms when the physical condition of the substratum is such as to furnish effective leverage. Once an animal is held, narrow perforation of the integument, intrusion of a mortiferous excrescence, extension of assimilative hyphae lengthwise, and appropriation of the degenerating fleshy contents, take place as in other species with adhesive predacious apparatus (FIG. 9, *C-E; F, a, b*).

The conidiophores (FIG. 9, *G-J*) arising here and there from the sparse mycelium in nematode-infested agar cultures, are rather frail in appearance when compared with those of most other fungi subsisting through the capture of eelworms. Usually and typically they are simple and bear a single conidium; yet at times a second conidium is produced on a short branch attached some distance below the apex (FIG. 9, *K*); and, more rarely still, two lateral branches are present, allowing a production altogether of three conidia (FIG. 9, *L*). Such distal ramification is no doubt akin to the proximal branching frequent in this as in related species, whereby young conidiophores are put forth to assume gradually an erect posture as the old axis declines to the substratum.

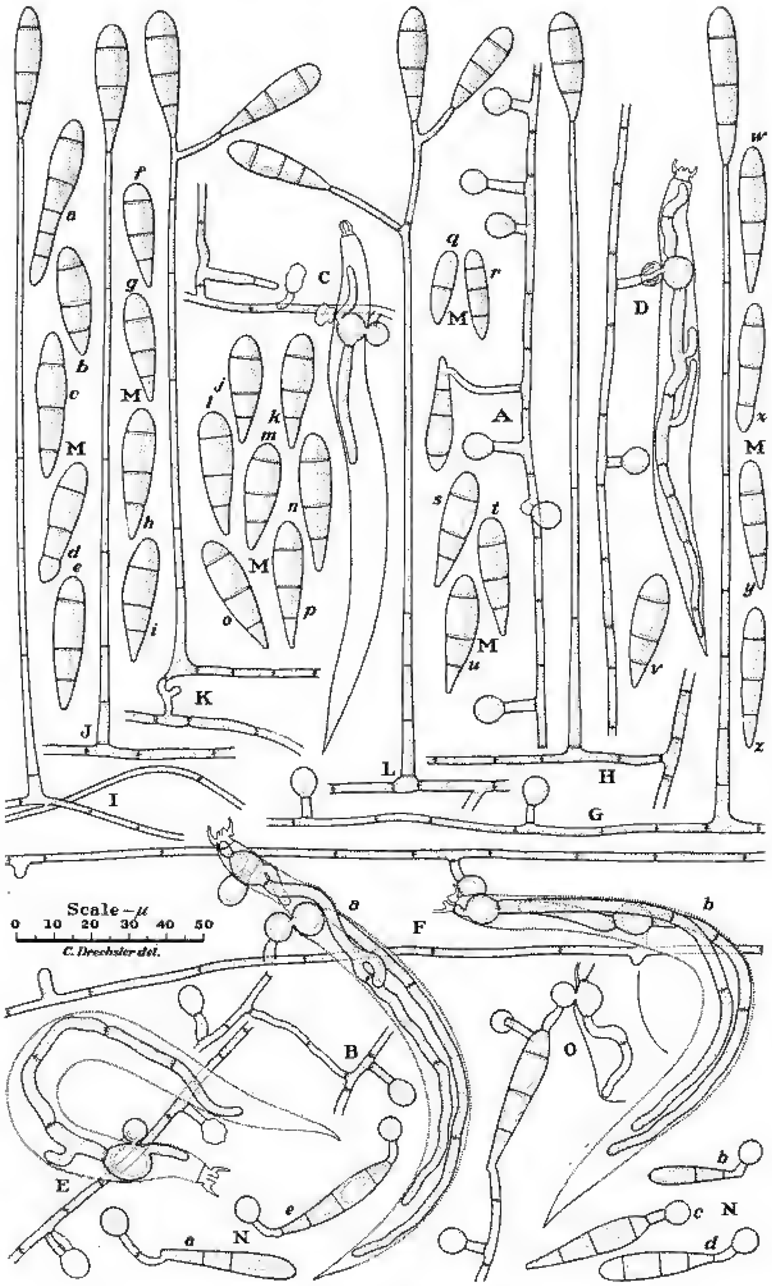

FIG. 9. *Dactylella asthenopaga.*

In pure culture on maizemeal agar the fungus grows readily, giving rise to a sparse stand of conidiophores, on which are borne conidia mostly rather irregularly clavate in shape, measuring 20 to 46 μ in length, and partitioned by one to five cross-walls (FIG. 9, *M, a-d, q, r, x*). On nematode-infested agar plate cultures, a better approximation to uniformity, and apparently a more trustworthy expression of the morphology of the species is obtained, the conidia here, more regularly clavate in shape, measuring 26 to 36 μ in length, and with few exceptions, containing three cross-walls (FIG. 9, *M, e-p, s-w, y, z*). Germination often is initiated by direct production of one or two stalked knobs (FIG. 9, *N, a-e*); the residual protoplasm in the conidium then being utilized to put forth a germ hypha likewise beset with these predacious organs (FIG. 9, *O*).

With respect to size and shape of conidium, the fungus would seem to fit fairly well the description of *Monacrosporium sarcopodioides* (Harz) Berl. & Vogl. as given by Saccardo (**62**) and by Lindau. However, the sporophores of *M. sarcopodioides*, characterized as continuous, ascending, and equal in length to the conidia, differ so much from the septate, erect and relatively tall fertile hyphae of the present form that identity of the two organisms appears unlikely. Nor, indeed, can a better agreement be discovered by consulting Harz's original account (**31**) of his *Acrothecium sarcopodioides*, wherein the fertile hyphae are described as "schwach aufsteigend oder neiderliegend."

The somewhat feebly predacious fungus under consideration is accordingly described as a new species under a name compounded of two words meaning "weak" and "trap" respectively.

Dactylella asthenopaga sp. nov.

Mycelium effusum; hyphis hyalinis, septatis, 1.7–3 μ crassis, bullas tenaces globosas vel ellipsoideas plerumque 6.5–8 μ longas, 6–7.5 μ latas ex ramulo recto, 3–10 μ longo, 2–3 μ crasso saepe proferentibus; his bullis vermiculos nematodeos tenentibus, integumentum perforantibus, tuber mortiferum saepe 8–10 μ crassum intrudentibus, hyphas 2–5 μ crassas evolventibus, quae carnem exhauriunt. Hyphae fertiles hyalinae, erectae, septatae, 100–200 μ altae, basi 2.5–4 μ crassae, sursum fastigatae, apice circa 1.5 μ crassae, plerumque simplices et unicum conidium ferentes, sed quandoque prope summum paululum ramosae tum 2 vel 3 conidia gerentes. Conidia hyalina, obconica vel clavata, basi truncata, apice rotundata, 20–46 μ (saepe circa

31.5 μ) longa, 6.5–9.5 μ (saepe circa 8.2 μ) crassa, 1–5 septata, fere 3-septata, loculo infimo tum saepe circa 8 μ longo, loculo antepaenultimo saepe circa 7.5 μ longo, loculo paenultimo saepe circa 9.8 μ longo, loculo summo saepe circa 6.2 μ longo.

Vermiculos nematodeos diversos pigros vulgo usque .3 mm. longos qui vulgo maximam partem specierum *Bunonematis* sunt capiens consumensque habitat exigue in humo silvestri sed abundius praecipue in glandibus quernis *Querci Prini* putrescentibus prope Beltsville, Maryland, et in Arlington, Virginia.

Mycelium spreading; composed of hyphae mostly 1.7 to 3 μ wide, that especially in the presence of nematodes give rise here and there, at angles approaching a right angle, to stalks 3 to 10 μ long and 2 to 3 μ wide, on each of which is borne a globose or prolate ellipsoidal unicellular adhesive knob, mostly 6.5 to 8 μ long and 6 to 7.5 μ wide; the knobs holding fast to nematodes, individually perforating their captive's integument, and intruding a globose mortiferous excrescence, often 8 to 10 μ in diameter, from which are extended lengthwise through the body assimilative hyphae, 2 to 5 μ wide, that appropriate the degenerating fleshy contents. Conidiophores hyaline, septate, erect, 100 to 200 μ, mostly 125 to 175 μ high, 2.5 to 4 μ wide at the base, tapering gradually upward to a width of approximately 1.5 μ, mostly unbranched and terminating in a single conidium, but occasionally giving off one or two branches some distance below the tip, and then bearing two or three conidia. Conidia hyaline, obconical or clavate, truncate at the narrow proximal end, broadly rounded at the distal end, 20 to 46 μ, mostly 26 to 36 μ (average 31.5 μ) long, 6.5 to 9.5 μ (average 8.2 μ) wide, containing 1 to 5 septa, but most often and most typically containing 3 septa, the basal of the 4 cells then delimited averaging about 8 μ in length, the antepenultimate cell about 7.5 μ, the penultimate cell about 9.8 μ, and the apical cell about 6.2 μ.

Capturing and consuming sluggish nematodes commonly up to .3 mm. in length, and for the most part belonging to species of *Bunonema*, it occurs sparingly in leaf mold but more abundantly within decaying acorns (*Quercus Prinus* L.) in Arlington, Va., and near Beltsville, Md.

DACTYLELLA LYSIPAGA

The fungus whose resemblance to *Dactylella ellipsospora* in morphology of reproductive structures has already been referred to, is easily distinguished from that species in cultures where its predacious apparatus has occasion to develop (FIG. 10, *A–O*). In part, to be sure, this apparatus consists of globose adhesive knobs similar in design to the homologous organs formed in *D. ellipsospora*, but differing from them in markedly smaller dimensions, as well as in their attachment to the parent filament by longish, slender, and often gracefully curved stalks, rather than on short, stout, straight ones. It would seem that in most agar substrata efficiency is associated more with size and sturdiness than with gracility; for the knobs of the present species have only rarely been found operative, and then only in the capture of larvae belonging to relatively lethargic nematodes. As was intimated earlier (**15**), the usual inefficiency of such knobs in a gelatinous culture medium need not preclude a greater degree of usefulness under the more different and varied physical conditions obtaining in natural substrata.

Development in nematode-infested agar cultures is made possible very largely through the more effective functioning of circular hyphal rings usually intermingled with the knobs, and like these produced terminally on short, slender, often gracefully circinate stalks. Nematodes ensnared in the rings are sometimes held in place, but more often they tear the encircling structure from its attachment and continue to move about, often only to be caught in a second ring, and occasionally even in a third. Accumulation of rings in larger numbers is perhaps somewhat infrequent in nature; yet as many as 8 have been seen encircling individual nematodes (FIG. 10, *P*) after large pieces of vigorous mycelium from pure cultures of the fungus on maizemeal agar had been transferred to agar plate cultures abundantly infested with roundworms. Devoid of all predacious apparatus at the time of transfer, the mycelium soon gave rise to rings and adhesive knobs in spectacular concentration, thereby providing opportunity for more frequently repeated ensnarement of visiting eelworms. In spite of extraordinary concentration of hyphal rings an animal would assuredly not become ensnared more than a few times if the fungus were not somewhat dilatory in accomplishing the death of encircled specimens. Although in cellular make-up the rings are not without similarity to the strangulating organs of *Arthrobotrys dactyloides* and *Dactylella bembicodes*, they exert no active constriction; and the bulbous body slowly intruded into the animal after delayed penetration of its integument apparently never becomes large

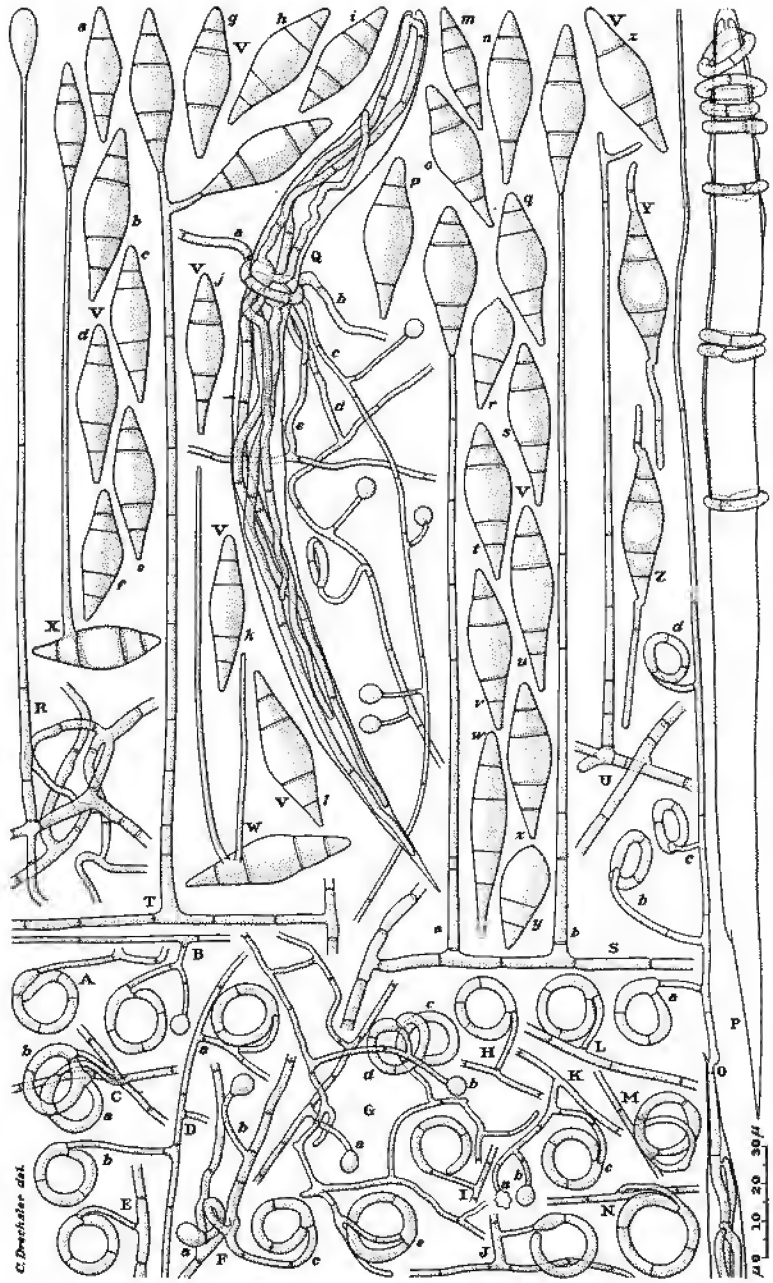

FIG. 10. *Dactylella lysipaga.*

enough to kill or paralyze promptly. The decline of the animal is accordingly rather slow at first, but with the gradual extension of assimilative hyphae from the intruded bulb through the fleshy interior, movement gradually comes to an end. Appropriation of the degenerating materials makes possible further mycelial growth in the underlying or surrounding substratum; the additional hyphae arising for the most part from the outer surface of the ring itself (FIG. 10, *A*, *a-e*), though here and there an assimilative branch occasionally breaks through the integument to grow out directly as a mycelial filament (FIG. 10, *O*). Whatever their source, the new external hyphae in their turn give rise to predacious organs, thus renewing the vegetative cycle.

The conidiophores (FIG. 10, *R-U*) and conidia (FIG. 10, *V*, *a-z*) produced usually in rather meager quantity, whether on nematode-infested substrata or in pure culture, closely resemble the homologous structures of *Dactylella ellipsospora*, but show on the whole somewhat smaller dimensions throughout. Measurements of conidia from representative material give average values for length and width corresponding very well to the values given by Smith (**65**); so that, as has been mentioned previously, it seems probable that this author was dealing with the species under consideration rather than with the one described by Grove. A conidium, after falling on a slightly moist substratum, often thrusts up an erect conidiophore (FIG. 10, *X*) to bear a secondary conidium, somewhat smaller but otherwise like its parent. Occasionally two conidiophores may be pushed up from a fallen spore (FIG. 10, *W*). On wetter substrata germination takes place, as in *D. ellipsospora*, by the production of two polar germ tubes (FIG. 10, *Y*, *Z*).

The fungus seems closely related also to *Dactylaria candida*, presenting obvious resemblance to that species in type of predacious apparatus, as well as in shape and septation of conidium. However, a capitate arrangement of the spores has never been observed here, though occasionally a second conidium may be borne on a short spur attached some distance below the tip of the axial hypha (FIG. 10, *T*, *U*).

It is hoped that an epithet compounded of words meaning "a loosing" and "snare," may appropriately suggest the combination of predacious and ectoparasitic relationships revealed by the species.

Dactylella lysipaga sp. nov.

Mycelium effusum; hyphis hyalinis, septatis, 1.5–3.5 μ crassis, non modo bullas tenacis globosas vel ellipsoideas plerumque 5–8 μ longas, 4.5–6 μ latas, sed etiam laqueos circulares 13–23 μ latos in 2–3 plerumque 3 loculis subaequalibus, arcuatis, 2.5–4 μ crassis consistentes ex ramulo saepe aliquantum curvato vel decore circinato 5–35 μ longo, 1.2–2 μ crasso ferentibus; bullis vermiculos nematodeos tenentibus, integumentum perforantibus, hyphas intus evolventibus quae carnem exhauriunt; laqueis vermiculos nematodeos irretientibus, modo hos capientibus, modo ipsis avolsis, sed tamen integumentum semper perforantibus, hyphas intus evolventibus quae carnem exhauriunt. Hyphae fertiles hyalinae, erectae, septatae, 125–250 μ altae, basi 3–5 μ crassae, sursum fastigatae, apice 1.1–1.8 μ crassae, plerumque simplices et unicum conidium ferentes sed quandoque secundum conidium ex ramusculo prope apicem orto gerentes. Conidia hyalina, vulgo fusoidea, apice rotunda, basi truncata, 28–55 μ (saepe circa 40.7 μ) longo, 9–14 μ (saepe circa 11.6 μ) lata, subinde 2 vel 3 septata, saepius 4-septata, loculo infimo tum fere circa 8.2 μ longo, huic proximo superiore loculo fere circa 6.8 μ longo, loculo medio fere circa 13.8 μ longo, loculo paenultimo fere circa 6.1 μ longo, loculo summo fere circa 6.3 μ longo.

Vermiculos nematodeos graciles multarum specierum interficiens consumensque habitat in humo silvestri prope Beltsville, Maryland, et in Arlington, Virginia.

Mycelium spreading; the vegetative hyphae hyaline, septate, mostly 1.5 to 3.5 μ wide, often especially in the presence of nematodes, giving rise on slightly curved or circinate stalks 5 to 35 μ long, 1.2 to 2 μ wide and composed of one or more cells, either to adhesive unicellular knobs, subspherical or prolate ellipsoidal in shape, 5 to 8 μ in length and 4.5 to 6 μ in width, or to generally discrete, approximately circular rings, 13 to 23 μ in diameter, composed usually of 3, more rarely of 2 or 4 subequal, arcuate filamentous cells mostly 2.5 to 4 μ wide—the knobs capturing nematodes through adhesion, individually perforating the integument of each, and intruding assimilative hyphae; the rings after individually ensnaring nematodes sometimes remaining attached, but often being torn loose from their attachments, yet in either event likewise perforating the integument and intruding assimilative hyphae to appropriate the fleshy contents. Conidiophores hyaline, septate, erect, 125 to 250 μ high, 3 to 5 μ wide at the base, tapering upward to a width of 1.1 to 1.8 μ, mostly simple and bearing a single terminal conidium but occasionally producing a second conidium on a short branch attached to the main axis some distance below the tip. Conidia hyaline, sometimes obovoid-fusoid, but much more frequently and more typically rather symmetrically fusoid, somewhat acutely rounded at the apex, truncate at the narrow base, 28 to 55 μ (average 40.7 μ) long, 9 to 14 μ (average 11.6 μ) wide, sometimes 2- or 3-septate, but more frequently and typically divided by 4 cross-walls into 5 cells, whereof the basal one averages 8.2 μ in length, the one adjacent to the proximal cell 6.8 μ, the middle one 13.8 μ, the penultimate one 6.1 μ, and the apical one 6.3 μ.

Destructive to slender nematodes belonging often to the genera *Rhabditis* and *Plectus,* it occurs in leaf mold in deciduous woods near Beltsville, Md., and in Arlington, Va.

DACTYLELLA LEPTOSPORA

The somewhat *Fusarium*-like predacious fungus whose main structural features were briefly described in an earlier summary (**14**: p. 355, lines 28–40; p. 356, lines 1–4; p. 357, lines 7–14, fig. 16, A, B, C) has been found only a few times, and then always in nematode-infested agar plate cultures to which pinches of leaf mold had been added. On the rather delicate hyphae that make up the sparse mycelium in such cultures, it gives rise under the surface of the substratum to stalked non-constricting hyphal rings (FIG. 11, *A-F*) closely similar to those produced by *Dactylella lysipaga* both in morphology and manner of operation. When conditions are provided for an abundant production of these rings in cultures infested with nematodes, the animals are ensnared in impressive numbers, some accumulating more than a half dozen of the annular structures (FIG. 11, *G*) before the gradual extension of assimilative hyphae through the fleshy interior finally brings locomotion to a halt. Appropriation of the degenerating cellular materials is accomplished much as in the case of *D. lysipaga*. The accession of nourishment naturally leads to production of new mycelial hyphae, which here arise in noticeably smaller proportion from the ring, and in correspondingly greater proportion consist of branches that are put forth directly from assimilative hyphae to reach the exterior through perforations in the integument (FIG. 11, *H*).

In comparison to the fertile hyphae of most fungi predacious on nematodes, the conidiophores of the present species appear of somewhat small stature (FIG. 11, *I, a-c; J-L*). Even in the pres-

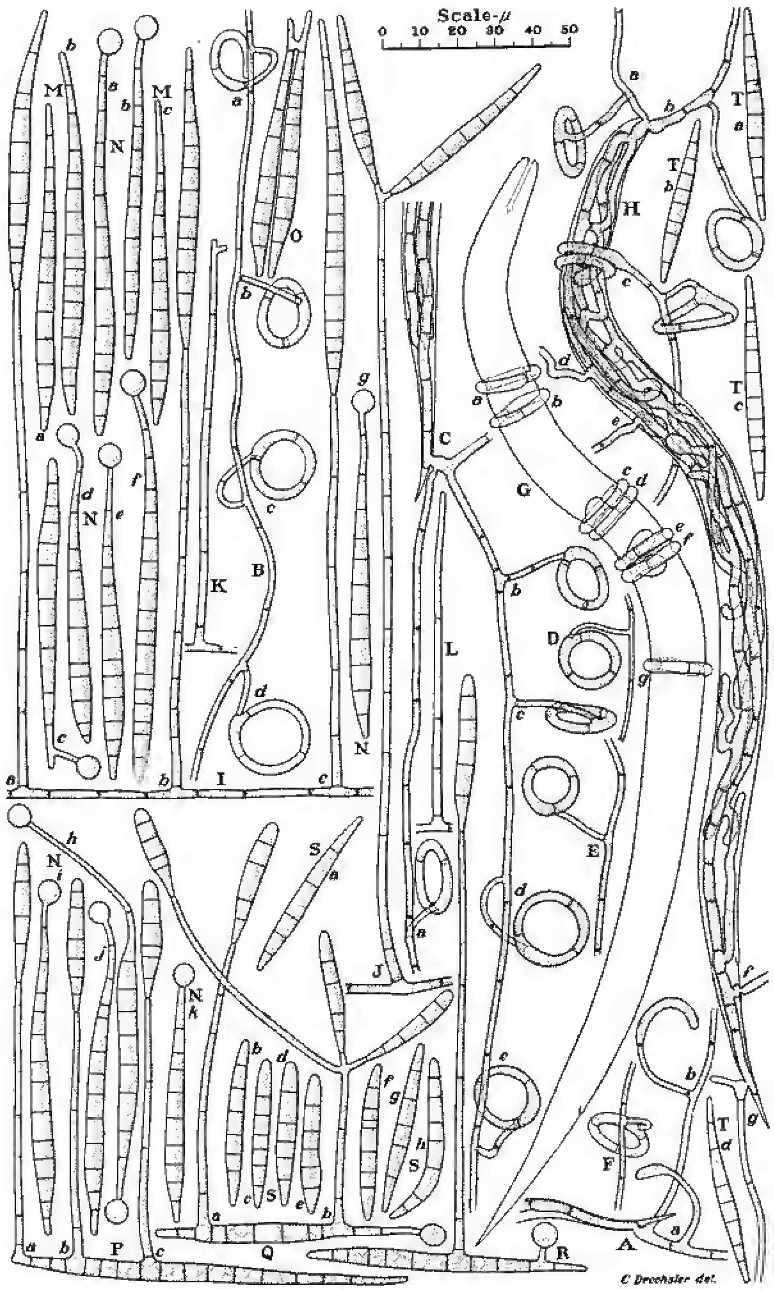

FIG. 11. *Dactylella leptospora.*

ence of an abundant supply of suitable animals they have never been seen produced in nematode-infested agar-plate cultures other than in meager quantity. However, in pure culture on maizemeal agar, reproduction is usually much more copious; and results, moreover, in conspicuously larger conidia. Thus, measurements of a representative assortment of conidia from a nematode-infested agar culture (FIG. 11, *T, a-d*) gave averages of 53 μ and 4.6 μ for length and width respectively; whereas measurements of primary conidia from pure culture on maizemeal agar (FIG. 11, *M, a-c*) gave corresponding averages of 73 μ and 5 μ respectively. Further variability in conidial dimensions is introduced through repetitional development, which especially in pure culture often takes place very abundantly (FIG. 11, *P-R*), some of the larger primary spores giving rise to two, three, or even four secondary ones. As might be expected under such circumstances, the secondary conidia are for the most part of decidedly smaller size (FIG. 11, *S, a-h*), measurements of specimens chosen at random giving averages of 36 μ and 4.8 μ for length and width respectively.

Aside from repetitional development and frequent vegetative fusions (FIG. 11, *O*), conidia produced in pure culture on maizemeal agar often show numerous globose cells, closely similar and undoubtedly homologous to the adhesive knobs in *Dactylella lysipaga*. Very often these globose cells are formed singly on the individual spore, either on a narrow apical prolongation (FIG. 11, *N, a-g, i-k*), or less commonly on a lateral stalk (FIG. 11, *R*); yet specimens with two such structures (FIG. 11, *N, h*) are not at all rare. That these cells represent predacious organs can hardly be questioned; though it must be admitted that so far they have been observed only a few times on mycelium in nematode-infested agar cultures, and then were never seen operative in taking prey.

In morphology of reproductive apparatus the fungus invites comparison more especially with three of the various species producing elongate conidia that have been compiled in the genera *Monacrosporium* and *Dactylella*, namely: *M. subtile* Oud. (**52**) with elongate clavate conidia, 45 to 70 μ long, 5 to 7 μ wide, and divided by septa up to 13 in number; *M. oxysporum* (**61**), with conidia 96 to 105 μ long, 9 to 10.5 μ wide, and divided by 10 to 12 cross-walls; and *D. minuta* var. *fusiformis* (**28**) with conidia

60 to 75 μ long, 7 to 9 μ wide, and containing 9 to 12 partitions. As the species mentioned were all described from substrata favorable for the development of microscopic animal life, the possibility of their occurrence in predacious relationships is not to be denied; and certainly the morphology of their reproductive apparatus strongly suggests true membership in the predacious series. Despite an approximate agreement in spore dimensions, the nematode-capturing fungus under consideration can not well be referred to *M. subtile*, since its conidia, when departing from a symmetrically fusiform shape, are much more inclined to become obclavate than clavate. Nor can assignment be made either to *M. oxysporum* or to *D. minuta* var. *fusiformis*, as the ranges for width of conidium given for these species lie beyond any values for this dimension attained in my fungus. Although the shorter, less frequently septate, and more pronouncedly *Fusarium*-like conidia of *D. passalopaga* are of equally small diameter, an epithet compounded in part of a word meaning " slender " may help to set off the species in question from the two other forms that employ nonconstricting rings in the destruction of nematodes.

Dactylella leptospora sp. nov.

Mycelium effusum; hyphis septatis, hyalinis, vulgo 1.2–3 μ raro usque 4 μ crassis, laqueos circulares 13–22 μ latos in 3 loculis subaequalibus arcuatis 2.3–4.5 μ crassis vulgo consistentes ex ramulo primo paulum curvato vel decore circinato 10–35 μ longo, 1.2–2 μ crasso ferentibus, raro bullas globosas vel ellipsoideas 6–7 μ longas, 5.5–6.8 crassas ex ramulo recto vel leviter curvato 3–35 μ longo, circa 1.5 μ crasso evolventibus—laqueis vermiculos nematodeos irretientibus, modo hos capientibus modo ipsis avolsis, sed tamen semper integumentum perforantibus, tuber bursiforme debilitans 7–10 μ longum 5–6 μ latum intrudentibus, hyphas intus evolventibus quae carnem exhauriunt. Hyphae fertiles hyalinae, septatae, erectae, 75–225 μ altae, basi 2.5–3.5 μ crassae, sursum paulo fastigatae, apice 1.3–2 μ crassae, fere simplices et unicum conidium ferentes sed quandoque secundum conidium ex ramusculo prope apicem orto gerentes. Conidia ordinis primi hyalina, fere recta, elongato-fusoidea vel cylindracea, 40–105 μ longa, 4–5.8 μ crassa, 5–15 septata; interdum bullas tenacis globosas proferentibus, interdum ex hyphis ferilibus germinationis erectis, septatis, simplicibus vel paulo ramosis, 50–125 μ longis, basi 2–3 μ apice 1.3–1.8 μ crassis, conidia ordinis secundi vulgo 25–50 μ longa, 4–5.8 μ crassa, 3–8-septata ferentia.

Vermiculos nematodeos graciles multarum specierum interficiens consumensque habitat in humo silvestri prope Beltsville, Maryland, et in Arlington, Virginia.

Mycelium spreading; the vegetative hyphae hyaline, septate, mostly 1.2 to 3 μ, rarely up to 4 μ wide, often, especially in the presence of nematodes, giving rise here and there on stalks frequently curved or circinate, 10 to 35 μ long and 1.2 to 2 μ wide, to generally discrete, approximately circular rings measuring 13 to 22 μ in diameter and composed of subequal arcuate cells, usually 3 in number and 2.3 to 4.5 μ in width; much less frequently giving rise on stalks 3 to 35 μ long and 1.5 μ wide to unicellular knobs, subspherical or prolate ellipsoidal in shape, 6 to 7 μ long and 5.5 to 6.8 μ wide: the rings after individually ensnaring a nematode, sometimes remaining attached, but very often, too, being torn loose from their attachments—in either case perforating the integument, intruding a bursiform excrescence 7 to 10 μ long and 5 to 6 μ wide, and therefrom extending assimilative hyphae lengthwise through the body to appropriate the fleshy contents. Primary conidiophores hyaline, erect, septate, 75 to 225 μ high, 2.5 to 3.5 μ wide at the base, tapering upward very slightly, 1.3 to 2 μ wide at the tip, mostly simple and bearing a single terminal conidium, but occasionally bearing an additional conidium on a short branch attached to the main axis near its apex. Primary conidia hyaline, mostly straight, elongate fusoid or cylindrical, 40 to 105 μ long, 4 to 5.8 μ wide, divided by 5 to 15 cross-walls,—after falling off, often giving rise individually to 1 or 2 globose knobs mostly on scarcely modified distal prolongations, more rarely on lateral stalks; often, too, producing on slightly branched conidiophores, 50 to 125 μ long, 2 to 3 μ wide at the base and 1.3 to 1.8 μ wide at the tip, secondary conidia mostly 25 to 50 μ long, 4 to 5.8 μ wide, and divided by 3 to 8 cross-walls.

Destructive to slender nematodes belonging often to the genera *Rhabditis* and *Plectus,* it occurs in leaf mold in deciduous woods near Beltsville, Md., and in Arlington, Va.

DACTYLELLA GEPHYROPAGA

The fungus with rectangular predacious meshes that was briefly described in an earlier summary (**13**: p. 268, lines 3–24; p. 269, fig. 12, A-C), has made its appearance frequently in nematode-infested agar-plate cultures following the addition of leaf mold from several widely separated localities in Iowa, Wisconsin, Maryland and Virginia. Its presence in such cultures is first made known through the production of perpendicular columnar processes at rather close intervals on the straightforward; sparsely distributed superficial mycelial hyphae (FIG. 12, *A*). These processes though resembling the predacious organs of *Dactylella ellipsospora* in stature and often also in number of component cells, show no constant differentiation into innocuous stalk and expanded adhesive knob, but seem, instead, to be of approximately equal width and adhesiveness from base to rounded apex. Moreover, while the stalked knobs of *D. ellipsospora* are largely formed immersed in the agar substratum, the columnar processes of the present species are commonly developed on the surface, usually, indeed, being thrust vertically into the air, sometimes, it is true, only to be brought down into prostrate positions through the violence of captured nematodes.

After attaining a length mostly of about 20 μ, the columnar processes abruptly change their direction of growth so that further elongation takes place along an axis parallel to the parent filament, and toward the apex of a neighboring process. When this apex is reached, as also when two elements growing directly toward one another meet midway in the manner of a bridge (FIG. 12, *B*), anastomosis occurs and a rectangular mesh is formed. Conjuncture frequently of closely spaced columnar processes in a continuous series of rectangular meshes results in a scalariform network extended usually in one plane (FIG. 12, *C*), which provides the most characteristic morphological feature of the species. The scalariform arrangement may later be partly obliterated through the production of a new series of columnar processes, followed by the superimposition of additional hyphal meshes often in other planes than the primary meshes and with little of their regular arrangement (FIG. 18, *D*, *E*).

Capture of nematodes is accomplished, as in other retiary species, through adhesion combined often with entanglement (FIG. 12, *D*). The columnar processes, which manifestly can operate only by adhesion, serve mainly in holding the younger and less vigorous animals; though their close, bristling arrangement facilitates multiple contact and thereby adds much to their effectiveness. Entanglement in closed meshes appears of importance chiefly in the capture of the larger and stronger eelworms. Whether the predacious unit engaged be one type or the other, it narrowly perforates the integument, and paralyzes the nematode by intruding a bulbous excrescence, from which assimilative hyphae are extended lengthwise through the inert body to appropriate the degenerating fleshy contents (FIG. 12, *E*).

In addition to nematodes, the fungus occasionally captures individuals of *Trinema enchelys* Ehrenb. found in agar cultures prepared with decaying vegetable material. Apparently the rhizopod in feeding is caught by its mouth on an adhesive columnar process, which then grows into the protoplasmic interior (FIG. 18, *M*). A yellow coloring substance is secreted around the invading filament, much as around filaments of *Dactylella tylopaga* invading specimens of *Amoeba verrucosa* Ehrenb. The predacious relationship here seems more or less incidental in the life of the species, yet offers more than negligible interest in illustrating an underlying character of the series. Apparently likewise representative of traits better developed in allied forms are the occasional instances that came under observation, wherein oöspores of *Pythium Butleri* Subr. were penetrated, invaded and successfully parasitized by lateral branches from submerged hyphae of the fungus.

The sturdy conidiophores (FIG. 12, *F–J*) that arise somewhat sparsely from the rangy hyphae in nematode-infested agar cultures, and in greater abundance from the fairly dense mycelium produced when the fungus is grown in pure culture on maizemeal agar, rather closely resemble those of *Dactylella bembicodes*. Similarly the conidia (FIG. 12, *K*, *a–w*) borne on them closely resemble the conidia of *D. bembicodes* in size and shape, though presenting a difference often useful for purposes of identification in that they commonly show a 4-septate condition coördinate with a 3-septate condition. The numerical proportion between the spores containing three cross-walls and those containing four is subject to considerable variation. In the 100 specimens whose measurements were used to obtain the relevant dimensional data submitted in the diagnosis below, 61 contained four partitions, 35 contained three partitions, and 4, possibly not all fully mature, contained two partitions. All of the 4-septate specimens had their partitions so spaced that two small cells were delimited at each of the ends leaving a relatively massive ventricose cell in the middle. Of the 3-septate conidia, 33 showed the ventricose cell in penulti-

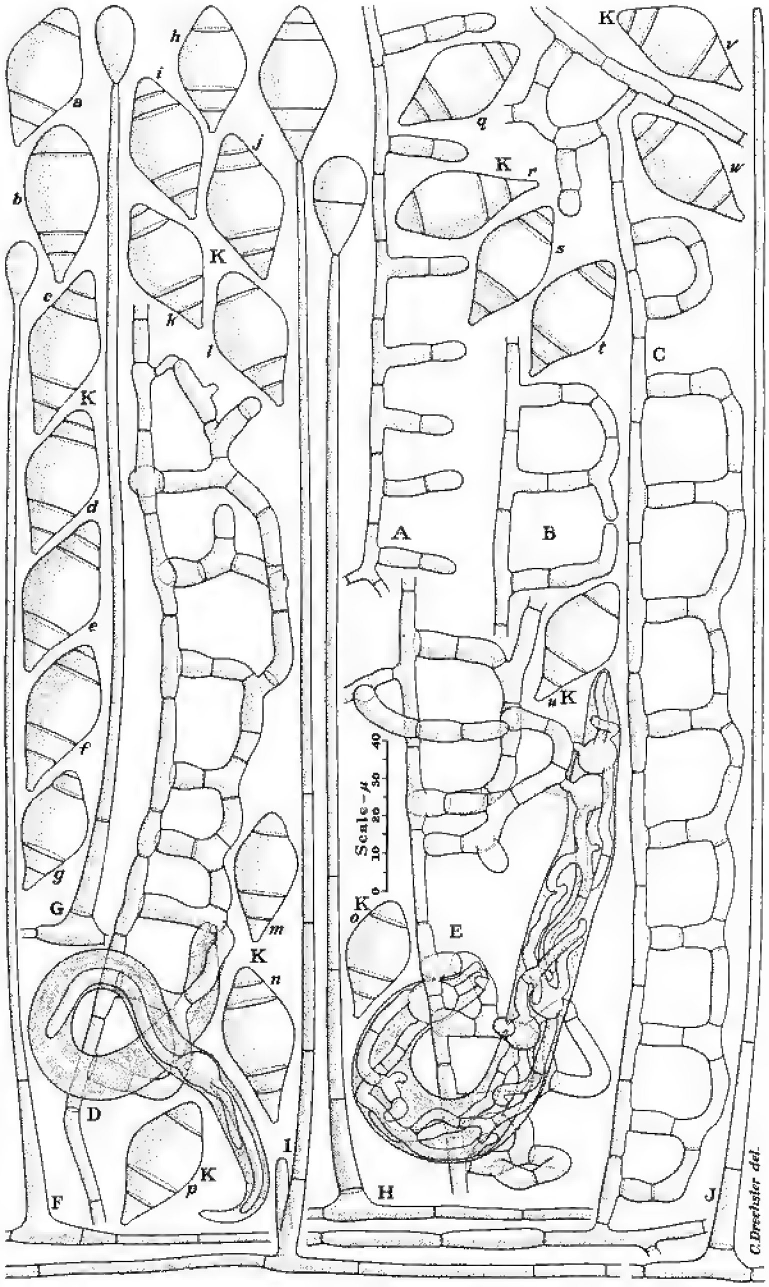

FIG. 12. *Dactylella gephyropaga.*

mate position between two small proximal cells and a single small distal cell; while the remaining two showed the ventricose cell in antepenultimate position, between a small basal segment and two small distal segments. As might be expected, the more abundantly septate conidia were slightly larger than those with fewer partitions, the 61 specimens with four cross-walls giving an average length of 39.5 μ, as contrasted with an average length of 38.2 μ for the random assortment. Without reference to septation, the 100 measurements gave a distribution of values for length, expressed to the nearest micron as follows: 27 μ, 1; 33 μ, 6; 34 μ, 8; 35 μ, 3; 36 μ, 7; 37 μ, 9; 38 μ, 19; 39 μ, 12; 40 μ, 11; 41 μ, 12; 42 μ, 4; 43 μ, 4; 44 μ, 3; 46 μ, 1; and a distribution of values for width as follows: 16 μ, 3; 17 μ, 7; 18 μ, 31; 19 μ, 32; 20 μ, 23; 21 μ, 4.

From *Monacrosporium elegans* the fungus is separated not only like *Dactylella bembicodes* by the smaller dimensions of its conidia, but also by their frequently 4-septate condition. On the other hand, the generous admixture of spores with no more than three cross-walls makes it ineligible for identification with *D. ellipsospora*, especially when considered in opposition to the more regularly 4-septate knobbed form treated herein under Grove's binomial. It is therefore described as a new species under a name compounded of two words meaning "bridge" and "trap" respectively.

Dactylella gephyropaga sp. nov.

Mycelium effusum; hyphis hyalinis, septatis, 2–5 μ crassis, ramulos glutinosos columnares 10–30 μ saepe circa 20 μ longos, 4–7 μ crassos, ex 1–3 cellulis compositos, inter se 20–30 μ distantes emittentibus; his ramulis diende subito recta hyphae originis regione saepe crescentibus, incrementis vicinis inter se ad instar ponticuli conjungentibus, ita laqueos quadrilateros modo separatos modo in rete mirabiliter scaliforme connectos texentibus; haerendo irretiendoque ramulis columnaribus et laqueis quadrilateris vermiculos nematodeos capientibus, integumentum perforantibus, tuber mortiferum intrudentibus, hyphas intus evolventibus quae carnem exhauriunt; atque alia animalia subinde tenentibus et carnem eorum assumentibus. Hyphae fertiles hyalinae, erectae, septatae, 225–500 μ altae, basi 5–7.5 μ crassae, sursum leviter fastigatae, propter apicem perspicuius attenuatae, ibi 1.5–2.7 μ crassae, unicum conidium ferentes. Conidia hyalina, turbinea, 27–46 μ (saepe circa 38.2 μ) longa, 16–21 μ (saepe circa 18.7 μ) lata, raro 2-septata, plerumque 3- vel 4-septata, quandoque 4-septata cellula infima obconica circa 7 μ longa, huic proxima superiore cellula disciformi ad 6.2 μ longa, cellula antepaenultima dolioformi vel ventricosa circa 17.6 μ longa, cellula paenultima disciformi circa 4.7 μ longa, cellula summa apice rotundata circa 4 μ longa.

Vermiculos nematodeos multarum specierum vulgo usque .6 mm. longos, subinde *Trinema enchelyn* capiens consumensque habitat in materiis plantarum putrescentibus et in humo silvestri prope Madison, Wisconsin; Ames, Iowa; Cumberland et Beltsville, Maryland; in Arlington, Virginia.

Mycelium spreading; the vegetative hyphae hyaline, septate, mostly 2 to 5 μ wide, often, especially in the presence of nematodes giving rise at intervals frequently of 20 to 30 μ, to adhesive columnar branches 10 to 30 μ long and 4 to 7 μ wide that consist generally of 2, less often of 1 or 3 cells—these branches later often abruptly changing their direction of elongation to grow parallel to the parent filament, the increments anastomosing with the neighboring branches, or with the similar increments put forth by the latter to form quadrilateral meshes, sometimes discrete but frequently compounded into scalariform networks of variable lengths, wherefrom adhesive columnar processes may be produced in turn; the columnar processes, meshes and networks capturing nematodes by adhesion and entanglement, then perforating the integument of each animal, and intruding a mortiferous excrescence that gives rise to assimilative hyphae which grow lengthwise through the body and appropriate the fleshy materials,—occasionally, also, capturing other animals to utilize their contents. Conidiophores hyaline, erect, septate, 225 to 500 μ high, 5 to 7.5 μ wide at the base, tapering gradually upward to within about 10 μ from the apex, from thence narrowing somewhat more markedly to a width of 1.5 to 2.7 μ at the tip whereon is borne usually a single conidium. Conidia hyaline, handsomely top-shaped, broadly rounded at the distal end, tapering toward the slightly protruded truncate base, 27 to 46 μ (average 38.2 μ) long, 16 to 21 μ (average 18.7 μ) wide, rarely 2-septate, commonly 3-septate and 4-septate; when 4-septate, the basal obconical cell averaging about 7 μ in length, the second and disciform cell about 6.2 μ, the central barrel-shaped or ventricose cell about 17.6 μ, the penultimate cell about 4.7 μ, the apical cell about 4 μ.

Capturing and consuming nematodes commonly up to .6 mm. in length, belonging to many species of *Acrobeles*, *Acrobeloides*, *Cephalobus*, *Diplogaster*, *Diploscapter*, *Plectus* and *Rhabditis*, and sometimes capturing also specimens of *Trinema enchelys*, it occurs in decaying vegetable materials and in leaf mold near Madison, Wis., Ames, Ia., Cumberland, Md., and Beltsville, Md., and in Arlington, Va.

DACTYLARIA BROCHOPAGA

The fungus bearing 3-septate cylindrical conidia in loose capitate arrangement, to which reference was made in an earlier summary (**13**: p. 268, lines 32–36; p. 269, fig. 14, A-C; p. 270, lines 1–6), has appeared occasionally in nematode-infested agar plate cultures following the addition of small quantities of leaf mold. In such cultures its straightforward vegetative hyphae bear at intervals stalked constricting rings (FIG. 13, *A-C*) that in manner of development as well as in shape, structure, and mode of operation, are indistinguishable from the predacious organs of *Arthrobotrys dactyloides* and *Dactylella bembicodes*. The assimilative hyphae extended through a captured nematode after the ring has squeezed it into a state of relative immobility, generally show no terminal modification in sharp-tailed animals (FIG. 13, *D*), but in blunt-tailed prey become distended at the tip (FIG. 13, *E*) like the haustorial filaments of *A. dactyloides*.

With ample nourishment the rather sparse mycelium in nematode-infested agar plate cultures gives rise to a scattering of erect fertile hyphae that terminate individually in a handsome radiating head containing mostly about a half dozen conidia (FIG. 13, *F*, *a*, *b*; *G*). The capitate arrangement of the multiseptate spores conforms to the reproductive habit specified in the phragmosporous Mucedinaceae for the genus *Dactylaria*, though the stubby sterigmata on which the conidia are borne appear to be broader and usually more distinctly separated from one another (FIG. 13, *H*, *J*, *a-e*) than would seem implied in the descriptions of most recognized members of this genus. In pure culture on maizemeal agar, where the fungus gives rise to lustrous, radiating, and rather dense mycelial growth, spores are sometimes borne on relatively short conidiophores (FIG. 13, *I*, *a-c*); and their arrangement may reveal all gradations between typically capitate and loosely racemose extremes (FIG. 13, *J*, *f-j*). In pure culture, too, the conidia exhibit somewhat more variability in size, shape and septation; though here, as also on wormy substrata, variations related to differences in cultural conditions can usually be distinguished from analogous variations referable to underlying differences between separate strains. The disparity in size evident between the as-

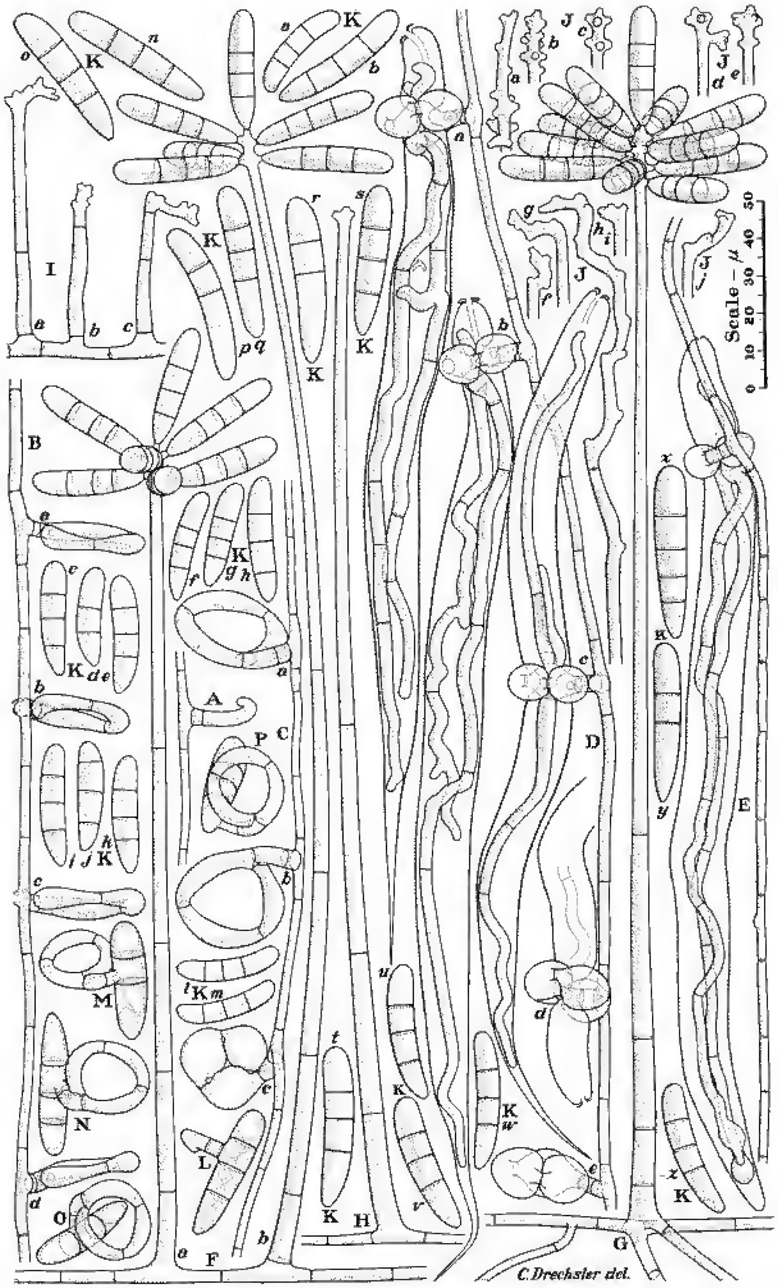

FIG. 13. *Dactylaria brochopaga.*

sortment of smallish spores shown in figure 13, *K, a-m* on the one hand, and the assortment of largish spores shown in figure 13, *K, n-z* on the other, is illustrative of a dimensional difference between two strains that has remained recognizable under varied conditions of culture.

Not infrequently conidia germinate by giving rise to predacious rings, often of smaller size but otherwise resembling those borne on mycelial filaments (FIG. 13, *L-P*). A nematode ensnared in such a ring continues to move about for some time, being impeded slightly, to be sure, by the conidium buckled absurdly to its side. With constriction becoming steadily more severe, its movements gradually slacken and finally come to a halt; whereupon extension of hyphae lengthwise through the paralyzed body and assimilation of the fleshy contents follow much as in captured specimens.

Both in pure and in nematode-infested cultures, the fungus, as has been intimated previously, shows a general parallelism with *Arthrobotrys dactyloides;* so that the more abundant septation of its conidia, because of which it needs to be referred to a different genus, provides at the same time the feature most decisively distinguishing it as a species. *Dactylaria echinophila* Massal., possibly to be reckoned among the members of the predacious series, offers similarity with respect to number of cross-walls in the conidium, but the dimensions given by Saccardo, 16–26 × 4–5 μ, would seem to indicate a definitely smaller fungus. Certainly the plant with conidiophores 25 μ high and conidia measuring 17–22 × 3.2–3.5 μ, that Rostrup (59) perhaps correctly listed under Massalongo's binomial, appears too small to be identified with the present species; and judging from the figure given by the Danish mycologist, differs besides in the delicate attachment and equidistant septation of its spores. *D. orchidis* Cooke & Mass. with 3-septate conidia 40 to 50 μ long and 7 to 9 μ wide, differs markedly in the much greater width, 10 to 12 μ, and orange coloration of its conidiophores. The dilute purple color tinging the reproductive parts of *D. purpurella* (Sacc.) Sacc., appears alien not only to the present species, but to the predacious series generally. Other congeneric forms likewise present quite decisive differences from the fungus under consideration: *D. acicularis* Rostrup (59) in the awl-like shape of its narrow conidia; *D. mucronulata* Ell. &

Langl. in its much smaller conidial dimensions—8–10 × 2.5–3 μ; and *D. pulchra* Linder (**39**) as well as *D. oogena* (Mont.) Sacc. in its more abundant conidial septation.

The species is therefore described as new under a name compounded of two words meaning "noose" and "snare" respectively.

Dactylella brochopaga sp. nov.

Mycelium effusum; hyphis hyalinis, septatis, 1.7–4.5 μ crassis, laqueos circulares 20–35 μ latos, in 3 cellulis arcuatis plerumque 14–28 μ longis medio 4–7 μ extremo 2.5–6 μ crassis consistentes, ex ramulo biloculari 7–13 μ longo, 3.5–6 crasso proferentibus; his laqueis vermiculos nematodeos illaquentibus, deinde tum per contractionem inflationemque trium loculorum animalia magnopere comprimentibus, ita haec interficientibus, statim integumentum perforantibus et hyphas intus evolventibus quae carnem exhauriunt. Hyphae fertiles hyalinae, septatae, erectae, 40–400 μ saepe 200–325 μ altae, basi 4–7 μ crassae, sursum leviter fastigatae, apice 2.4–3.5 μ crassae, ibi ex sterigmatibus brevibus obtusis 2–12 saepius 3–8 conidia in capitulum pulchrum radians aggregata ferentes vel subinde usque 15 conidia in parte superiore rarius digesta gerentes. Conidia recta vel curvata, cylindracea vel elongato-ellipsoidea, apice rotundata, basin versus paulo attenuata, 26–46 μ longa, 5–9 μ crassa, 2–4 septata, plerumque tribus septis in 4 loculos divisa, loculis infimo et apicali tum fere inter se subaequalibus sed aliquanto longioribus quam loculis antepaenultimo et paenultimo qui inter se etiam aequales sunt.

Vermiculos nematodeos multarum specierum vulgo usque .6 mm. longos laqueans consumensque habitat in humo silvestri prope Cumberland, Maryland, et in Arlington, Virginia.

Mycelium spreading; the vegetative hyphae hyaline, septate, 1.7 to 4.5 μ wide, often especially in the presence of nematodes producing underneath and at right angles to their axes approximately circular rings 20 to 35 μ in outside diameter, composed individually of 3 arcuate cells 14 to 28 μ long, 4 to 7 μ wide in the middle and 2.5 to 6 μ wide at the ends—the first and third of the cells being united usually to one another as well as to the distal end of the slightly curved supporting branch 7 to 13 μ long, 3.5 to 6 μ wide, and consisting mostly of 2 cells whereof the basal one is usually the shorter; after 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 assimilative hyphae lengthwise through the interior to appropriate the fleshy contents. Conidiophores hyaline, septate, erect, 40 to 400 μ, more typically 200 to 325 μ high, 4 to 7 μ wide at the base, tapering gradually upward to a width of 2.4 to 3.5 μ near the tip, there bearing on short blunt sterigmata 2 to 12, mostly 3 to 8 conidia in beautiful radiating capitate arrangement—or less often and less typically producing up to 15 conidia in more scattered, irregularly racemose arrangement. Conidia hyaline, straight or slightly curved, cylindrical or elongate ellipsoidal, broadly rounded at the apex, usually tapering noticeably toward the somewhat truncate base, 26 to 46 μ long, 5 to 9 μ wide and containing 2 to 4 cross-walls, though most frequently divided by 3 septa into 4 cells—the basal and apical cells then approximately equaling one another in size, but exceeding in length by a third or even a half the antepenultimate and penultimate cells, which also are approximately equal to one another.

Ensnaring and consuming nematodes commonly up to .6 mm. in length, belonging to many species of *Acrobeles*, *Acrobeloides*, *Cephalobus*, *Diplogaster*, *Diploscapter*, *Plectus*, *Rhabditis* and *Mononchus*, it occurs in leaf mold in deciduous woods near Cumberland, Md., and in Arlington, Va.

DACTYLARIA THAUMASIA

The fungus whose production of 3-septate obovoid conidia in loose heads was referred to in an earlier summary (**12**: p. 139, 7, 8, 18–20, fig. 5, A, D) occurs widely in decaying plant remains. After having been first obtained in old isolation agar plate cultures planted with decaying rootlets of spinach, it has frequently made its appearance in nematode-infested cultures following addition of leaf mold from supplies of this materials collected as opportunity offered in deciduous woods in several widely separated localities. Often, especially under moist conditions, when the surface of the substratum is lubricated with bacterial slime in a manner greatly reducing the effective leverage of nematodes, it destroys these animals in such large numbers that here and there accumulations of their remains become plainly visible to the naked eye as scabby deposits. The apparatus through which this destruction is accomplished, closely resembles that of *Arthrobotrys oligospora* and *A. conoides*, similarly consisting of rather wide hyphal bails and loops, which at first are discrete but later usually become compounded into more or less extensive reticula (FIG. 14, *A*, *B*). Capture is brought about through adhesion combined frequently, especially under drier conditions, with physical entanglement. It promptly leads to perforation of the animal's integument, intrusion of one

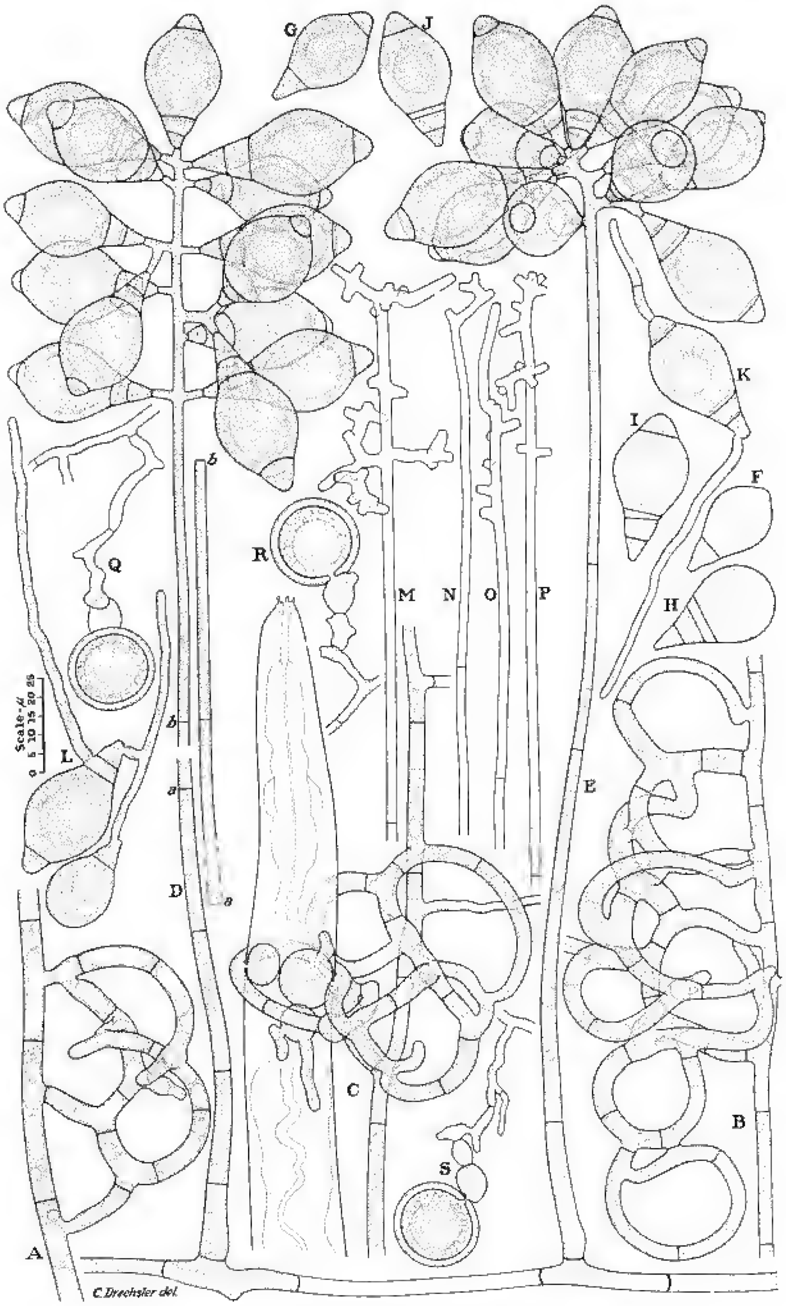

FIG. 14. *Dactylaria thaumasia.*

or more globose structures, and extension of assimilative filaments lengthwise within the paralyzed body precisely as in other retiary species (FIG. 14, *C*).

In the beginning the conidiophores arising at intervals from the straightforward vegetative filaments that make up the sparse mycelium of the fungus in nematode-infested cultures, might easily be mistaken for fertile hyphae of *Dactylella bembicodes* and *D. gephyropaga*, which they closely resemble in stature and in production of large obovoid conidia. With an ample supply of eelworms to provide continued nourishment, a distinctive difference soon becomes evident in that additional conidia are developed by the individual sporophores, either on terminal prolongations or on rather broad stubby sterigmata that project at wide angles from the distal portion of the axis. Though on wormy substrata the spores borne on a sporophore ordinarily do not exceed three or four in number, their arrangement in terminal heads makes for a handsome appearance under a microscope of low magnification. Even more impressive reproductive apparatus is obtained in pure culture on maizemeal agar if the fungus is permitted to continue development for several weeks by being protected against early desiccation of the medium. Very often about a dozen (FIG. 14, *D, E*) and sometimes more than a score of conidia may then be found in beautiful capitate clusters held aloft on tall conidiophores. In very copiously laden conidial apparatus the sterigmata are frequently borne in large part on short lateral branches (FIG. 14, *M*), whereas in apparatus more moderately prolific the sterigmata arise mainly from the axis itself (FIG. 14, *N-P*).

The conidia closely resemble those of *Dactylella bembicodes* and *D. gephyropaga* not only in shape but also in size. A somewhat greater variability in dimensions is usually apparent here, the 100 presumably representative conidial measurements from which were obtained the relevant metric data submitted in the diagnosis below, giving a distribution of values for length expressed to the nearest micron, as follows: 27 μ, 1; 28 μ, 1; 30 μ, 5; 31 μ, 5; 32 μ, 5; 33 μ, 5; 34 μ, 11; 35 μ, 10; 36 μ, 13; 37 μ, 4; 38 μ, 7; 39 μ, 5; 40 μ, 7; 41 μ, 5; 42 μ, 5; 43 μ, 3; 45 μ, 1; 46 μ, 3; 47 μ, 2; 48 μ, 1; 49 μ, 1; and a distribution of values for width as follows: 15 μ, 1; 16 μ, 3; 17 μ, 12; 18 μ, 19; 19 μ, 20; 20 μ, 19; 21 μ, 14; 22 μ, 9;

23 μ, 3. Of the 100 conidia, which were taken at random in equal numbers from maizemeal agar plate cultures of four separate strains, 4, probably somewhat immature, contained one septum delimiting a small basal cell from a large distal one (FIG. 14, *F*); 17 contained two septa, which, except in one specimen with two small proximal cells below a large distal cell, delimited a small basal and a small apical segment from a large central segment (FIG. 14, *G*; FIG. 18, *L, b-e*) much as in the atypical biseptate swollen spores of *Arthrobotrys dactyloides* (FIG. 18, *K, d-f, i, j, l, m, n, p*); 77 contained three septa which, except in one specimen with three small proximal cells below a large distal cell (FIG. 14, *H*), delimited, after the manner usual in *D. bembicodes*, a small basal, a small antepenultimate, a large penultimate, and a small apical cell (FIG. 14, *D, E*; FIG. 18, *L, a*); and 2 contained four cross-walls, these partitions in one specimen being spaced symmetrically after the manner usual in *D. ellipsospora* to delimit two small proximal cells below and two small distal cells above a large middle cell, while the other specimen showed an arrangement of three small proximal segments, a large penultimate and a small apical segment (FIG. 14, *I, J*; FIG. 18, *L, f*).

Like the three larger retiary species of *Arthrobotrys*, the fungus produces yellow thick-walled chlamydospores (FIG. 14, *Q-S*) within the substratum. In pure culture on maizemeal agar these bodies are sometimes formed in numbers so large that the substratum is given a perceptibly rusty color. When examined under a microscope of high magnification, two layers can usually be recognized in the enveloping wall, though perhaps more from differences in transparency than from spatial separateness.

Since on decaying natural materials with meager nematode infestation its poorly nourished conidiophores often give rise to only a single conidium, or at most to two or three conidia, the fungus obviously can not always be reliably distinguished on natural opaque substrata from *Dactylella bembicodes* or from *D. gephyropaga*. Positive identification of the species accordingly requires either cultivation on some transparent nematode-infested substratum to reveal its predacious apparatus, or somewhat prolonged development in pure culture under favorable conditions to bring to light its distinctive capitate reproductive habit. From *Monacro-*

sporium elegans it is separated not alone by its capitate habit, but also, like *D. bembicodes* and *D. gephyropaga*, by its definitely shorter conidia. *M. megasporum*, presumably, too, a closely related member of the predacious series, and in any case a truly capitate form, appears (4) no less clearly distinct from the present species by virtue of larger conidial dimensions, 35–57.5 μ × 15.5–27.5 μ, an ellipsoid rather than turbinate shape of its conidia, and the small size of the warty spore-bearing protuberances that beset the slightly enlarged tip of the sporophore somewhat as in *Arthrobotrys dactyloides*.

As the fungus under consideration evidently is different from any hitherto named in the literature, its description as a new species seems justified. The frequently spectacular appearance of its conidial apparatus suggests employment of a word meaning "wonderful" as a suitably expressive specific epithet.

Dactylaria thaumasia sp. nov.

Mycelium effusum; hyphis hyalinis, septatis, plerumque 2–8 μ crassis, laqueos tenaces arcuatos vel circulares in reticula fere conjunctos saepe evolventibus; his laqueis vermiculos nematodeos illaqueantibus, deinde tum integumentum perforantibus, tuber mortiferum intrudentibus, hyphas intus evolventibus quae carnem exhauriunt. Hyphae fertiles septatae, erectae, 250–450 μ altae, basi 4–8 μ crassae, sursum paulo fastigatae, prope apicem 2.2–3.3 μ crassae, ibi saepe plus minusve ramosae et ex sterigmatibus obtusis vulgo 2–10 μ longis, 2–3 μ crassis 3–15 raro usque 25 conidia in capitulum laxum pulchrum aggregata gerentes. Conidia hyalina, speciose turbinea, 27–49 μ (saepe circa 37 μ) longa, 15–23 μ (saepe circa 19.2 μ) lata, 1–4-septata, saepissime in 4 cellulis consistentia—cellula infima obconica saepe circa 5.8 μ longa, cellula antepaenultima disciformi saepe circa 4.9 μ longa, cellula paenultima ventricosa dolioformi saepe circa 22.7 μ longa, cellula summa apice rotundata saepe circa 4.6 μ longa. Chlamydosporae flavidae, globosae, plerumque 18–28 μ latae, maturitate membrana vulgo 1.4–2.5 μ crassa.

Vermiculos nematodeos multarum specierum vulgo usque .6 mm. longos irretiens consumensque habitat in radicibus *Spinaciae oleraceae* putrescentibus prope Norfolk, Virginia, etiam in humo silvestri prope Beltsville, Maryland; Madison, Wisconsin; et in Arlington, Virginia.

Mycelium spreading; the vegetative hyphae hyaline, septate, 2 to 8 μ wide, often, especially in the presence of nematodes producing bail-like arches and loops mostly 25 to 35 μ wide, which may remain discrete but are frequently compounded into networks,—the hyphal bails, loops, and networks capturing nematodes through adhesion and entanglement, then perforating the integument of each animal and intruding a mortiferous excrescence that gives rise to assimilative hyphae which grow lengthwise through the body and appropriate the fleshy materials. Conidiophores hyaline, erect, septate, 250 to 450 μ high, 4 to 8 μ wide at the base, tapering upward to a width of 2.2 to 3.3 μ, simple or often somewhat branched near the tip, and there bearing on blunt sterigmata, mostly 2 to 10 μ long and 2 to 3 μ wide, usually 3 to 15, rarely up to 25 conidia in beautiful loose capitate arrangement. Conidia hyaline, handsomely top-shaped, rounded at the apex, tapering toward the frequently somewhat protruding truncate base, 27 to 49 μ (average 37 μ) long, 15 to 23 μ (average 19.2 μ) wide, containing 1 to 4 septa, but most often divided by 3 cross-walls into 4 cells—the obconical basal cell then averaging 5.8 μ in length, the disciform antepenultimate cell 4.9 μ, the broadly ventricose or barrel-shaped penultimate cell 22.7 μ, and the apical cell 4.6 μ. Chlamydospores yellow, globose or ellipsoidal, mostly 18 to 28 μ in diameter, at maturity surrounded by a wall commonly 1.4 to 2.5 μ thick.

Capturing and consuming nematodes generally up to .6 mm. long, referable to many species of *Acrobeles, Acrobeloides, Cephalobus, Diplogaster, Diploscapter, Plectus* and *Rhabditis*, it occurs in decaying roots of *Spinacea oleracea* near Norfolk, Va., and also in leaf mold in deciduous woods near Beltsville, Md., near Madison, Wis., and in Arlington, Va.

DACTYLARIA CANDIDA (Nees) Sacc.

The predacious fungus that was sketchily characterized in a synoptic account (**12**: p. 139, lines 20–24, fig. 6, A, B) as producing narrow spindle-shaped conidia in loose capitate arrangement, and that later (**15**) on somewhat more detailed consideration was identified with *Dactylaria candida*, has been observed from time to time in nematode-infested agar plate cultures to which small quantities of leaf mold had previously been added. Its effuse mycelium is somewhat delicate in comparison with the mycelium in most other nematode-capturing members of the series, the rather straightforward hyphae composing it measuring generally between 1.2 μ and 3 μ in width. On these hyphae, under conditions inviting its development, and more especially in the presence of free-living nematodes, is formed predacious apparatus consisting as in *Dactylella lysipaga* and *D. leptospora* of unicellular knobs and non-constricting rings. The knobs, globose or prolate ellipsoidal in shape, measuring commonly 4 to 7 μ in length and 3.8 to 6 μ in width, are supported on slender stalks mostly 4 to 15 μ long and 1 to 1.4 μ wide (FIG. 15, *A, a-e*). The rings, usually 15 to 23 μ in outside diameter, are composed generally of three arcuate cells 2.5 to 4 μ in width; the proximal segment often being noticeably inflated where it joins the stalk, which is frequently circinate or otherwise curved, and measures commonly 10 to 35 μ in length and 1.2 to 1.8 in width (FIG. 15, *B-J*).

The stalked knobs have rarely been seen operative, and then only in the capture of the smallest and feeblest nematodes; though as was intimated earlier their usual ineffectiveness in agar media need not imply any lack of competence in natural substrata of much different physical texture. Ensnarement in a ring, on the other hand, always results in destruction of the nematode concerned, regardless of whether the encircling structure remains attached to its stalk (FIG. 15, *K*), or is torn off therefrom (FIG. 15, *L*). The bursiform body, often about 8 μ long and 6 μ wide, that is intruded after the integument has been penetrated by a narrow process from the inner surface of the ring, is not sufficient to disable the animal, which therefore continues to move about with gradually diminishing briskness until assimilative hyphae have been extended well through its interior. In fairly large nematodes these hyphae, sometimes as much as 4 μ wide, attain rather luxuriant development (FIG. 15, *L*). Appropriation of the fleshy contents makes possible the growth of new mycelial filaments arising mainly from the outer surface of the ring.

Thus both in structure and in operation of its predacious organs the fungus shows an obvious parallelism to *Dactylella lysipaga* that is extended, though with a smaller degree of exactness, in its conidial apparatus. Sporulation, especially in pure culture, is inclined to be capricious, sometimes taking place only on a very meager scale despite a vigorous condition of the underlying mycelium. Exposure to sunlight for brief periods has often proved helpful in stimulating reproductive development in refractory material; yet even under the most favorable conditions the conidiophores scarcely ever become clearly visible to the naked eye. Commonly 3 to 5 μ in diameter at the base, they taper gradually upward

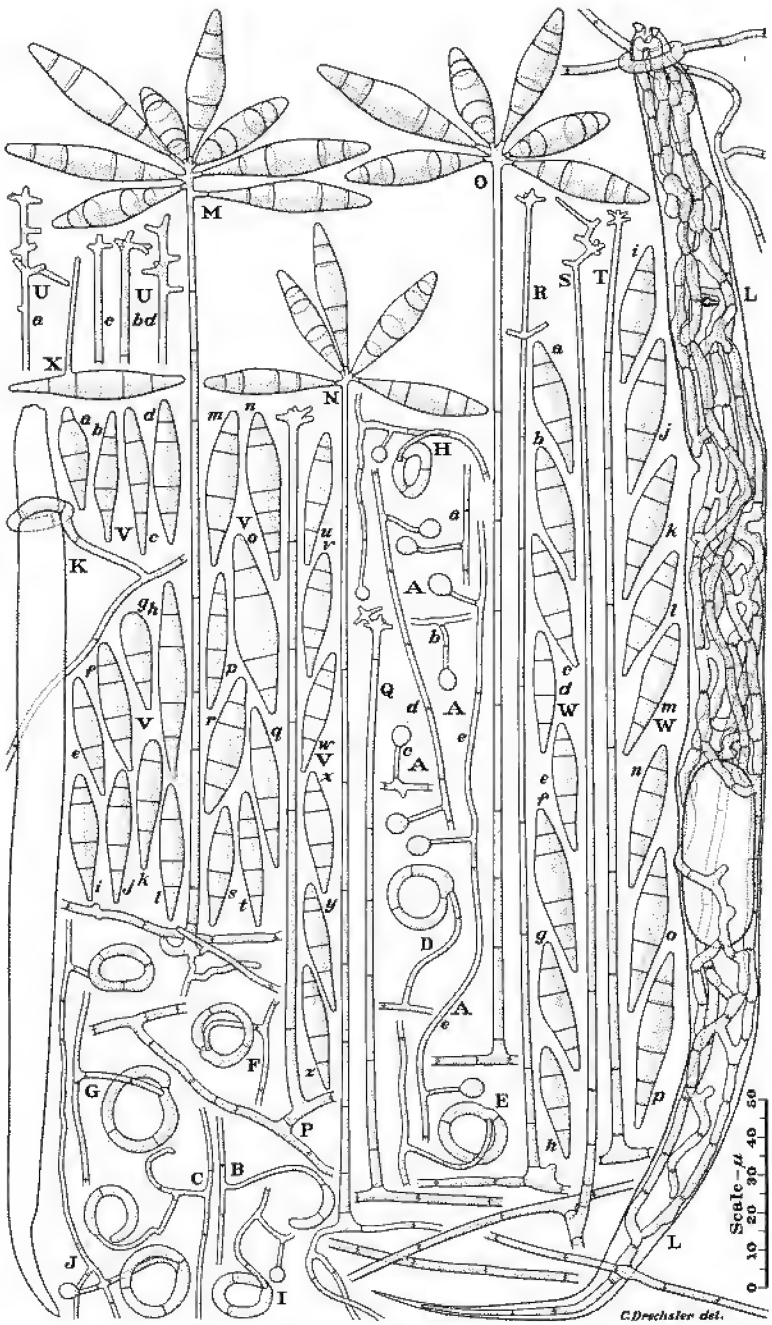

FIG. 15. *Dactylaria candida.*

to a width of 1.3 to 2.4 μ near the tip, where, 150 to 300 μ or even 400 μ above the substratum, 3 to 10 conidia are borne in strikingly handsome capitate arrangement (FIG. 15, *M, N, O*). As was set forth earlier, the spores are attached individually to stubby sterigmata, usually simple yet occasionally branched, and measuring commonly 2 to 12 μ in length, 1 to 2 μ in width at the base, and .8 to 1.4 μ in width at the apex (FIG. 15, *P-T; U, a-d*). The conidia themselves vary in shape from clavate-fusoid to fusoid; in length from 26 μ to 52 μ, mostly from 30 μ to 45 μ; and in diameter from 5.5 μ to 11.5 μ, mostly from 7 μ to 10 μ (FIG. 15, *V, a-z; W, a-p*). While the number of cross-walls dividing the conidia varies from two in some of the shorter specimens, to six in some of the longer ones, the 4-septate condition, with the partitions so spaced as to give greater length to the median or antepenultimate cell than to any of the other segments, generally predominates. On rather dry substrata fallen conidia often show repetitive development in giving rise to small conidiophores (FIG. 15, *X*) and secondary conidia.

From *Dactylella lysipaga* the fungus under discussion differs mainly in the lesser diameter of its conidia, and in the production of these bodies in heads rather than singly or, at most, in pairs. The capitate habit here can not be considered as resulting from luxuriant development any more than the usually solitary sporulating habit of *D. lysipaga* or of *D. ellipsospora* can be regarded as expressive of a depauperate condition. For however abundantly spores may be formed in cultures of the latter two species, a capitate arrangement is never brought about; whereas in cultures of the present form the conidia are disposed in heads even when produced only in meager quantity.

The fungus is identified as *Dactylaria candida* mainly because of its general agreement with the diagnosis given by Saccardo (**61**) for that species. Historically the species dates back to 1816 when the elder Nees von Esenbeck (**50**) described under the binomial *Dactylium candidum* a white, gregarious, inconspicuously pulverulent mold found on the inner surface of old loosened oak bark—erecting on it a genus characterized by simple upright hyphae bearing terminally three or four elongate-clavate, short-celled conidia. No statement was made regarding the number of cross-walls in the conidia, but the minute figure accompanying the description shows a decided predominance of 3-septate over 4-septate spores. Conidia with three cross-walls preponderate seemingly to the exclusion of 4-septate specimens in the equally minute figures of the species published by Chevallier (**7**) a decade later. In 1837 the younger Nees von Esenbeck and Henry (**51**) published illustrations of *D. candidum* showing some 3-septate conidia together with a smaller number of 4-septate ones. Later Bonorden (**5**) in a figure of *D. candidum*, drawn presumably at first hand and to a slightly less parsimonious scale, represented conidia containing four cross-walls in equal number with conidia having five cross-walls. Oudemans (**52**), who recognized as *D. candidum* a form growing on goat dung and producing spores 46 to 56 μ long and 7 to 9.3 μ wide, disapproved of Bonorden's illustration on the ground that it exaggerated the number of conidial septa, which he considered more accurately set forth in Nees' figure. Nevertheless, when soon thereafter Saccardo transferred the species to the newly erected genus *Dactylaria*, his diagnosis brought together Bonorden's representations concerning spore septation with the metric data supplied by Oudemans. The description thus compiled was adopted by Lindau without significant change.

References to *Dactylaria candida* in the more recent as also in the older literature are so few that an established usage relative to the binomial can hardly be said to exist. The substrata on which the species has been reported, decaying oak bark and goat dung are materials congenial for the development of nematodes, and consequently also for the development of fungi that subsist on these animals. The reproductive habit described and figured in the older accounts conforms at least in a general way with that of predacious fungi when found on natural substrata. Finally, whether by accident or because of specific identity, the morphological details set forth in the diagnosis generally accepted for the species agree so well with those revealed in the predacious fungus under consideration, that for the present at least, disposition of the latter elsewhither could not readily be defended.

DACTYLARIA POLYCEPHALA

A fungus of more than ordinary taxonomic interest made its appearance a few times in nematode-infested agar plate cultures to