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THREE HYPHOMYCETES THAT CAPTURE NEMATODES IN ADHESIVE NETWORKS

THREE HYPHOMYCETES THAT CAPTURE NEMATODES IN ADHESIVE NETWORKS

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(WITH 5 FIGURES)

In several previous papers (**4**, **5**, **6**) descriptive treatment was given to 22 interrelated hyphomycetes found subsisting by the capture and destruction of eelworms infesting transparent agar plate cultures started from diseased rootlets or from other decaying vegetable materials. Similar treatment is devoted herein to 3 additional fungi of like biological habit and manifestly belonging to the same predaceous series. Capture of eelworms is accomplished, in all 3 fungi, by means of adhesive bail-like hyphal loops, which, as in allied forms, may occur singly, or may be compounded into networks of variable intricacy. Two of the fungi are referred to *Arthrobotrys*, one being presented as a new variety, while the other is identified with a long-established though somewhat unfamiliar species of that genus. The third fungus is described as a new species of *Dactylaria*. In relation to a subsidiary spore form apparently connected with the new species, preliminary discussion is devoted to a delicate *Trichothecium* found producing stalked adhesive knob-cells.

A VARIETY OF ARTHROBOTRYS CLADODES WITH DISTINCTLY PEDICELLATE ELONGATED CONIDIA

A maizemeal-agar plate culture which after being permeated with *Pythium* mycelium had been further planted with small quantities of leaf mold collected near Beltsville, Md., early in October 1936, showed on subsequent examination numerous eelworms being captured and consumed by a small *Arthrobotrys*

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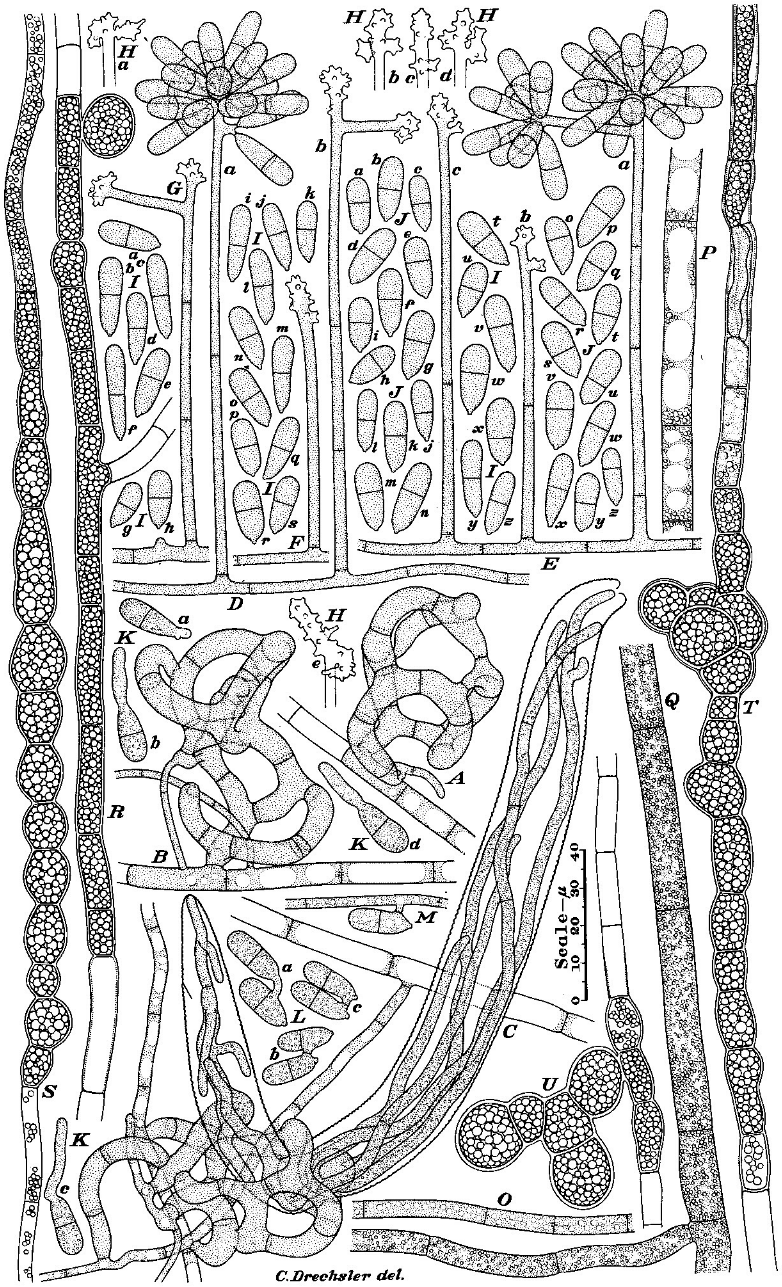
having the general aspect of *A. superba* Corda or *A. cladodes* Drechsl. (**4**, p. 450–464). Since these two species, unlike most hyphomycetes of similar predaceous character, usually can not be distinguished well in nematode-infested agar cultures owing to the frequent failure of their conidiophores to develop beyond a simple monocephalous condition, the fungus was isolated by removing some of its conidia aseptically from their supporting hyphae to sterile agar in Petri dishes. When the plate cultures started in this way had grown for a few weeks, they showed little tendency toward the prolific uniaxial development of successive conidial clusters so characteristic of *A. superba*, but revealed instead a slower, more moderate multiplication of larger conidial heads through lateral branching of the conidiophores. Although with respect to sporulating habit the fungus thus agreed closely with the several strains of *A. cladodes* then familiar to me, it displayed readily noticeable differences in the more elongated shape and consistent pedicellation of its conidia, as well as in its production of more or less indurated resting bodies. Because of these differences the fungus was excluded from consideration at the time the specific description of *A. cladodes* was drawn up. It made its appearance more recently in some maizemeal-agar plate cultures started from decaying pansy roots collected in Mt. Rainier, Md., on May 21, 1943.

Grown in pure culture on Petri plates of maizemeal agar the fungus produces a commonplace mycelium composed of colorless branching filamentous hyphae, septate at moderate intervals, with the aperture of each cross-wall guarded on both sides by "Woronin bodies." When sizable slabs of agar medium newly permeated with young mycelium are removed to agar plate cultures abundantly infested with actively motile eelworms, hyphal bails and anastomosing networks are formed everywhere in the transferred slabs, and later are also produced at variable intervals along the rangy filamentous hyphae that grow out rather sparingly in all directions from the slabs. The networks often become 4 or 5 times more extensive than the examples illustrated in figure 1, *A*, *B*. They closely resemble the networks of *Arthrobotrys superba* and *A. oligospora* Fres. with respect to the width of their anastomosing hyphal elements, as well as with respect to the size of their meshes. The resemblance extends also to manner of operation: relatively small, weak nematodes are often held merely through adhesion, while capture of larger and more energetic eelworms usually requires, besides, some degree of enmeshment (FIG. 1, *C*). Perforation of the animal's integument soon ensues through intrusion of a delicate process at some place where the network makes intimate contact with the prey. Often when enmeshment is rather loose, one of the hyphal elements nearest to the animal may give rise to a short stout branch that grows firmly against the integument and then narrowly penetrates it (FIG. 1, *C*). After penetration is accomplished the fungus produces within the integument a globose enlargement which soon puts forth assimilative hyphae to permeate the animal's body from head to tail. If the integument is penetrated in several places, a corresponding number of globose enlargements are usually intruded, all of them generally sharing in the invasion of the prey, though not necessarily in equal measure.

As invasion proceeds the animal's musculature and organs undergo globulose degeneration, the softer parts disintegrating more rapidly than the firmer tissues of the oesophagus and valve. During the period when the newly extended assimilative filaments are most active in appropriating contents of the prey, they likewise contain numerous globules, which, however, are generally smaller than those formed directly from the tissues of the nematode. Later, as the animal's substance nears exhaustion, the globules of the haustorial system diminish markedly. Since the assimilative filaments never grow out through the enveloping integument, nor give rise to erumpent branches, it is clear that the materials absorbed by the fungus are transferred backward into the hyphal loop or network from which the invasion began. As the last remnants of degenerating flesh disappear, the contents of the assimilative filaments begin to share in the backward movement; with the result that apart from the indurated spicules present in male specimens, the empty collapsing integument of the eelworm eventually surrounds only the equally empty membranous remains of the haustorial system.



C. Drechsler del.

FIG. 1. *Arthrobotrys cladodes* var. *macroides*.

The conidial apparatus produced in nematode-infested cultures is ordinarily too sparse to be seen with the naked eye. However, in pure culture on maizemeal-agar plates, the fungus sporulates more freely; so that after about 5 days of growth a mycelium will usually reveal a delicate turf near its center. The conidiophores making up this downy turf closely resemble those formed in eelworm-infested cultures, since like the latter they commonly measure only 3 to 4 μ in width, and bear at the tip a bristling cluster of conidia (FIG. 1, *D*, *a*) together sometimes with a subsidiary cluster at the tip of a subapical spur (FIG. 1, *E*, *a*). While the clusters are mostly borne 110 to 150 μ above the surface of the substratum, relatively short conidiophores may bear their conidial heads at heights less than 100 μ (FIG. 1, *E*, *b*) or even less than 75 μ (FIG. 1, *F*). In its denuded condition the sporiferous tip of the main hypha (FIG. 1, *E*, *b*, *c; F*), as also the tip of the subapical spur (FIG. 1, *D*, *b; G*)—where a spur is present—reveals fairly pronounced, truncate denticulations. Often the sporiferous tip is found irregularly expanded or lobed in a manner to afford increased spatial capacity for attachment of conidia (FIG. 1, *H*, *a–e*).

During their earlier development in a Petri-plate culture conidiophores evidently arise only from filaments prostrate on the surface of the substratum, but after 2 or 3 weeks restricted areas often become covered with whitish aerial wefts, in which numerous conidiophores commonly arise from aerial filaments. These conidiophores, on declining toward the substratum, or even while still in an erect posture, frequently branch out near the base to give rise to secondary conidiophores; and the same process may be repeated several times. In instances where the older conidiophores remain more or less erect, those of secondary, tertiary, or quaternary origin may show rather pronounced curvature. Conidiophores resulting from the somewhat indeterminate development usual in aerial wefts often attain lengths varying between 200 and 300 μ, and basal widths between 4 and 6 μ.

As has been mentioned the conidia of the present fungus (FIG. 1, *I*, *a–z; J*, *a–z*) would seem appreciably longer and narrower than those produced in the cultures on which the description of *Arthrobotrys cladodes* was based. The relevant metric data given in the diagnosis below were obtained by measuring 200 specimens taken at random in microscope mounts prepared from abundantly sporulating material. Expressed as the nearest integral number of microns, the values for length were distributable thus: 13 μ, 1; 14 μ, 2; 15 μ, 15; 16 μ, 29; 17 μ, 47; 18 μ, 48; 19 μ, 34; 20 μ, 14; 21 μ, 8; 23 μ, 1; 26 μ, 1; while the values for width were distributable as follows: 5 μ, 5; 6 μ, 102; 7 μ, 84; 8 μ, 9. Aside from dimensional differences the conidia diverge from those of *A. cladodes* in being drawn out at the proximal end into a distinct basal protrusion. Germination ensues very readily, much as in other members of the predaceous series. Often a germ tube is put forth from the proximal end (FIG. 1, *K, a–d*), but at other times, especially when anastomosis with another conidium (FIG. 1, *L, a–c*) or with a mycelial filament (FIG. 1, *M*) takes place, germination and vegetative union may be effected elsewhere than at the base.

On prolonged aging many of the submerged hyphae in maizemeal-agar cultures of the fungus gradually increase in width (FIG. 1, *O*), some becoming conspicuously vacuolate (FIG. 1, *P*), others becoming filled with numerous minute globules (FIG. 1, *Q*). Eventually most of the granular and globuliferous contents are collected in portions of filament consisting usually of 5 to 20 indurated segments. The segments may retain a cylindrical shape (FIG. 1, *R*), or, again, they may become more or less prominently inflated (FIG. 1, *S*). A branched arrangement of the segments is by no means uncommon (FIG. 1, *R, T, U*). Manifestly the groups of cells make up resting bodies of the same type as those produced abundantly in maizemeal-agar cultures of the predaceous species I have recently described as *Dactylella heterospora* (**6**, p. 339–349). Their resistance to desiccation would seem more than commensurate with the moderate induration suggested by their faintly yellowish coloration and the rather meager thickening of their walls. Like the chlamydospores of *Arthrobotrys oligospora* and of the two allied retiary species I presented earlier under the binomials *A. conoides* (**4**, p. 473–477) and *Dactylaria thaumasia* (**4**, p. 518–523), they remained alive in maizemeal-agar cultures fully 4 years old, although during the last 30 months of storage the medium was in a completely air-dry horny state (6, p. 346).

The fungus appears to merit recognition as a distinct variety; and is accordingly described under a varietal term meaning "of long form."

Arthrobotrys cladodes var. **macroides** var. nov.

Mycelium effusum; hyphis hyalinis, septatis, primo plerumque 2–7 μ crassis, postea usque 11 μ crassis, laqueos tenaces arcuatos vel circulares in reticula saepe conjunctos evolventibus; his laqueis vermiculos nematoideos tenentibus, deinde integumentum cuiusque animalis perforantibus, tuber debilitans vel mortiferum intrudentibus, hyphas intus evolventibus quae carmen exhauriunt. Hyphae fertiles hyalinae, erectae, septatae, simplices vel aliquid ramosae, plerumque 75–300 μ altae, basi 2–6 μ crassae, subter apicem 1.5–2.5 μ crassae, apice dilatatae vel coralloideae, ibi ex denticulis obtusis 5–30 conidia in capitulum confertum ferentes. Conidia hyalina, elongato-ellipsoidea vel elongato-obovoidea, apice rotundata, basi obtuse pedicellata, 13–26 μ (saepe circa 17.6 μ) longa, 5–8.2 μ (saepe circa 6.4 μ) crassa, loculis duobus inter se nunc paene aequalibus, nunc inaequalibus, loculo superiore 5.5–13.4 μ (saepe circa 8.4 μ) longo, loculo inferiore 6.4–12.4 μ (saepe circa 9.2 μ) longo. Corpora perdurantia intra matricem orta, flavidula, protoplasmatis valde guttulosi repleta, modo simplicia modo paulum ramosa, vulgo 50–250 μ longa, in 5–20 cellulis saepius consistentia, cellulis vulgo 7–35 μ longis, 7–20 μ crassis.

Mycelium spreading; vegetative hyphae hyaline, septate, at first varying in width mostly from 2 to 7 μ, some later becoming wider and then occasionally attaining a diameter of 11 μ, in their young condition often, especially in the presence of nematodes, giving rise to sturdy hyphal bails and loops, which, though discrete in the beginning, are later frequently compounded into more or less extensive networks; the bails and networks capturing nematodes through adhesion and enmeshment, then perforating the integument of each captured animal and intruding one or more globose mortiferous excrescences from which are extended assimilative hyphae to appropriate the fleshy contents. Conidiophores hyaline, erect, septate, simple or somewhat branched, mostly 75 to 300 μ high, 2 to 6 μ wide at the base, 1.5 to 2.5 μ wide below the tip which frequently is somewhat widened or irregularly lobed and on which are borne 5 to 30 conidia in capitate arrangement. Conidia hyaline, elongate ellipsoidal or elongate obovoid, rounded at the distal end, provided with a distinct apiculum-like basal prominence at the proximal end, 13 to 26 μ, mostly 15 to 21 μ (average 17.6 μ) long, 5 to 8.2 μ (average 6.4 μ) wide, divided by a cross-wall at the middle, above the middle, or below the middle, the upper cell 5.5 to 13.4 μ (average 8.4 μ) long, the lower cell 6.4 to 12.4 μ (average 9.2 μ) long. Resting bodies formed tardily in the substratum, faintly yellowish, filled with pronouncedly globuliferous contents, mostly intercalary, simple or somewhat branched, commonly 50 to 250 μ long, usually composed of 5 to 20 segments measuring individually 7 to 35 μ in length and 7 to 20 μ in width.

Capturing and consuming eelworms up to 600 μ long referable to species of *Acrobeloides*, *Cephalobus*, *Plectus*, *Rhabditis* and other genera it occurs in decaying roots of *Viola tricolor* L. and in leaf mold in Maryland.

ARTHROBOTRYS ARTHROBOTRYOIDES (BERLESE) LINDAU

From time to time examination of agar plate cultures wherein nematodes were being destroyed by predaceous hyphomycetes has disclosed sparsely scattered conidiophores of robust stature, bearing aloft individually a terminal cluster of conidia which with respect to their largish dimensions appeared rather similar to the conidia of *Arthrobotrys oligospora*, but which with respect to their lesser tapering and nearly equal partitioning more nearly resembled those of *A. superba* or *A. cladodes*. Because of its ambiguous morphology the conidial apparatus in question was excluded from consideration in my treatment of the 3 species mentioned. More recently the fungus here concerned was isolated from leaf mold gathered in deciduous wood near Presque Isle, Me., on Oct. 1, 1941, as well as from leaf mold gathered in deciduous woods near Fairfax, Va., on Nov. 10, 1942.

In pure culture on maizemeal agar the fungus, like most other hyphomycetes of similar biological adaptation, grows rather rapidly to form a dense mycelium devoid of any modification for capture of animals. When a sizable slab permeated with young hyphae is removed from a growing culture to an agar plate culture infested with nematodes, adhesive hyphal bails and networks (FIG. 2, *A; B, a, b*) soon come to light, first appearing promiscuously throughout the transferred slab, and later developing at intervals along the straightforward, rangy filaments extended sparsely in all directions into the adjacent substratum. As might be expected the retiary apparatus promptly begins to capture some of the eelworms whose presence evoked its formation,

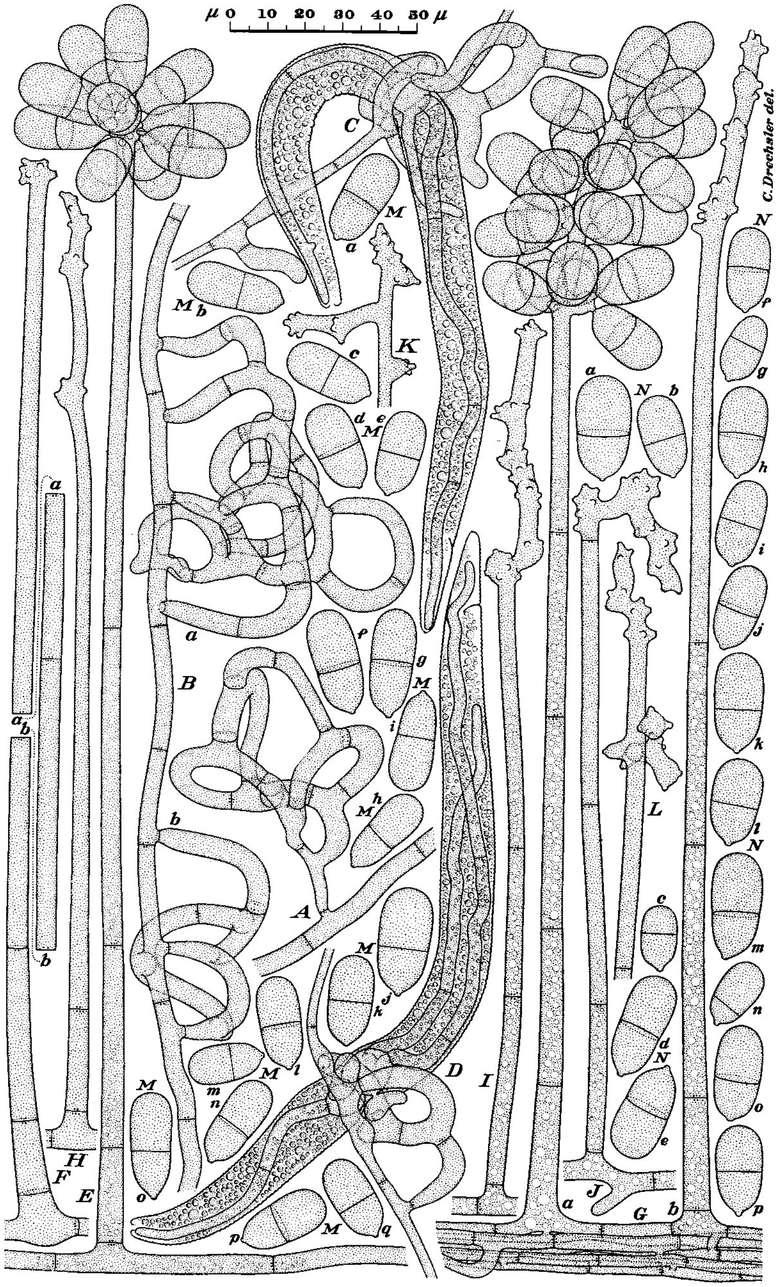


FIG. 2. *Arthrobotrys arthrobotryoides.*

capture being effected through adhesion and enmeshment. Before long the integument of each hapless animal is narrowly perforated by a delicate bud put forth from an enveloping (FIG. 2, *C*) or adjacent hyphal element; or, often, especially in instances where envelopment is loose at the beginning, from one or more short branches that grow firmly against the prey (FIG. 2, *D*). After being disabled from rapid intrusion of one (FIG. 1, *C*) or more (FIG. 1, *D*) bulbous excrescences, the eelworm is invaded from head to tail through the longitudinal extension of assimilative hyphae. Progressive globulose degeneration of musculature and fleshy organs, absorption of the resulting products by the assimilative hyphae, transfer of appropriated or elaborated materials backward through these hyphae into the external parts of the fungus, and withdrawal of protoplasm from the assimilative filaments—all these processes ensue in the same sequence as in allied forms.

When the fungus thus obtains its nourishment from eelworms rather than from the mass of substratum infested by them—presumably the infested substratum ordinarily becomes unusable as a food supply because of foulness brought on by heavy bacterial contamination—it gives rise to a relatively sparse array of conidiophores. These conidiophores, as has been intimated, are of robust stature, usually attaining a height of 300 to 450 μ before they produce from 5 to 10 conidia in a single terminal cluster (FIG. 2, *E*, *F*). Often they measure 5.5 to 8 μ, or even as much as 9 μ, in basal diameter, while varying from 4 to 5 μ in width some distance below the apex. When fully developed they frequently contain 4 or 5 or 6 cross-walls. After the conidia have fallen off, the somewhat expanded tip is revealed as being beset with bluntly truncate sterigmatic protuberances (FIG. 2, *F*).

When the fungus grows in pure culture, so that the more abundant nourishment of the substratum itself can be utilized, vegetative development and spore production are much more luxuriant. Under moist conditions aerial filaments often cohere longitudinally, and thereupon, as in *Arthrobotrys oligospora*, where similar hyphal fasciation was noted by Matruchot (**10**), become united through multiple anastomoses to form coarse mycelial strands from which conidiophores are given off erectly (FIG. 2, *G, a, b*) or in somewhat promiscuous radial arrangement. Although some conidiophores formed here are fully as stout as those formed on nematode-infested materials, others are slenderer (FIG. 2, *H*), not a few measuring only from 4 to 5 μ in diameter (FIG. 2, *I, J*). Many of the conidiophores here produce a cluster of conidia at a height of 200 μ (FIG. 2, *H*), or even at substantially lesser heights (FIG. 2, *I, J*). If evaporation is reduced to prevent early desiccation the conidiophores continue to elongate distally and to form additional conidia, though not on a scale as spectacular as in cultures of *A. oligospora* and *A. superba* that have benefited from similar treatment. Apart from its lesser prolongation the extended conidiiferous spike here is marked by less distinct separation into a series of spore clusters. For although localization of conidial attachments at nodes is at times readily recognizable (FIG. 2, *H*), no less often a rather haphazard arrangement of sterigmatic prominences along a crooked (FIG. 2, *I, J*) or irregularly branched rachis (FIG. 2, *K, L*) denotes botryose aggregation rather than seriate clustering.

Conidiophores of the fungus can be distinguished with moderate certainty from those of *Arthrobotrys oligospora* even when, as usually in nematode-infested cultures, they are bearing aloft only between 5 and 10 conidia in a simple head (FIG. 2, *E*); the capitate arrangement here being noticeably more open with respect to the distal portions of the spores. The looser distal spacing can not be considered a fortuitous feature, but must be held to result from the shape of the conidia making up the cluster, since these, as a rule, taper less markedly from apex toward base than conidia of *A. oligospora*. Because of this lesser tapering, and because, further, their single cross-walls are generally placed in more nearly median positions than in *A. oligospora*, the conidia of the present species, on the whole, show less pronounced inequality in size between the larger distal cell and the smaller proximal cell (FIG. 2, *M, a–q; N, a–p*). In some conidia the 2 cells appear of nearly equal volume, and occasionally, indeed, the lower cell is larger than the upper one (FIG. 2, *N, c, g*).

Spore morphology, as in allied species, is strongly affected by the environmental conditions that attend development. Owing to their relatively large dimensions, and to the relatively high degree of uniformity in size, shape, and septation revealed by them, the conidia produced in nematode-infested cultures at a temperature of about 20° C. (FIG. 2, *M*, *a–q*) may perhaps be regarded as most distinctive of the fungus. When development takes place at 20° C. in pure culture on a suitable medium like maizemeal-agar (FIG. 2, *G*, *a; N*, *a–p*), almost equal uniformity of size, shape, and septation prevails, especially if the substratum and sporiferous layer remain free of troublesome deposits of water. Measurements of 100 conidia selected at random in equal numbers from nematode-infested and pure cultures, which in both instances had developed at 20° C., gave values for length, expressed as the nearest integral number of microns, with a distribution as follows: 17 μ, 1; 18 μ, 2; 19 μ, 2; 20 μ, 4; 21 μ, 8; 22 μ, 3; 23 μ, 13; 24 μ, 16; 25 μ, 16; 26 μ, 14; 27 μ, 9; 28 μ, 6; 29 μ, 4; 30 μ, 2; and values for greatest width distributable thus: 10 μ, 6; 11 μ, 19; 12 μ, 37; 13 μ, 25; 14 μ, 11; 15 μ, 1; 16 μ, 1. The measurements yielded averages of 24.4 μ and 12.1 μ for length and width, respectively; and averages of 13.2 μ and 11.2 μ for length of upper cell and length of lower cell, respectively. In 85 of the 100 conidia the upper cell was clearly longer than the lower one; in 8 the two cells were of about equal length; in the remaining 7 the basal cell (including the basal prominence) was longer than the upper cell, though, owing to its usually somewhat smaller diameter, not always of greater volume.

The conidia (FIG. 3, *A*, *a–z; B*, *a–j*) developed in pure culture on maizemeal-agar at 28 to 32° C., a usual daily range of indoor temperatures near Beltsville, Md., include a large proportion of short ovoid and ellipsoidal specimens. Very often the plump spores of such origin reveal no cross-wall, apparently remaining continuous in their definitive state (FIG. 3, *B*, *a–j*). In septate specimens the two cells appear frequently of nearly equal size, though, on the whole, the upper cell here, too, would seem slightly to exceed the lower one in volume (FIG. 3, *A*, *a–z*).

In the morphology of its conidial apparatus the fungus agrees rather well with the illustrated description wherein more than half a century ago a hyphomycete found occasionally on moist rotten mulberry (*Morus alba* L.) wood at Padua in Northern Italy was presented by Berlese (**1**, **2**) as a new variety, *arthrobo-*

tryoides, of *Cephalothecium roseum* Corda. The conidial dimensions given by Berlese, 20 to 22 μ for length and 9 to 10 μ for width, though somewhat smaller than the dimensions I consider most characteristic of my cultures, are yet very frequent when my cultures are grown at summer temperatures. Berlese's characterization of the conidia produced by his fungus as elongate-ovoid, uniseptate, rounded distally, often obtusely apiculate at the base, and with the upper cell only slightly more distended than the lower, applies accurately to the conidia produced by mine. Taken collectively, his figures, moreover, show very much the same approximation to equality in size of the two conidial segments that comes to light in my material. If, perhaps, in general, these figures show slightly greater constriction at the septum than is commonly evident in my cultures, or, for that matter, than might be justified by the term "vix" in Berlese's diagnosis, it may be profitable to recognize that at the small magnification employed a really minute feature could not have been represented clearly without some exaggeration.

As the Italian fungus bore its conidia on denticulations constantly present on the expanded apex of the erect fertile hypha, and sometimes present likewise on an intercalary node below the apex, Berlese recognized its resemblance to *Arthrobotrys superba*. That he nevertheless assimilated it to *Cephalothecium roseum* may very probably be attributed to the persistent misunderstanding through which, as has been related earlier (**4**, p. 469–471), *Arthrobotrys* was long confused with *Trichothecium* and *Cephalothecium;* though this misunderstanding would hardly seem to account for his very puzzling interpretation of *Cephalothecium* as a more developed form (una forma più sviluppata) of *Arthrobotrys*. Four years later, Matruchot (**10**), after distinguishing anew the basipetal development of conidia in *C. roseum* from the truly capitate sporulation of *Arthrobotrys*, pronounced Berlese's fungus to be beyond doubt *A. oligospora*.

The transfer of Berlese's fungus to *Arthrobotrys* can be viewed with more satisfaction than its identification with *A. oligospora*. Since Matruchot's text gives no ground for supposing that he had received authentic material from Berlese, the identification may be presumed to have been made solely from Berlese's description and figures, and these, as has been intimated, appear better applicable to a fungus specifically alien to the one described by Fresenius. Rather curiously, Matruchot may actually have dealt at first hand with the same organism as Berlese, for his illustrated account of the fungus he formally denominates as *A. superba* Corda var. *irregularis* Matr.—his other designations "la forme *irregularis* Matruchot" (**10**, p. 74) and "*Arthrobotrys irregularis*" (**10**, p. 109) are mentioned casually—presents fea-

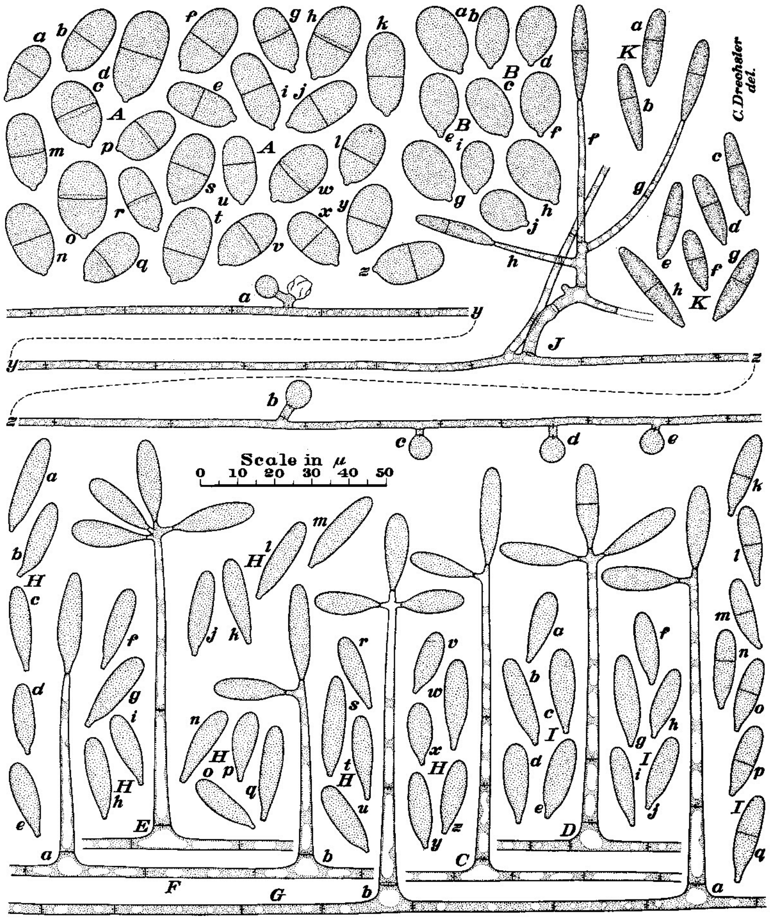


FIG. 3. *A*, *B*, *Arthrobotrys arthrobotryoides; C–I*, small hyphomycete resembling subsidiary sporlating stage of *Dactylaria psychrophila; J–K*, predaceous knob bearing fungus with a delicate *Trichothecium* stage.

tures more or less distinctive of the cultures I hold to be conspecific with Berlese's hyphomycete. Thus, Matruchot ascribes to the prolonged conidiophores of his variety a conspicuous irregularity with respect both to length of internodal portions and to the angles subtended at the nodes. To the nodes, moreover, he attributes a strong tendency toward lateral elongation whereby they sometimes acquire a somewhat branched or coralloid arbuscular form. The conidia he describes as having a length of 25 μ, a maximum width of 12 μ in the distal cell, and a greatest width of 8 μ in the proximal cell. In several of the 9 conidia figured by him the inequality between the upper and the lower segment is not pronounced either with respect to width or with respect to size.

As the several peculiarities which Matruchot detected in material developing on rotten wood persisted during artificial cultivation on different substrata, he held them, not unjustifiably, to represent constant characteristics. In view, however, of what he considered extreme polymorphism in the fungi here concerned, he deemed it inadvisable to propose a separate species. Accordingly he subsumed his fungus under *Arthrobotrys superba* as a new variety, whereby it yet was given equal rank with *A. oligospora*, which likewise he recognized as a variety of Corda's species. It can only be presumed that apart from the variety *irregularis* all the *Arthrobotrys* material studied by Matruchot was referable to *A. oligospora*. In discussing briefly the "forme polyspore," which he observed on dry horse dung and which he held to be typical *A. superba*, he makes no mention of any distinctiveness attaching to the conidia. Most probably Matruchot, like other authors whose observations led them on the score of priority to apply Corda's binomial to *A. oligospora*, did not happen to encounter the much less frequent, less robust, but not less repeatedly capitate fungus that from the smaller dimensions and more nearly equal partitioning of its conidia corresponds much more closely to Corda's illustrated account, and therefore is better deserving of being identified with Corda's species.

It remains uncertain how much significance can properly be ascribed to the wide difference in the statements relating to length of conidiophorous filaments given respectively by Berlese and

Matruchot. In the diagnosis of *Cephalosporium roseum* var. *arthrobotryoides* a range of 150 to 200 μ is given for this dimension, whereas the erect branches of *Arthrobotrys superba* var. *irregularis* are stated to attain readily a length of several millimeters. Berlese's material may have developed on the natural substratum under conditions favoring cessation of growth in the individual conidiophore after development of a single conidial head—under conditions comparable, for example, to those operative in nematode-infested agar plate cultures, where as a rule *A. superba*, *A. oligospora*, and *A. conoides*, despite their strong tendency toward production of successive conidial clusters on a greatly prolonged uniaxial filament, are found in a monocephalous state almost as constantly as the purely monocephalous congeneric species I described under the binomial *A. musiformis* (**4**, p. 477–482). Yet Berlese's statement on length of fertile hyphae is not lacking in taxonomic import; for in my cultures of the fungus under discussion, the conidiophores, regardless of their ultimate length, often form their first conidial clusters at heights less than 200 μ, while, by way of contrast, conidiophores of *A. oligospora* only rarely produce the first conidial cluster less than 300 μ from the base.

The rather satisfactory agreement of my fungus with Berlese's description can be turned to account for nomenclatorial purposes all the more readily because Lindau (**9**, p. 371) in 1905 raised Berlese's variety to specific rank within the genus *Arthrobotrys* as *A. arthrobotryoides* (Berl.). The somewhat abridged German diagnosis given under the new binomial includes nearly all important details of the original account, though its failure to mention anything about the upper cell of the conidium being only slightly more distended than the lower cell appears unfortunate. However, in accordance with the type method of nomenclature, now firmly established, the omitted detail would seem to apply to the species no less than it applied to the variety; there being no question here of an intended factual correction as the transfer was made apparently without any first-hand examination of relevant material. Nor, apparently, has any usage intervened to modify the original characterization. Accordingly, in the absence of serious adverse considerations, I am referring my fungus to *A. arthrobotryoides*.

Lindau expressed some uncertainty whether the species he renamed might not belong to *Arthrobotrys superba;* the latter being interpreted by him, as by Matruchot, to include *A. oligospora* as a somewhat depauperate variety. The fungus under discussion assuredly is separate from the congeneric form I hold referable to Corda's species; its separateness being manifest in parallel cultures despite the intimate interrelationship between all typical species of *Arthrobotrys*.

In old maizemeal-agar plate cultures the fungus occasionally gives rise to multicellular resting bodies through gradual distension and induration of uniaxial (FIG. 4, *A*) or branched (FIG. 4, *B*) portions of submerged hyphae. These resting bodies, like the similar structures of *Dactylella heterospora* and *Arthrobotrys cladodes* var. *macroides*, reveal pronouncedly globuliferous contents within walls that in many instances are thickened somewhat less markedly than the walls surrounding the more deeply colored chlamydospores produced in cultures of *A. oligospora*, *A. conoides*, *A. musiformis*, and *Dactylaria thaumasia*.

A RETIARY FUNGUS WITH UNUSUALLY LARGE PLURISEPTATE CONIDIA

A maizemeal-agar plate culture which after being permeated with *Pythium* mycelium had been further planted with a pinch of decaying material from old potato vines collected near Presque Isle, Me., on Oct. 2, 1941, showed, on examination 10 days later, development of a nematode-capturing fungus that presented some features in an unfamiliar combination. On its tall, sparsely scattered conidiophores were borne, for the most part singly, swollen ellipsoidal conidia, which, if predominantly triseptate, nevertheless very often contained 4 cross-walls (FIG. 4, *C*). The reproductive apparatus thus offered obvious parallelism with *Dactylella gephyropaga* Drechsl. (4, p. 508–513), except that the conidia here were of conspicuously greater length, often measuring more than 60 μ in this dimension. Further, the adhesive networks operative in capture of eelworms showed no scalariform development, but consisted throughout of arcuate or bail-like elements, and hence greatly resembled the retiary apparatus displayed, among pluriseptate species, by *Dactylaria thaumasia* and *Dactylaria polycephala* Drechsl. (**4**, p. 527–531). As both of these species are sometimes difficult to identify with complete certainty in nematode-infested cultures, the fungus of ambiguous morphology was isolated by transferring aseptically some of the large conidia from their supporting hyphae to sterile maizemeal-agar plates.

The conidia germinated promptly, their germ tubes soon growing out into a compact branching mycelium, with numerous hyphal anastomoses and with all septa guarded by Woronin bodies. In the pure culture thus obtained the mycelium has never been found giving rise to predaceous organs. For a time no success was achieved in inducing development of predaceous apparatus by transferring sizable slabs of agar newly permeated with hyphae to Petri-plate cultures abundantly infested with active nematodes. The reason for this unexpected failure became clear when the temperature of the laboratory, ordinarily kept at about 25° C., went down to 17° C. for a period of several days. Under the cooler conditions hyphal bails and networks promptly came into being everywhere in the transferred slabs, and then were formed more gradually at intervals along the straightforward hyphae pushed out sparsely into the subjacent medium. Similarly luxuriant production of bails and networks took place whenever cultures containing the fungus in association with eelworms were kept at the lower temperature; many of the reticula becoming 5 or 6 times more extensive than the examples shown in figure 5, *A*, *a–c*. Contrary to expectations suggested by the robust dimensions of the conidia from which the pure culture was started, the networks have for the most part been rather more delicate than those of any other retiary species except *Dactylaria polycephala*. In their manner of operation they have shown no special distinctiveness. Eelworms measuring from 150 to 600 μ in length are held fast, partly by adhesion and partly by enmeshment. The integument of each eelworm is narrowly penetrated in one or more places; penetration being accomplished in each instance by a fine outgrowth that sometimes is extended from a thick stumpy branch thrust firmly against the animal after its capture (FIG. 5, *B*), but at other times is extended from the inner side of an enveloping loop or from an adhesive hyphal element merely in close contact with the animal (FIG. 5, *C*). Wherever the integument has been perforated a globose enlargement is intruded, severing the animal internally and thus disabling it. Each globose enlargement soon gives off a few assimilative hyphae, which push their way lengthwise through musculature and organs, everywhere bringing about globulose degeneration. After the hyphae have completely taken up the globulose materials, their protoplasm is withdrawn backward into the external mycelium.

The relatively low temperatures between 15° and 20° C. not only permit a lively display of predaceous activity, but also are far more favorable than temperatures near 25° C. for development by the fungus of asexual reproductive apparatus. Under the cooler conditions the fungus promptly gives rise to numerous erect conidiophores, most of which soon come to support 2 (FIG. 5, *D*), 3 (FIG. 5, *E*) or 4 (FIG. 5, *F*) elongate ellipsoidal conidia. In large part the arrangement of plural conidia indicates successive development. Where, as is frequently the case, a spore is attached laterally at a slight geniculation a short distance below the apex bearing the terminal spore (FIG. 5, *D*, *a*, *b*; *E*, *b*, *c*), it may be presumed that the laterally sessile spore was formed originally at the tip of the supporting hypha, and was later pushed aside as the hypha resumed growth to produce another spore on its newly extended tip. Through repetition of this process 2 spores (FIG. 5, *F*, *b*, *c*) often come to be attached at successive geniculations below the apex bearing the terminal spore (FIG. 5, *F*, *d*); a strictly acropetal sequence of development being manifest in such instances. Frequently, in addition, a conidiophore may produce a conidium on the tip of a short spur-like branch (FIG. 5, *E*, *a*; *F*, *a*) arising usually from a position somewhat below that of the original axial tip; and, indeed, sometimes two lateral spurs are present, each bearing a conidium. Production of spores on such branches would seem more or less indeterminate with respect to time, except that it probably never precedes development of the first conidium on the main hyphal axis.

The conidia thus produced are the largest formed by any of the hyphomycetes so far known to subsist through capture of nematodes. Spores developed plentifully in maizemeal-agar plate cultures at temperatures near 17° C. were used for the measurements underlying the data on conidial dimensions supplied in the diagnosis. The 100 specimens selected at random gave values for length, expressed as the nearest integral number of microns, with a distribution as follows: 46 μ, 1; 49 μ, 1; 53 μ, 1; 54 μ, 1; 55 μ, 2; 56 μ, 5; 57 μ, 2; 58 μ, 3; 59 μ, 2; 60 μ, 9; 61 μ, 13; 62 μ, 4; 63 μ, 12; 64 μ, 12; 65 μ, 12; 66 μ, 8; 67 μ, 2; 68 μ, 3; 69 μ, 4; 70 μ, 1; 71 μ, 2; and values for width distributed thus: 21 μ, 3; 22 μ, 7; 23 μ, 12; 24 μ, 20; 25 μ, 21; 26 μ, 19; 27 μ, 14; 28 μ, 2; 29 μ, 2. Of the 100 conidia 50 showed the triseptate partitioning usual in *Dactylella bembicodes* Drechsl. (**4**, p. 487–492), each consisting of a small basal cell, a small antepenultimate cell, a large penultimate cell, and a small apical cell (FIG. 5, *D, a; E, c; F, b, d; G–K*); the lengths of the 4 cells averaging, respectively, 8.2 μ, 8.5 μ, 37.6 μ, and 8.8 μ. Thirty-five of the 100 conidia showed the quadriseptate partitioning frequent in *D. ellipsospora* Grove (**8**; **4**, p. 492–496), each consisting of a small basal cell, a small parabasal cell, a large median cell, a small penultimate cell, and a small apical cell (FIG. 5, *E, a, b; F, a, c; L–P*); the lengths of the 5 cells here averaging, respectively, 7.8 μ, 7.7 μ, 36.7 μ, 6.6 μ, and 4.2 μ. The remaining 15 conidia showed several types of partitioning: six were biseptate after the manner familiar in *D. heterospora*, each consisting of a small basal cell, a large median cell, and a small apical cell (FIG. 5, *Q*); one, though also biseptate, was divided into a small basal cell, a small penultimate cell, and a large distal cell (FIG. 5, *R*); three were composed individually of a small basal cell, a small parabasal cell, a small antepenultimate cell, a large penultimate cell, and a small apical cell (FIG. 5, *S, T*); four consisted individually of a small basal cell, a large antepenultimate cell, a small penultimate cell, and a small apical cell (FIG. 5, *U*); a single specimen with 5 cross-walls had its two large median cells intercalated between two smaller proximal cells and two smaller distal cells (FIG. 5, *V*).

Sporulation is less prompt and less abundant when the fungus is grown in maizemeal-agar plate cultures at the relatively high temperatures—mostly between 28° and 32° C.—prevailing indoors near Beltsville, Md., during the summer. Further, the conidia then produced are, in general, of smaller dimensions. This difference in size, appreciable even in the specimens that with regard to shape and septation (FIG. 4, *D*, *a–d; f–i*) show little divergence from those formed under cooler conditions, is especially marked in the frequently very numerous examples that clearly betray thwarted development in obovoid shape and meager partitioning by 1 or 2 proximal cross-walls (FIG. 4, *D*, *e*, *j–l*). A large proportion of the conidia germinate while still attached to their supporting hyphae by extending a germ tube from the distal end (FIG. 4, *E*). Where germination occurs after the spore has fallen off, the germ tube is more usually sent up from a position closer to the basal end (FIG. 4, *F*).

As the fungus never shows scalariform development but always forms its predaceous networks by adding one bail-like loop after another, it must be held to differ decisively from *Dactylella gephyropaga* in its vegetative stage. The composition and texture of its predaceous networks offer strong similarities with *Dactylaria polycephala*, which, however, is very adequately distinguished by conidial apparatus wherein pluriseptate conidia are frequently arranged in a succession of distinctly capitate clusters. As the 3 or 4 conidia commonly produced by conidiophores of the present fungus at suitably low temperatures are attached in positions often 5 to 25 μ apart, they offer a more or less capitate appearance mainly by virtue of their large dimensions. The difficulty of recognizing such loose arrangement as capitate clustering for diagnostic purposes is aggravated through the circumstance that with meager nourishment the conidiophores often bear only a single conidium or, perchance, two conidia, and then reveal a sporulating habit much like that of *D. gephyropaga* or of *Dactylella bembicodes*. Nevertheless, since its more luxuriant sporulation is apparently more expressive of good development than is its meager sporulation, the fungus would seem somewhat better referable to the capitate genus *Dactylaria* than to *Dactylella*. Assignment to the capitate genus, moreover, conveniently brings the fungus into the same fold with *Dactylaria thaumasia*, to which, from resemblances in character of predaceous networks as well as from similarities in shape and arrangement of conidia, it seems most closely related. When grown in parallel cultures with *D. thaumasia* its separateness from that species is sufficiently evidenced in the larger dimensions of its conidia, in the production of these conidia in lesser numbers on the individual conidiophores, and in complete absence of chlamydospores.

Among the various hyphomycetes which have been made known without reference to any predaceous relationship, yet which from similarities of their conidial apparatus may be presumed to subsist by capture of nematodes, are two species with large swollen conidia that in respect to dimensions approach, even if they do not equal, the aerial spores produced in pure cultures of the present fungus under congenially cool conditions. One of these species, *Monacrosporium elegans* Oudemans (**11**), found on rabbit dung in The Netherlands, was set forth as giving rise to solitary, triseptate, mostly pyriform conidia, 50 to 60 μ long and 16 to 21 μ wide, on conidiophores about 250 μ high, 4 to 6 μ wide at the base and 2 to 3 μ wide at the tip. As the solitary condition of the conidium was affirmed not only in Oudemans' diagnosis of the species (Hyphae conidiophorae . . . singulae conidium solitarium gerentes . . .) but also in his definition of the genus *Monacrosporium* he erected at the time (Hyphae conidiophorae . . . apice unicum tantum conidium . . . gerentes) it may be inferred that in his material the tendency toward production of plural conidia, if present at all, was much feebler than in my cultures. The second of the two large-spored species here in question was found on a partly decayed male inflorescence of the oil palm, *Elaeis guineensis* Jacq., in Sumatra. It was presented by Boedijn as a new member of Oudemans' genus under the binomial *M. megasporum*, though its erect, unbranched, septate conidiophores, 300 to 500 μ long and 5.5 to 7.5 μ wide, were described as having at the tip several warty protuberances, each functional in serving as support of a separate conidium. Boedijn's figure shows several of the sterigmatic warts closely aggregated on the somewhat expanded apex of each conidiophore —an arrangement certainly much closer than that prevailing in my fungus. The conidia of *M. megasporum*, described in part as being elliptical, as containing usually 3 septa, and as measuring 35 to 57.5 μ in length by 15.5 to 27.5 μ in width, would seem from the several examples illustrated, to taper less markedly toward base and apex than the conidia produced in my cultures, besides differing in being drawn out abruptly at the proximal end into a minute hilar protrusion.

Aside from comparison of reproductive structures, determination of predaceous hyphomycetes, and especially of hyphomycetes subsisting by capture of eelworms, necessarily entails consideration of agreement or disagreement with respect to predaceous apparatus. Unfortunately the literature pertaining to the group of fungi here concerned was written, for the most part, without any suspicion of predaceous relationships, so that treatment of the vegetative stage usually affords scope for comparison only with respect to the commonplace features of undifferentiated mycelium. In some instances, it is true, a fungus found capturing and consuming nematodes may be satisfactorily assigned to an established species even where no information is given as to the existence or character of predaceous organs in the material on which the species was based. Thus, since the several typical representatives of the genus *Arthrobotrys* which have been appropriately studied in living cultures—*A. dactyloides* Drechsl. (**4**, p. 482–487) must be held aberrant because of its production, now and then, of swollen biseptate conidia—have all been found capturing nematodes by means of adhesive networks composed of bail-like hyphal loops,[2] there is good reason to presume that similar biological adaptation and similar predaceous apparatus belonged likewise to the similar fungi described as species by

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[2] Very recently, however, an undeniable exception to the general rule has come to light in a predaceous hyphomycete specially adapted to capture minute Sminthurid springtails; the insects being held through adhesion to ovoid glandular cells borne aloft individually on short unicellular erect columnar stalks arising from different segments of a prostrate anastomosing hyphal network. Although the concomitant conidia, mostly about 22 μ long and 5 μ wide, are borne on longish sterigmatic spurs and thus appear in looser capitate arrangement than is prevalent in the better known congeneric nematode-capturing species, their consistently uniseptate condition, together with their production in well defined clusters that are formed terminally one after another on a slender conidiophore given to repeated uniaxial elongation, makes the fungus unreservedly eligible for inclusion in *Arthrobotrys*.

earlier observers. Consequently the determination of two retiary nematode-capturing fungi as *A. superba* and *A. arthrobotryoides* need arouse no serious misgiving with regard to correspondence in the vegetative stage, however silent the relevant descriptions by Corda and Berlese may be in respect to predaceous features. Lack of positive knowledge on adaptations for holding prey is, however, very serious where, as in the case of the fungus from Maine, comparison must be made with descriptions of broad-spored species of *Dactylella* (including *Monacrosporium*) and *Dactylaria*. For among such species are utilized all types of specialized apparatus known to be operative in capture of nematodes—constricting rings, adhesive networks compounded of bail-like hyphal loops, scalariform adhesive networks, adhesive knob-like cells on sturdy stalks, and smaller adhesive cells on frail stalks together with non-constricting rings; so that here the conidiophores and conidia, in themselves, give little indication as to which type of predaceous apparatus might be associated with them. Hence, even if the fungus from Maine agreed well in its reproductive structures to the description of *M. elegans* or of *M. megasporum*, a strong possibility of outright disagreement in the vegetative stage would nevertheless remain.

The fungus, therefore, is described as a new species. A specific term compounded of words meaning, respectively, "cold" and "to love" may serve conveniently to direct attention to its thermal preference.

Dactylaria psychrophila sp. nov.

Mycelium effusum; hyphis sterilibus hyalinis, septatis, plerumque 2–6 μ crassis, laqueos tenaces arcuatos vel circulares in reticula saepe conjunctos proferentibus; his laqueis reticulisque vermiculos nematodeos illaqueantibus, deinde tum integumentum animalis captivi perforantibus, tuber debilitans vel mortiferum intrudentibus, hyphas intus evolventibus quae carnem exhauriunt. Hyphae fertiles incoloratae, septatae, erectae, plerumque 150–500 μ altae, basi 5–9 μ crassae, apice 2.5–4.5 μ crassae, modo simplices modo subter apicem uno ramulo usque 35 μ longo (quandoque duobus ramulis ejusmodi) instructae, primum 1 vel 2 conidia gignentes, mox semel vel bis recrescentes et 1 vel 2 alia conidia deinceps gerentes, itaque postea 3 vel 4 conidia in capitulum laxum saepe ferentes. Conidia hyalina, ellipsoidea vel fusoideo-ellipsoidea, sursum rotundata, deorsum truncata, 1–5 septata vulgo triseptata vel quadriseptata, plerumque 46–71 μ (saepius circa 62.3 μ) longa, 21–29 μ (saepius circa 24.7 μ) crassa.

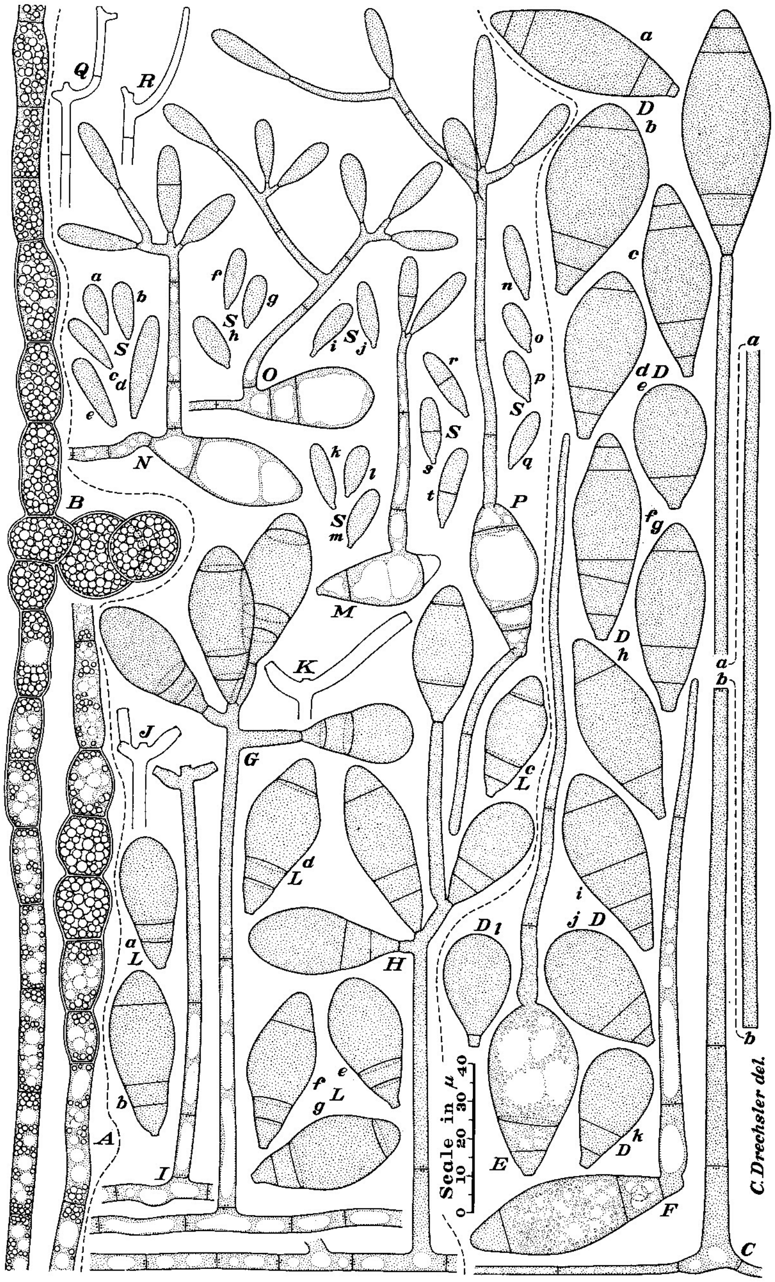

FIG. 4. *A*, *B*, *Arthrobotrys arthrobotryoides*; *C–F*, *Dactylaria psychrophila* (typical strain); *G–S*, *Dactylaria psychrophila* (aberrant strain).

Mycelium spreading; vegetative hyphae hyaline, septate, mostly 2 to 6 μ wide, often, especially in the presence of nematodes, giving rise to hyphal bails and loops which though at first discrete are later usually 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 mortiferous excrescences from which are extended assimilative hyphae to appropriate the fleshy contents. Conidiophores hyaline, erect, septate, mostly 150 to 500 μ high, 5 to 9 μ wide at the base, 2.5 to 4.5 μ wide at the tip, sometimes simple and sometimes bearing near the tip a branch (occasionally 2 branches) up to 35 μ long, often on giving rise terminally to 1 or 2 conidia elongating once or twice to produce 1 or 2 additional conidia, and thus frequently coming to bear 3 or 4 conidia in a loose head. Conidia hyaline, ellipsoidal or fusoid-ellipsoidal, rounded at the distal end, somewhat truncate at the proximal end, when developed under favorable conditions measuring mostly 46 to 71 μ (average 62.3 μ) in length and 21 to 29 μ (average 24.7 μ) in greatest width, containing from 1 to 5 cross-walls but mostly divided by 3 or 4 cross-walls into 4 or 5 cells whereof one, as a rule—the penultimate cell usually in triseptate specimens and the median cell usually in quadriseptate specimens—greatly exceeds the others in size.

Capturing and consuming eelworms that measure usually 150 to 600 μ in length and that belong to species of *Acrobeloides*, *Cephalobus*, *Plectus*, *Rhabditis*, and other genera, it occurs on decaying leaves and stems of *Solanum tuberosum* L. near Presque Isle, Maine.

A SECONDARY CONIDIAL STAGE APPARENTLY REFERABLE TO DACTYLARIA PSYCHROPHILA

Although the foregoing account of *Dactylaria psychrophila* is based primarily on study of a single culture, it applies equally well to more than a dozen other cultures, similar in behavior and morphology, that were derived from other specimens of decaying potato vines also collected near Presque Isle, Me., on Oct. 2, 1941. Mention must be made, however, of differences noted in an aberrant culture isolated from the same general collection of old potato vines. Under congenially cool conditions and on suitable substrata, the strain in question shows very satisfactory agreement with the other strains; but when unfavorably high temperatures supervene it responds by even more pronounced shortening of the conidiophores, which, as a result, then often bear their first conidia at heights between 80 and 130 μ (FIG. 4, *G, H, I*). Plural production of conidia in loose heads (FIG. 4, *G, H*), following subapical branching or prolongation of the supporting hyphae (FIG. 4, *I–K*), continues with little abatement, but rather generally the conidia then formed measure only 30 to 50 μ in length and 15 to 20 μ in greatest width (FIG. 4, *L, a–g*). Premature germination, while the conidia are still attached, occurs only rarely. In aging maizemeal-agar plate cultures, especially in cultures where species of *Penicillium* have partly overgrown the substratum, a fallen conidium often puts forth an erect or ascending germ-conidiophore, which may be simple (FIG. 4, *M*), or somewhat branched (FIG. 4, *N, O*), or successively prolonged (FIG. 4, *P*). On these germ-conidiophores are frequently borne 4, 5, or 6 secondary conidia, mostly elongate ellipsoidal or elongate obovoid in shape, and often drawn out noticeably at the basal end. Varying in length from 14 to 35 μ, and in width from 4.8 to 7.5 μ, the secondary conidia are much smaller than the primary spores that produce them. While most of them evidently remain continuous (FIG. 4, *S, a–q*), some become divided by a median septum (FIG. 4, *S, r–t*).

Conidial apparatus closely resembling the subsidiary reproductive stage just described came to light in a maizemeal-agar plate culture planted with leaf mold taken from deciduous woods near Presque Isle, Me., on Oct. 2, 1941. A tract about 25 square millimeters in extent adjoining the deposit of forest refuse afforded development of a sparse mycelium consisting of colorless septate filaments mostly 2.5 to 3 μ in width. From these filaments, not any of which were supplied with predaceous organs, arose hyaline, meagerly septate, tapering, erect hyphae, mostly 50 to 90 μ high, 4 to 5 μ wide at the base and 1.5 to 2.5 μ wide near the tip, where they gave off usually 1 to 3 lateral spurs (FIG. 3, *C–E; F, a, b; G, a, b*). As the axial tip and each of the spurs supported a conidium, most of the erect hyphae bore aloft 2, 3, or 4 conidia in loose capitate arrangement. These conidia were of elongate ellipsoidal or elongate obovoid shape, and usually tapered noticeably toward the blunt narrow basal end. They measured from

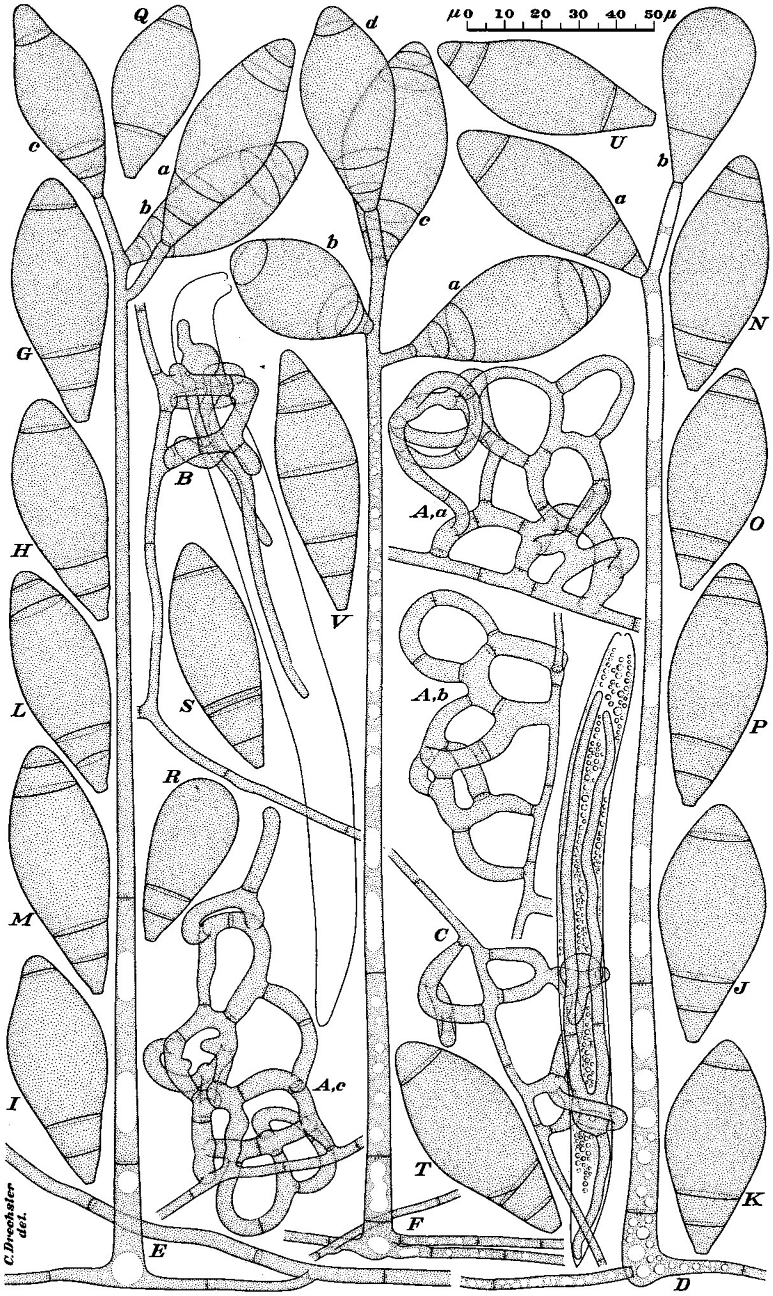

FIG. 5. *Dactylaria psychrophila* (typical strain).

16 to 27 μ in length and from 5.4 to 7.2 μ in greatest width. Though they were predominantly unseptate in their definitive state (FIG. 3, *H*, *a–z; I*, *a–j*), some of them became partitioned by a median cross-wall (FIG. 3, *K*, *k–q*).

Owing in part to the low stature of the sporiferous hyphae and their tendency to collapse rather quickly on exposure to normal evaporation, efforts to isolate the fungus by aseptic removal of conidia proved unsuccessful. Consequently it remains uncertain whether the modest conidial apparatus represented the principal reproductive stage of a small hyphomycete, or an accessory stage of some relatively large mucedinaceous form. That it may belong to *Dactylaria psychrophila* is suggested by its occurrence in decaying vegetable material collected in the same locality at the same time, and by the resemblance of its conidia to the secondary conidia formed occasionally in the aberrant strain of the very robust nematode-capturing hyphomycete.

A KNOBBED NEMATODE-CAPTURING HYPHOMYCETE WITH A TRICHOTHECIUM STAGE

A similarly perplexing fungus appeared in a maizemeal-agar plate culture which after being permeated with *Pythium* mycelium had been further planted with leaf mold collected in deciduous woods near Fairfax, Va., on Nov. 10, 1942. Its straightforward, sparingly branched, colorless, vegetative hyphae, septate at intervals of 15 to 35 μ, and measuring 2 to 2.4 μ in width, bore globose cells, mostly 5.8 to 7.2 μ in diameter, on stalks 1.5 to 5 μ long and 2 to 2.5 μ wide (FIG. 3, *J*, *a–e*). The resemblance of these globose cells to the adhesive predaceous organs of *Dactylella ellipsospora* and of the two allied species I have described as *Dactylella asthenopaga* (**4**, p. 496–499) and *Dactylaria haptospora* (**5**, p. 456–461) identified them unmistakably as organs for capture of nematodes, though, owing very probably to scarcity of suitable prey, nematodes were not actually seen captured by them. Apart from the predaceous structures formed on the surface of the substratum as well as in submerged positions, the mycelial filaments were found bearing a sparse array of colorless, sparingly septate, erect, tapering conidiophores often 35 to 65 μ high, 2 to 3.5 μ wide at the base, and 1 to 1.5 μ wide at the tip. In many instances these conidiophores showed no branching, though rather often, after they had produced a single spore at the tip and had fallen over on the substratum, they would give rise from one of their basal cells to a new conidiophore. Now and then, however, a conidiophore (FIG. 3, *J, f*) would give off one or even two fertile branches (FIG. 3, *J, g, h*) while still in an erect posture. The conidia were generally of elongate ellipsoidal shape, with the distal end bluntly rounded and the basal end perceptibly truncate (FIG. 3, *K, a–h*). They measured mostly 17 to 27 μ in length by 4.2 to 5.6 μ in greatest width, and were consistently divided by a single crosswall at the middle or slightly above the middle.

As all efforts to isolate the fungus by aseptic removal of bacterium-free conidia proved unsuccessful, it has not been possible to determine whether the reproductive apparatus found associated with the knob-bearing mycelium is to be considered a primary sporulating stage or a subsidiary stage. *Dactylella ellipsospora*, the most frequent of the 3 species known to form predaceous organisms of the type here in question, had developed abundantly in the same culture, though no hyphal connection with it could be discovered. The globose cells appeared, in general, somewhat smaller than those characteristic of *D. ellipsospora;* so that with respect to size they more closely resembled the predaceous organs of *Dactylella asthenopaga* and *Dactylaria haptospora.* The latter two species, however, were not observed in the same culture with the fungus under discussion, nor, for that matter, in any of the several dozen other cultures planted with material from the same collection of leaf mold. Nothing that could be taken for a subsidiary sporulating stage has ever been noted in my pure cultures of *D. ellipsospora*, *D. asthenopaga*, and *D. haptospora*.

If the conidial apparatus under discussion should represent a primary sporulating stage, as seems not unlikely, the fungus would be properly referable to *Trichothecium.* In this genus it would offer close similarity to *T. arrhenopum*, a delicate species I have recently described (**7**) as a destructive parasite on oospores of *Pythium graminicolum* Subr. With respect to natural relationship it appears far removed from the widely familiar *T. roseum* Link.

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EXPLANATION OF FIGURES

FIG. 1. *Arthrobotrys cladodes* var. *macroides;* drawn with the aid of a camera lucida to a uniform magnification; ×500 throughout. *A*, *B*, Portions of mycelial filament, on each of which a predaceous network has been produced. *C*, Portion of mycelium with a predaceous network that has been operative in capturing a nematode referable to *Acrobeloides* sp.; from the 3 bulbous enlargements intruded into the animal to disable it assimilative hyphae have grown lengthwise through the fleshy interior. *D*, Portion of prostrate hypha with 2 conidiophores, one of which, *a*, is shown with its cluster of conidia attached, while the other, *b*, a distally branched specimen whereon 2 clusters had been borne, is shown in a denuded state. *E*, Portion of prostrate hypha that has given rise to 3 conidiophores; the conidiophore *a*, bearing a subapical branch, is shown with its 2 clusters of conidia attached, while the simple conidiophores, *b* and *c*, are shown denuded of their spores. *F*, Portion of prostrate hypha bearing an unusually short conidiophore.

G, Portion of prostrate hypha with a denuded conidiophore bearing a subapical branch rather markedly expanded at its tip. *H*, Denuded terminal portions of conidiophores, *a–e*, showing arrangement of the denticulations on which the conidia were borne. *I*, *J*, Assortment of conidia, *a–z*, showing variations in shape, in size, and in position of the cross-wall. *K*, Conidia, *a–d*, germinating by emission of a basal germ tube. *L*, Three pairs of conidia, *a–c*, united by vegetative anastomoses. *M*, Conidium anastomosed with a mycelial filament. *O*, Vegetative hypha, with small vacuoles beginning to form within cellular contents otherwise nearly homogeneous in appearance. *P*, Strongly vacuolate enlarged hypha with some accumulation of small globules. *Q*, Branched portion of mycelial hypha with more pronounced accumulation of small globules. *R*, Resting body consisting of 11 cylindrical cells and 1 strongly inflated cell. *S*, *T*, *U*, Resting bodies with their component cells more or less strongly inflated and filled with relatively large globules.

FIG. 2. *Arthrobotrys arthrobotryoides;* drawn with the aid of a camera lucida to a uniform magnification; ×500 throughout. *A*, Portion of mycelial hypha on which a small predaceous network has been formed. *B*, Portion of mycelial hypha that has produced a somewhat extensive network, *a*, as well as a smaller network, *b*, compounded of only 4 bail-like elements. *C*, Portion of mycelial filament with a small predaceous network that has been operative in capturing a nematode referable to *Acrobeloides* sp.; the mortiferous enlargement from which 3 assimilative hyphae have grown through the fleshy interior was intruded directly from the inner aspect of an enveloping bail-like element, the narrow communication through the perforated integument being shown in profile. *D*, Portion of mycelial filament with a small predaceous network that has been operative in capturing a nematode belonging to *Acrobeloides* sp.; the 2 mortiferous enlargements whereby the animal was disabled were intruded from 2 short branches which manifestly grew firmly against the animal after its capture; only the larger of the mortiferous bodies—the one from which 2 assimilative hyphae were extended toward the tail end—is shown connected in profile view with the external branch from which it originated. *E*, Conidiophore with 10 conidia borne in the typically monocephalous arrangement usual in nematode-infested cultures. *F*, Denuded conidiophore from a nematode-infested culture; for lack of space it is shown in 3 portions separated at the cross-walls *a* and *b*. *G*, Portion of a fasciated mycelial strand formed aerially in pure culture under humid conditions; from the component hypha shown uppermost are given off 2 conidiophores; one of the conidiophores, *a*, bears 20 conidia in 4 clusters so indistinctly separated as to present the appearance of botryose arrangement; the other conidiophore, *b*, shows in its denuded state similarly indistinct separation of its 4 denticulate nodes. *H*, *I*, *J*, Denuded conidiophores from a pure culture, showing arrangement of denticulations on the prolonged axis. *K*, *L*, Somewhat branched distal portions of denuded conidiophores that developed in a pure culture on maizemeal agar under humid conditions. *M*, Random assortment of conidia, *a–q*, from a nematode-infested culture kept at about 20° C., showing normal variation in size, in shape, and in position of cross-wall. *N*, Assortment of conidia, *a–p*, developed in pure culture under humid conditions at a temperature of about 20° C.; some of the spores (*c*, *g*, *n*) illustrate rather extreme variations in shape, in size, or in position of septum.

FIG. 3. Drawn with the aid of a camera lucida to a uniform magnification; ×500 throughout.

A, B, Arthrobotrys arthrobotryoides: A, Assortment of uniseptate conidia, *a–z*, formed in pure culture on maizemeal agar at temperatures varying mostly between 28° and 32° C. *B*, Assortment of unseptate conidia, *a–j*, formed likewise at temperatures between 28° and 32° C.

C–I, Sporulating stage possibly belonging to *Dactylaria psychrophila: C, D, E*, Portions of prostrate hyphae, each with a conidiophore; on the conidiophores are borne, respectively, 2, 3, and 4 conidia. *F*, Portion of a prostrate hypha from which has arisen a young conidiophore, *a*, bearing only a single conidium, and a slightly older conidiophore, *b*, bearing 2 conidia. *G*, Portion of a prostrate hypha with a rather young conidiophore, *a*, bearing 2 spores, and a somewhat older conidiophore, *b*, bearing 3 spores. *H*, Unseptate conidia, *a–z*, showing variations in size and shape. *I*, Assortment of conidia including some continuous specimens, *a–j*, and some uniseptate specimens, *k–q*.

J, K, Predaceous knob-bearing fungus with delicate *Trichothecium* stage: *J*, Portion of mycelial filament bearing 5 predaceous knob-like organs, *a–e*, and a conidiophore, *f*, with 2 branches, *g* and *h*. *K*, Assortment of conidia, *a–h*, showing normal variations in size, in shape, and in position of cross-wall.

FIG. 4. Drawn with the aid of a camera lucida to a uniform magnification; ×500 throughout.

A, B, Arthrobotrys arthrobotryoides: A, Somewhat immature resting body from a maizemeal-agar plate culture 3 months old. *B*, More nearly mature resting body from same culture.

C–F, Dactylaria psychrophila (typical strain): *C*, Conidiophore bearing only a single conidium, as found frequently in nematode-infested cultures. *D*, Assortment of conidia, *a–l*, formed in a maizemeal-agar plate culture kept at temperatures between 28° and 32° C. *E*, Conidium with an apical germ tube, as often found while still attached to the conidiophore in cultures kept at 28° to 32° C. *F*, Conidium germinating after falling on moist substratum.

G–S, Dactylaria psychrophila (aberrant strain): *G, H*, Conidiophores, each bearing 4 conidia, from a pure culture on maizemeal agar grown at temperatures between 28° and 32° C. *I*, Denuded conidiophore from same culture. *J, K*, Distal portions of denuded conidiophores likewise from same culture. *L*, Assortment of conidia, *a–g*, from same culture. *M–P*, Conidia which, after falling on the surface of a 40-day-old maizemeal-agar plate culture contaminated with *Penicillium* sp., have given rise to erect or ascending germ conidiophores whereon are borne a number of smaller secondary conidia. *Q, R*, Denuded distal portions of germ conidiophores. *S*, Random assortment of secondary conidia, showing normal variations in size and shape; with the more numerous continuous specimens, *a–q*, are included a few uniseptate specimens, *r–t*.

FIG. 5. *Dactylaria psychrophila* (typical strain) as found in cultures kept at temperatures near 17° C.; drawn with the aid of a camera lucida to a uniform magnification; ×500 throughout. *A*, Portions of hyphae, *a–c*, on each of which a predaceous network has been produced. *B*, Portion of mycelial filament with a predaceous network that has been operative in the capture of an eelworm referable to *Acrobeloides* sp.; 3 assimilative hyphae are being extended into the fleshy interior from the single mortiferous enlargement

intruded by one of the 2 short branches that grew firmly against the animal after its capture. *C*, Portion of mycelial hypha with a predaceous network that has been operative in the capture of an eelworm referable to *Acrobeloides* sp.; 2 mortiferous enlargements are visible within the integument, the one shown uppermost having been intruded from a hyphal branch curving only half-way around the animal, the other, nearer the tail, having been intruded from an enveloping loop; the second and older of the globose enlargements has given rise to 3 assimilative hyphae whose advance lengthwise through musculature and organs has resulted in globulose degeneration of the invaded parts. *D*, Conidiophore which after giving rise on its original apex to the conidium *a* resumed growth to produce a second conidium, *b*, on its new apex. *E*, Conidiophore with a short subapical spur on which the conidium *a* has been produced; on the original tip of its main axis it first gave rise to the conidium *b*, and then resumed growth to form the conidium *c* on a new apex. *F*, Conidiophore which, apart from producing the conidium *a* on a short subapical spur, has given rise on its axial hypha first to the conidium *b*, and then in succession, with repeated renewal of growth, to the conidia *c* and *d*. *G–P*, Representative assortment of conidia showing normal variations in size, in shape, and in partitioning with 3 or 4 cross-walls. *Q–V*, Conidia showing more unusual partitioning by cross-walls varying in number from 2 to 5.