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A CLAMP-BEARING FUNGUS PARASITIC AND PREDACEOUS ON NEMATODES

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(WITH 7 FIGURES)

Among 10 Hyphomycetes which in a paper (**12**) published 4 years ago I set forth as attacking nematodes after the manner most familiar in such fungous parasites, that is, through invasion by means of hyphae resulting from the germination of conidia affixed to the animal host, were included 2 species whose filaments bore clamp-connections characteristic of various groups within the Basidiomycetes. Owing to some minor differences, particularly in their sterigmata, the 2 species could not both be aptly referred to any one mucedinaceous genus then known. As assignment to separate genera would almost certainly have obscured the intimate kinship of the 2 species, a new genus, *Nematoctonus,* was erected for them; this disposition being deemed all the more advantageous since it would serve to bring into relief how unusual the biological relationship here concerned—parasitism on animals normally free-living and motile from the moment of hatching until the approach of death—was among fungi belonging in the Basidiomycetes. The diagnosis of the new genus was intentionally phrased so as to make provision not only for the 2 parasitic species then described under

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the binomials *N. tylosporus* and *N. leiosporus,* but also for a third form generally similar to them in its production of conidia and clamp-connections, as well as in its habitual subsistence on nematodes, but differing significantly in attacking eelworms for the most part in a predaceous manner—that is, by holding the animals through adhesion to specialized vegetative organs, eventually to extend into the helpless captives assimilative hyphae of mycelial origin. Since the third form had been available for examination only in cultures obtained from Hawaii, which when received by ordinary mail were too old to allow preparation of satisfactory figures, it was left unnamed in the hope that an accession of younger material might later make possible a better description. This hope has so far not been fulfilled, owing to failure of the fungus to appear in such cultures as I have subsequently had occasion to prepare from decaying plant detritus collected mostly in Virginia, Maryland, Delaware, Maine, Wisconsin, and Colorado; though 2 additional clamp-bearing species parasitic on nematodes have come to light and have been described (**13**) under the binomials *N. pachysporus* and *N. leptosporus.* More recently, again, a sixth member of the genus, which, besides attacking eelworms parasitically, operates very destructively in a predaceous manner much like the Hawaiian species, has been observed under favorable conditions and in adequate abundance.

The fungus in question was obtained from 2 collections of friable vegetable refuse gathered by W. J. Zaumeyer near Greeley, Colorado, in October, 1944; one of the collections consisting mainly of partly decayed cucumber (*Cucumis sativus* L.) vines and partly decayed lilac (*Syringa* sp.) leaves, while the other was composed largely of decayed remnants of tamarisk (*Tamarix* sp.) leaves, cottonwood (*Populus* sp.) leaves, and oleaster (*Elaeagnus angustifolia* L.) leaves. In accordance with routine procedure pinches of material from both collections were planted in Petri dishes on maizemeal agar already well permeated with oömycetous mycelium; opportune utilization being made, in this instance, of old cultures of *Pythium arrhenomanes* Drechsl. and *P. undulatum* Petersen *sensu* Dissmann. Before long a flourishing population of eelworms was present in all the cultures, with the result that after about 10 days the predaceous hyphomycetes *Arthrobotrys*

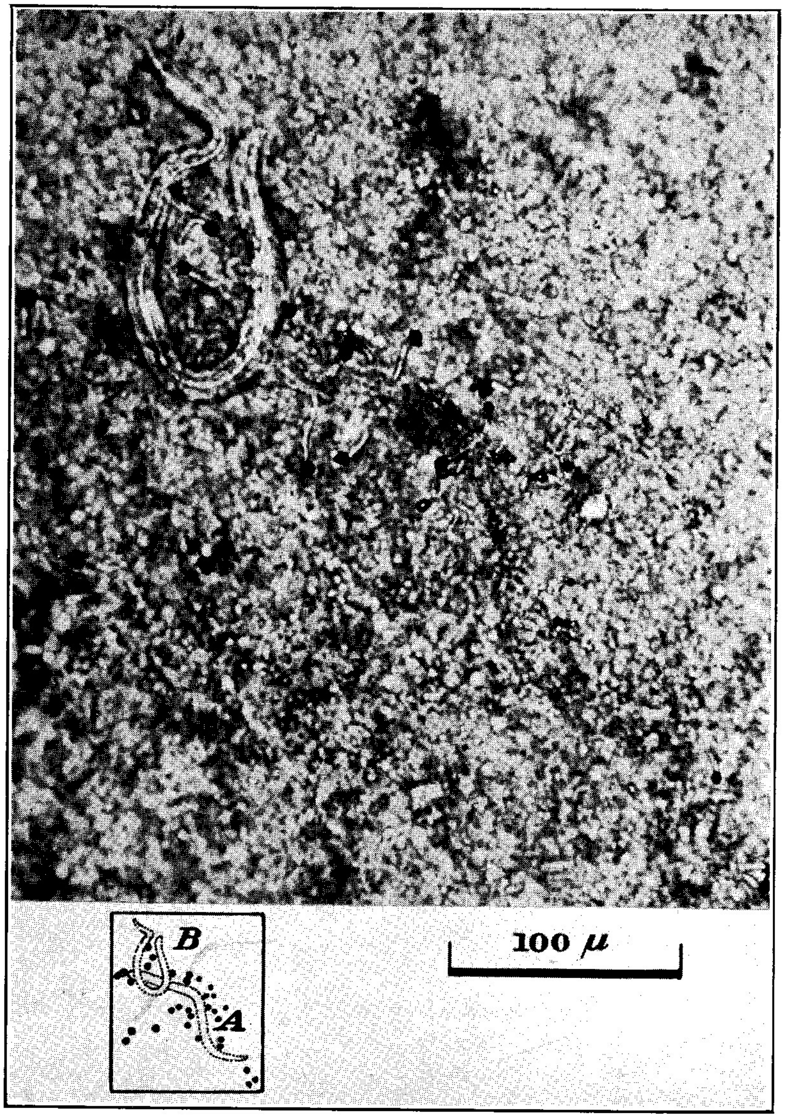

FIG. 1. *Nematoctonus haptocladus* × 300.

oligospora Fres. and *A. arthrobotryoides* (Berl.) Lindau, as also the hyphomycetous parasite *Harposporium anguillulae* Lohde, were developing extensively. Usually it was not until these familiar hyphomycetes had been active for several days that the new clamp-bearing fungus could be found beginning to destroy eelworms in numbers sufficient to arrest attention, though its destructiveness in many cultures soon became very severe. A nematode identified as an undescribed species of *Panagrolaimus*,[2] which predominated numerically over all other species, was often found killed in spectacular quantity. A stylet-bearing nematode identified as *Paraphelenchus pseudoparietinus* Micoletzky [2] and several species of the genera *Rhabditis* and *Mononchus* incurred destruction in a measure corresponding approximately to their lesser abundance.

While as a general rule the predaceous fungi, including both the nematode-capturing hyphomycetes and the nematode-capturing Zoöpagaceae, begin their visible development in Petri plate cultures containing deposits of decaying plant material by extending mycelial filaments from the opaque deposits into the surrounding transparent agar medium, the clamp-bearing fungus more often makes its initial appearance in growing out of dead nematodes (FIG. 1, *A*) lying at some distance—frequently 10 to 20 mm.—from the nearest mass of vegetable detritus. In their earlier stages of development the mycelial filaments growing out into the clear culture medium offer no unusual features (FIG. 2, *A*). Except for the cross-walls associated with the clamp-connections studding them at moderate intervals, they contain few septa. The longer hyphae show moderate branching at rather wide angles; some, though not all, of the branches manifestly arising from individual clamps. Neither vacuoles nor granular constituents are at all abundant in young hyphae; so that the protoplasmic contents present a rather clear, nearly homogeneous appearance.

The commonplace morphology just described pertains more especially to mycelial elements formed under the surface of agar substratum, and consequently is displayed on a greater scale in

[2] For identification of these species I am indebted to Dr. G. Steiner, Principal Nematologist, Division of Nematology, Plant Industry Station, Beltsville, Maryland.

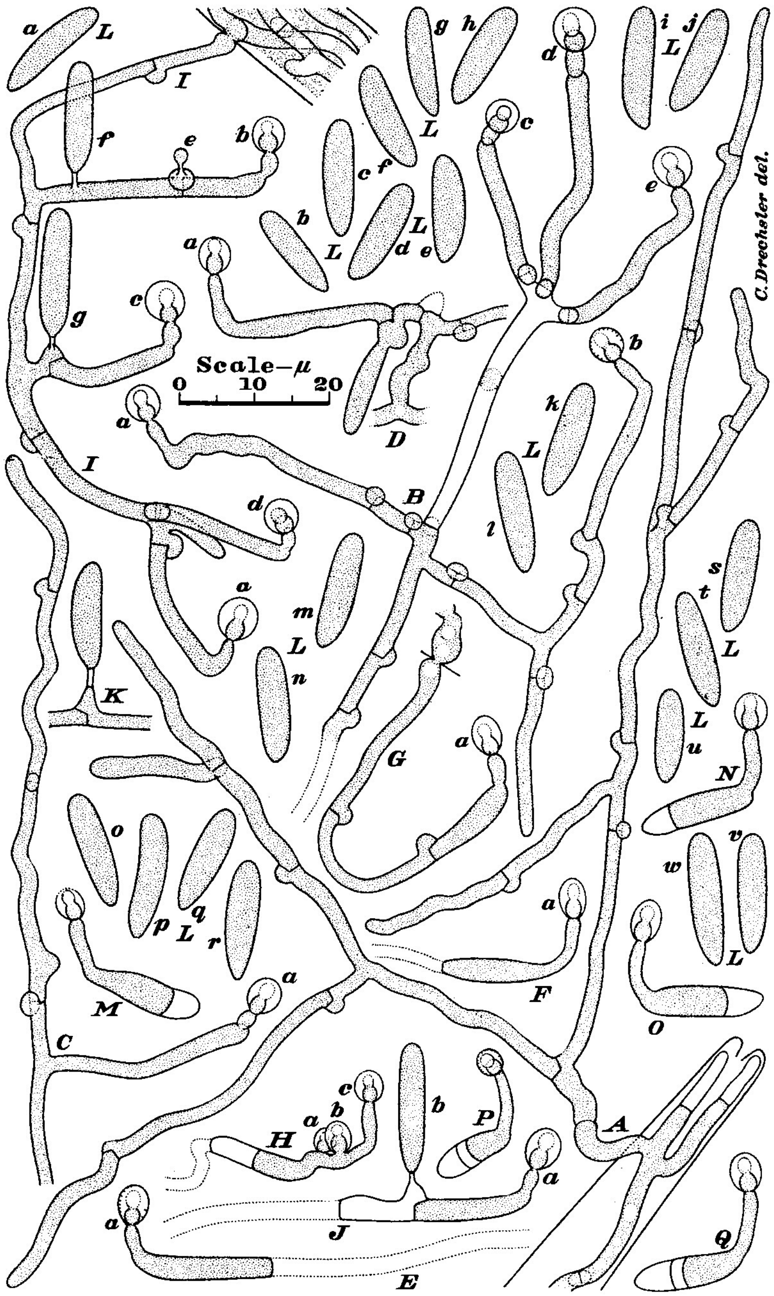

FIG. 2. *Nematoctonus haptocladus.*

instances where the nematode has happened to succumb in a deeply submerged position than in instances where it succumbed on the surface. Once the hyphae from a submerged animal reach the surface they continue their development for the most part procumbently, and then are capable of undergoing the same distinctive modification (FIG. 2, *B*) which hyphae growing out from animals lying on the surface can achieve with little preliminary expenditure of their substance (FIG. 3, *A, B*). To accomplish this modification the prostrate axial filament, as also its prostrate branches, stops elongating procumbently, and gives rise abruptly from its tip to a short, erect or ascending process terminating in a glandular cell that soon is surrounded by a transparent adhesive secretion (FIG. 2, *B, a–e; C, a; D, a; E, a; F, a; G, a; H, a–c; I, a–d.* FIG. 3, *A, a–g; B, a, b; C, a; D, a–j.* FIG. 4, *A, a, b*). The glandular cell usually has a shape somewhat like the Arabic numeral 8. Generally its proximal lobe is noticeably wider than its distal lobe, and appears to be surrounded by thicker, more substantial membrane. As the boundary of the distal lobe, especially at the rounded tip, is often only vaguely discernible, it may be surmised that this lobe is the more directly active one in the elaboration of adhesive material. When viewed under the microscope, in a moist preparation covered with a cover glass, the adhesive drop shows a distinct boundary, as if it were surrounded by a thin peripheral film. Sometimes short rod-like markings appear to extend radially inward from the peripheral contour of the droplet (FIG. 2, *E, a.* FIG. 3, *A, a–g; B, a; D, e–j*). It is quite possible that these markings may represent only minute folds in the peripheral film such as might readily result from the pressure of the overlying cover glass. Not infrequently a predaceous branch, after putting forth one adhesive body, will elongate slightly to put forth a second (FIG. 3, *A, b, c; D, h, i.* FIG. 4, *A, a, b*); and occasionally elongation is repeated in the development of a third adhesive body (FIG. 2, *H, a, b, c*). This rejuvenation of predaceous branches has an obvious parallel in the repeated elongation of the outgrowth put forth by abjointed conidia of *Nematoctonus pachysporus*.

As the glandular cells with their envelopes of adhesive secretion are borne aloft in the air 2 to 8 μ above the substratum they stand out in bold relief when cultures containing them are examined

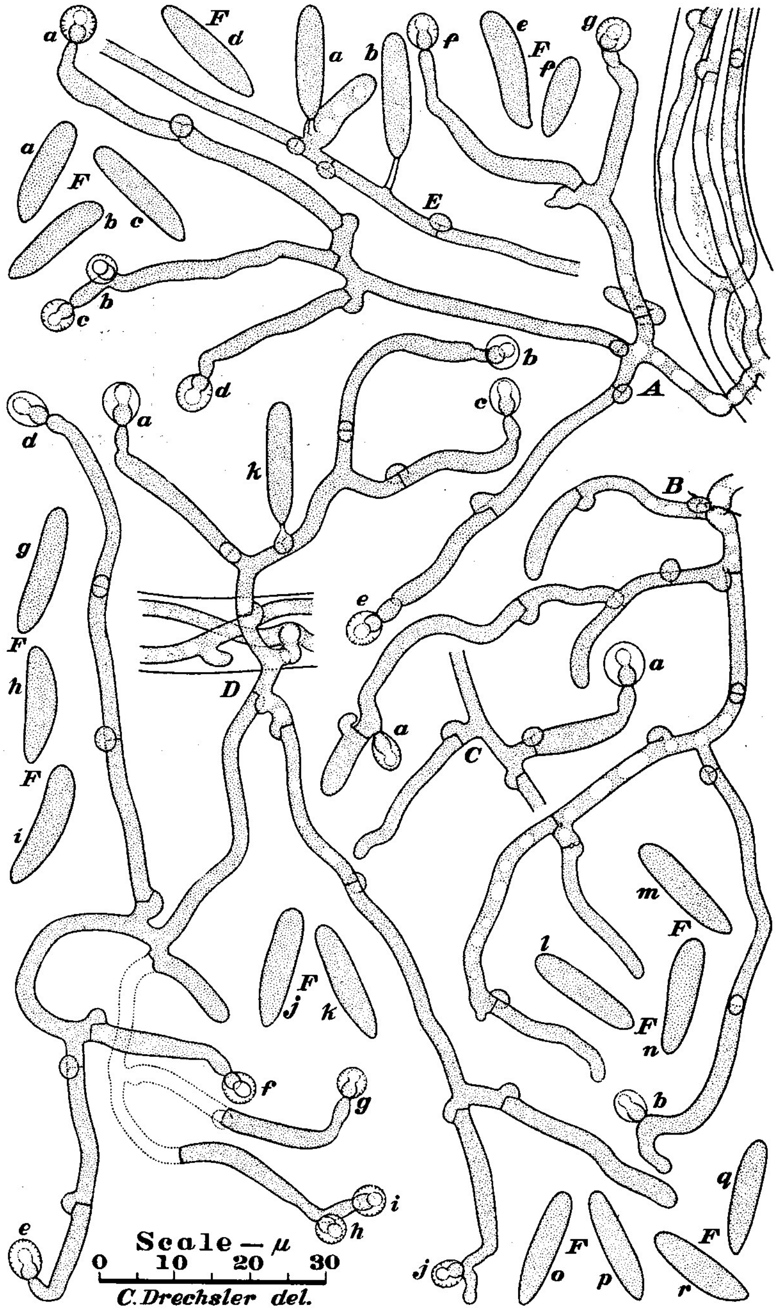

FIG. 3. *Nematoctonus haptocladus.*

microscopically in an uncovered state by means of a dry objective (FIGS. 1, 5, 6). Owing to their raised position they adhere only to nematodes moving along on the surface of the culture. Small eelworms, as, for example, young specimens of the undescribed *Panagrolaimus* species mentioned, are usually held securely despite all struggles, even when attached only by a single adhesive branch (FIG. 7, *A, a*); and somewhat larger animals are frequently held captive if two (FIG. 1, *B*) or more branches become fastened upon them. Like the nematode-capturing Zoopagaceae, but unlike most of the clampless hyphomycetous forms familiarly exemplified in *Arthrobotrys oligospora,* the fungus shows no special development operative in killing or disabling quickly any nematode captured by it. It accordingly delays invasion—certainly invasion on an extensive scale—until the animal has become quiescent from prolonged struggle. A small specimen of *Paraphelenchus pseudoparietinus,* whose capture happened to come under direct observation, remained capable of some slight movement fully 31 hours later. Forty-eight hours after capture the animal was motionless (FIG. 7, *B*), though death had probably taken place only a short time earlier, judging from the meager display of assimilative hyphae inside its body.

While the smaller, weaker nematodes are usually held captive on the adhesive branches, the larger and stronger animals more often tear these branches away, and continue moving about, carrying the adhesive organs with them (FIG. 7, *C, a–f*). Such escape, however, brings little advantage, for the affixed fungous structures penetrate the integument and intrude infective hyphae, eventually killing the fugitives, much as if they had been held captive. Because of the long period required to bring about their disablement, the fugitive animals roam about widely, often entering other areas of infestation and thus becoming burdened with additional predaceous apparatus. In cultures where the fungus was abundant, large specimens of the unnamed *Panagrolaimus* measuring .75 to 1 mm. in length could often be seen encumbered with 15 to 20 adhesive branches; and much more frequently somewhat less robust specimens were found still moving about feebly, though a half-dozen adhesive branches had intruded assimilative hyphae of some length (FIG. 7, *C, a–f*). Infected eelworms, thus capable of prolonged locomotion are, of course, wont to succumb in scattered positions, much like eelworms killed by fungi attacking wholly after the ordinary manner of parasites. Its failure to hold the more robust nematodes not only explains largely why the fungus often makes its first appearance in Petri plate cultures at a distance from the deposit of decaying material whence it must have originated, but also explains for the most part why nematodes are often found succumbing to it in submerged positions, despite its production of predaceous organs only on the surface of the agar substratum. Again, partly because of the limited mechanical strength of the filaments terminating in adhesive organs, and partly because of the limited elongation of hyphae extended from dead nematodes, flourishing cultures of the fungus show a characteristic distribution of dead and dying eelworms in numerous colony-like groups—the groups including often 5 to 25 small eelworms held captive through adhesion to the abundant predaceous apparatus originating from the body of a conspicuously larger eelworm that had earlier succumbed to invasion from predaceous apparatus which it manifestly had torn off but had not succeeded in shedding.

There are grounds for believing that the frequent tearing away of adhesive organs by the stronger eelworms is a normal and more or less advantageous feature in the development of the fungus. Often a ramifying predaceous hyphal system, still in a fairly youthful condition, undergoes evacuation of protoplasm from intercalary portions, with the result that the adhesive branches distal in relation to these portions remain attached only very weakly by empty membranes so unsubstantial as to be hardly visible (FIG. 2, *B, c, d, e; E; H; J*. FIG. 3, *D, g, h*. FIG. 7, *A, c, d; B, a, b*). Through weakening of the hyphal attachments the fungus achieves a condition analogous to that found in 3 species of the clampless nematode-capturing hyphomycetes—*Dactylella lysipaga* Drechsl., *Dactylella leptospora* Drechsl., and *Dactylaria candida* (Nees) Sacc.—whose predaceous organs, consisting of adhesive knobs and non-constricting rings, are borne on longish, slender, and evidently frail filamentous stalks. As was set forth in an earlier account (**8**: p. 499–508; p. 523–527), the rings of these species are often torn from their attachments, permitting the ensnared eelworm to proceed on its way. Since the earlier account was written I have had occasion further to observe in cultures of *Dactylella lysipaga* and *Dactylaria candida* nematodes moving about with predaceous knobs of these fungi adhering externally to them; the knobs in time infecting the encumbered animals and bringing about their death, after a considerable period of motility, in widely scattered positions. Such an extended period of motility after predaceous organs—whether adhesive knobs or non-constricting rings—have been affixed to prey would seem very helpful in spreading the fungus; so that it may well be significant that the 3 clampless hyphomycetes named, much like the clamp-bearing form from Colorado, but wholly unlike most other clampless nematode-capturing hyphomycetes, are not wont to kill eelworms quickly. The frail attachment of predaceous branches consequent to withdrawal of protoplasmic contents from intercalary hyphal parts may thus with some justification be regarded as an adaptation not only advantageous in allowing development of additional predaceous branches from the protoplasmic materials withdrawn, but profitable, moreover, in utilizing the animal's locomotion to extend the region of infestation. It must be admitted, however, that similar extension, though on a lesser scale, would seem to be accomplished quite fortuitously now and then in behalf of clampless hyphomycetes whose predaceous organs are not only attached very firmly to the mycelium but, besides, operate in a manner calculated to inflict death quickly; as, for example, in instances when powerful specimens of *Rhabditis* or *Mononchus,* after tearing off, through sheer violence, the firmly attached constricting rings of *Arthrobotrys dactyloides* Drechsl., *Dactylella bembicodes* Drechsl., or *Dactylaria brochopaga* Drechsl., continue their locomotion for an hour or two, until they are completely disabled.

With respect to its development inside nematodes the fungus shows, in general, little departure from the 4 congeneric species that have previously been described and named. During the earlier stages of invasion the assimilative hyphae are often found conspicuously distended for short distances (FIG. 7, *C, b, c, e*). Apart from these swollen portions the internal mycelium is usually not clearly discernible until the animal's contents have been largely expropriated (FIG. 4, *A, C*). It is then revealed as being moderately branched and moderately beset with clamp-connections;

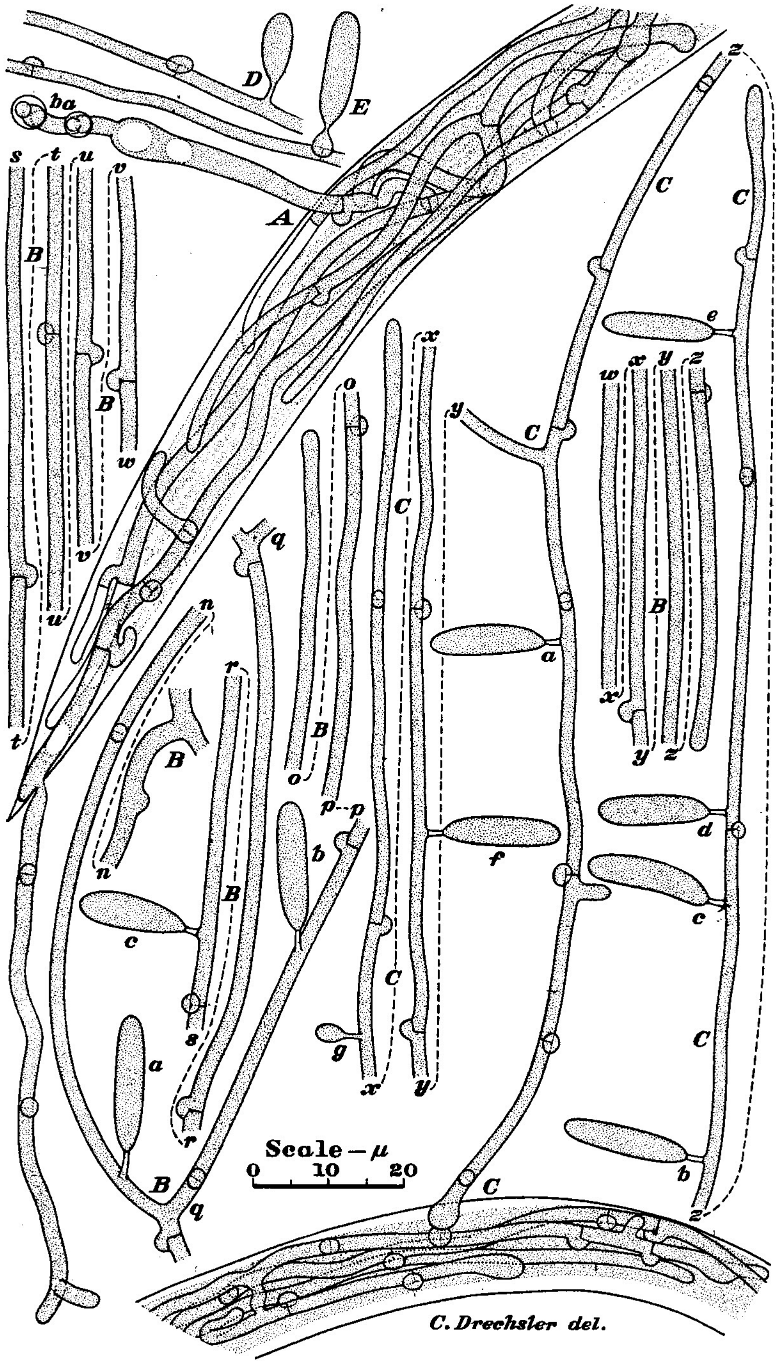

FIG. 4. *Nematoctonus haptocladus.*

many of the branches, indeed, arising from individual clamps. The assimilative hyphae, compared with those of other members of the genus, appear of intermediate coarseness,—being, on the one hand, somewhat wider than the corresponding hyphae of *Nematoctonus tylosporus, N. leiohypha,* and *N. leptosporus,* and, on the other hand, slightly narrower than the assimilative hyphae of *N. pachysporus.* At first they are filled with protoplasmic contents of rather homogeneous aspect, but as materials are withdrawn to provide for the growth externally of predaceous and conidiophorous filaments, vacuoles appear and evacuation takes place progressively until little is left within the animal's integument except empty hyphal membranes,—the remains of the eelworm being then visible only in faint outline amid the array of adhesive organs elaborated from its fleshy materials (FIG. 1, *A*). The time required to permeate the body of an eelworm after its death, and to convert its digestible contents into predaceous and conidial apparatus would seem not greatly to exceed the time taken to kill the animal after its capture. Thus, in one observed instance, a captured motionless specimen of the undescribed *Panagrolaimus,* about 325 μ long, which when first photographed (FIG. 1, *B*) showed so little internal disorganization that it could have succumbed only a little earlier, was only faintly discernible 48 hours later when it was photographed again (FIG. 5); its fleshy substance having in 2 days been completely expropriated by the fungus, and utilized in the production of approximately 30 predaceous branches and one conidium.

The paucity of reproductive apparatus, relative to the output of predaceous branches from this particular nematode, can hardly be considered unusual for the fungus. The array of approximately 34 adhesive bodies amid which the animal succumbed came from an individual nematode without the supplement even of a single conidium (FIG. 1, *A*); such failure of sporulation being rather frequent in instances where nematodes of only moderate size die in isolated positions. Where only a few conidia are produced, they usually are borne on sterigmata arising exclusively from prostrate hyphae; some of the sterigmata originating from clamp-connections (FIG. 2, *I, e, g; J, b; K.* FIG. 3, *D, k*), others from undifferentiated portions of filament (FIG. 2, *I, f.* FIG. 3, *E, a, b*). More liberal sporulation commonly takes place where nematodes have succumbed in colony-like groups; for in addition to the scattered conidia here likewise arising from prostrate hyphae (FIG. 6, *a, b*) a larger number of conidia are produced on aerial hyphae, often several hundred microns long, which seem given over entirely to

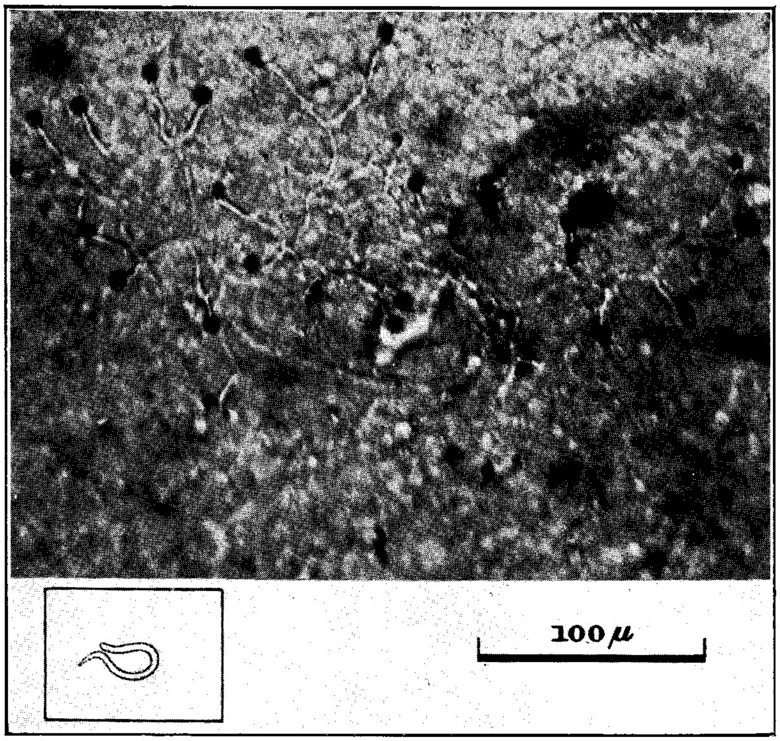

FIG. 5. *Nematoctonus haptocladus.*

asexual reproduction. These aerial hyphae (FIG. 4, *B, C*) are sometimes sparingly branched, and like the assimilative filaments are studded with clamp-connections at moderate intervals. In their earlier condition they ascend usually at a narrow angle with the horizontal. They bear their spores nearly vertically on sterigmata arising much more frequently between the clamps (FIG. 4, *B, a–c; C, a–g; D*) than directly from the clamps (FIG. 4, *E*). After their contents have largely been spent in production of conidia they decline to the substratum, much like the aerial conidiophorous hyphae of *Nematoctonus leiosporus* and *N. pachysporus.*

The sterigmata of the fungus rather closely resemble those of *Nematoctonus leiosporus* in length and distal width; but being evidently, in general, somewhat narrower at the base, they taper less markedly, and often, indeed, hardly seem to taper at all. The conidia borne on them (FIG. 2, *L*, *a–w*. FIG. 3, *F*, *a–r*) are conspicuously wider and shorter than those of *N. tylosporus* and *N.*

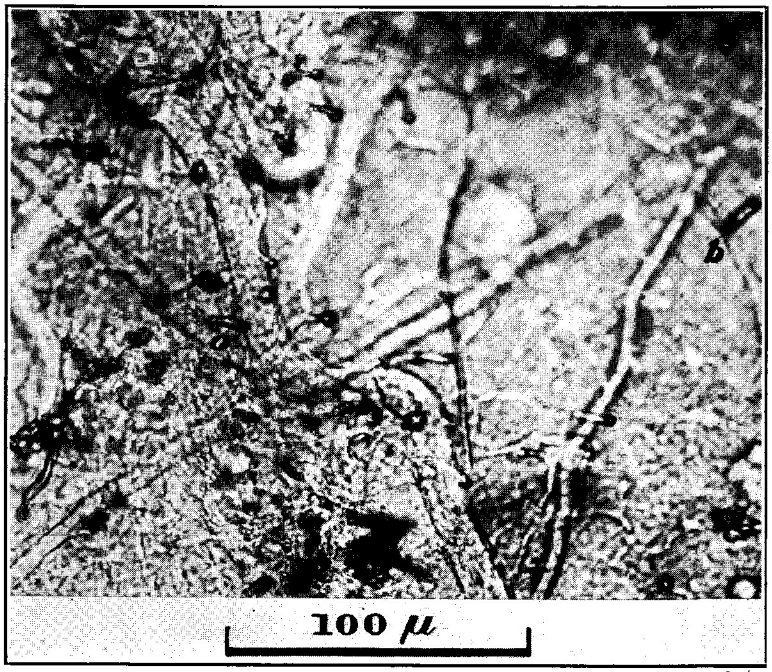

FIG. 6. *Nematoctonus haptocladus.*

leptosporus; and they have a cylindrical or elongate-ellipsoidal shape differing markedly from the tapering shape distinctive of the spores of *N. leiosporus,* as well as from the plumper strobiliform shape characteristic of the conidia of *N. pachysporus.* With respect to volume they would seem equal or very nearly equal to the conidia of *N. pachysporus,* and perhaps are slightly larger than those of *N. leiosporus;* their greater width in comparison with the latter probably more than making up for their lesser length. From the strongly curved conidia of the congeneric predaceous Hawaiian species they differ not only in their lesser length and lesser width, but more especially in that they are straight or at most slightly curved (FIG. 2, *L, p*. FIG. 3, *F, i*).

When a conidium falls on the moist surface of an agar culture, it gives rise at its distal end to a short, erect or ascending outgrowth which terminates in a glandular cell that soon becomes surrounded by a globule of adhesive secretion (FIG. 2, *M–Q*). The material required for production of the outgrowth is provided through evacuation of protoplasmic contents from the basal portion of the

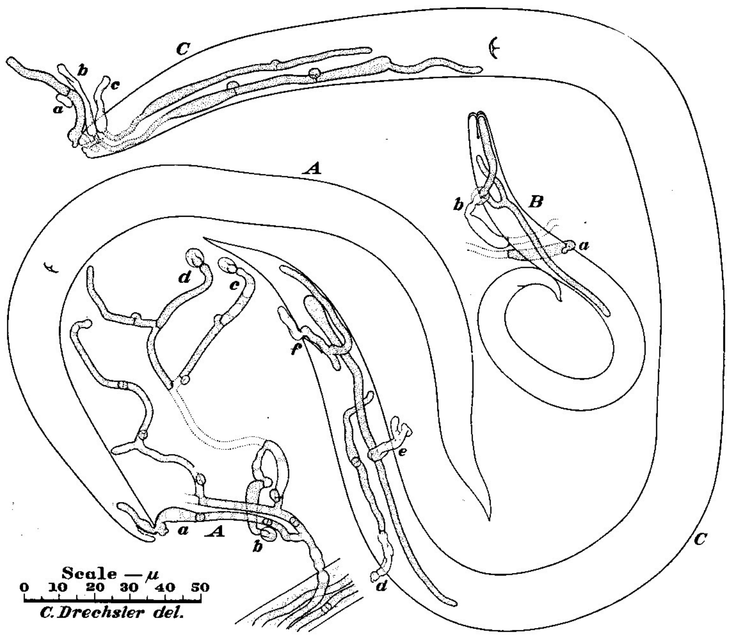

FIG. 7. *Nematoctonus haptocladus*.

spore. When this germinative development is concluded, a wall is laid down to delimit the living part from the emptied part (FIG. 2, *M–O*). In some instances, a retaining wall is laid down earlier, while evacuation is still in progress, so that in the end the spore comes to contain 2 transverse walls (FIG. 2, *P, Q*).

The adhesive outgrowth put forth by a disarticulated conidium corresponds, of course, to the erect or ascending terminations of predaceous branches; and operates quite similarly in effecting attachment to motile nematodes. Since, however, the disarticulated spore lacks all anchorage below, and in itself is not bulky enough to impede seriously the locomotion of even a small eelworm, effective attachment of a nematode to the adhesive germ hypha results invariably in a parasitic rather than in a predaceous relationship. In fine, the conidia of the Colorado fungus are limited no less strictly to a parasitic mode of attack than the conidia of the 4 exclusively parasitic species of *Nematoctonus* previously described and named.

Infection of microscopic animals more or less directly by conidia of predaceous fungi is not unusual. Among the predaceous Zoopagaceae such infection has often been noted, for example, in the amoeba-destroying forms *Acaulopage marantica* Drechsl. (**10**: p. 144, *fig. 6, B*) *Zoöpage rhabdospora* Drechsl. (**6**: p. 375. *fig. 4, C*), and *Z. thamnospira* Drechsl. (**9**: p. 143, *fig. 2, F, G*). As the elongate conidia of these species are being carried about by the actively moving animal to whose integument they have become affixed, they intrude haustoria much like conidia of the curiously ectoparasitic *Bdellospora helicoides* Drechsl. (**4**: p. 20–26), though often revealing an essentially predaceous characteristic in continuing simultaneously to germinate by putting forth a commonplace germ hypha (**6**: p. 375, *fig. 4, C*). Sometimes minute *Amoebae* much smaller than the animals habitually serving as prey become affixed to the conidia, as also to the mycelium, of members of the Zoopagaceae,—a relevant instance being given in a figure (**5**: p. 179, *fig. 2, J*) showing a filamentous conidium of *Acaulopage macrospora* Drechsl., 52 μ long and 1.7 μ wide, from which haustoria have been intruded into 2 affixed pulvinate *Amoebae,* each about 6 μ in its greatest dimension. Naturally the very feeble *Amoebae* are easily held captive by the larger adhering conidia, which therefore can be regarded as having established a predaceous relationship even though completely lacking hyphal anchorage. Likewise conidia of the predaceous hyphomycete *Pedilospora dactylopaga* Drechsl., after directly burgeoning forth several digitiform adhesive processes (**3**: p. 396, *fig. 1, S*), have been observed capturing and destroying specimens of the small testaceous rhizopod *Geococcus vulgaris* Francé. The same rhizopod has been seen immobilized, invaded, and destroyed also by the large conidia of the predaceous hyphomycete *Dactylella passalopaga* Drechsl. (**7**: p. 398, *fig. 1, M*).

Among the clampless predaceous hyphomycetes the manner and prevalence of attack by loose conidia varies greatly, owing in large part to the diversity of predaceous organs utilized in this group. When lying on the surface of a moist substratum the conidia of the several species employing adhesive networks sometimes germinate by giving rise exclusively to hyphal loops, or, again, sometimes produce several hyphal loops before the ordinary germ hyphae are long enough to insure good anchorage; several figures of such germination being included in Woronin's early illustrations of *Arthrobotrys oligospora* (**18**: *pl. 6, figs. 12–14*). Naturally when predaceous apparatus so weakly moored fastens on to an active nematode the whole array of loops is carried away together with the spore; the animal, nevertheless, being destined to succumb unless it should succeed in shedding the encumbering material rather promptly. At least two of the hyphomycetes that capture nematodes in constricting rings, namely *Arthrobotrys dactyloides* and *Dactylaria brochopaga*, are occasionally given to producing their remarkable predaceous organs directly on conidia (**8**: p. 483, *fig. 6, K;* p. 515, *fig. 13, L–P*) without putting forth any ordinary mycelial hyphae. A nematode caught in a predaceous ring of such origin continues to move about, carrying the spore clamped to its side, until disablement ushers in its death. When the conidium of *Dactylella asthenopaga* Drechsl. germinates, as it frequently does, by putting forth 1 or 2 predaceous organs (**8**: p. 497, *fig. 9, N, a–e*)—which in this species consist individually of a globose adhesive cell borne on a short sturdy stalk—it often adheres to specimens of *Bunonema,* and after being carried around a while, infects the sluggish animal (**8**: p. 497, *fig. 9, O*). Similar development has not been observed in *Dactylella leptospora* Drechsl., but should take place there also, since its conidia, when formed in pure culture, are frequently found bearing 1 or 2 globose cells (**8**: p. 505, *fig. 11, N, a–k*). Of all the clampless nematode-capturing hyphomycetes, *Dactylaria haptospora* Drechsl. (**11**: p. 456–461) undoubtedly displays the most consistently aggressive parasitic attack. Adaptation for such attack is clearly manifest in the curious morphology distinguishing the conidium of this aberrant member of the predaceous series of hyphomycetes; the adhesive terminal cell, constantly present on the spore, providing ready attachment to an animal; and the slender shape of the spore being helpful in maintaining attachment by offering little resistance to movement through substratum, and consequently affording little opportunity for removal by the scraping or shearing action attending the animal's continued locomotion.

In whatever measure disarticulated conidia of the predaceous Zoopagaceae and predaceous clampless hyphomycetes may attack animals, it yet remains true that the conidia in all predaceous species referable to these two series are capable of putting forth a mycelium extensive enough, as a rule, to afford secure anchorage against the struggles of the animals habitually serving as prey; such germination being, indeed,—except possibly for the conidia of *Dactylaria haptospora*—their more usual or preferred manner of development. However, the conidia of the clamp-bearing Colorado fungus, like those of the 4 parasitic congeners previously named, have never been seen to put forth anything but the short aerial adhesive outgrowths so obviously designed to effect attachment to roving eelworms without directly halting their locomotion. Once an adhesive outgrowth has been produced, all further extensive development appears restricted to intrusion of assimilative filaments into a animal host. Among aquatic predaceous fungi similar limitation of asexual spores to attack of animals after the usual manner of parasites, would seem present at least in *Sommerstorffia spinosa,* where according to Arnaudow's (2) original account the zoospores after rounding up a second time regularly extend a short germ tube or infection tube, and subsequently infect living rotifers through the mouth. As the empty cysts of the zoospores were reported to measure only up to 10 μ in diameter, production of germ hyphae robust enough for capture of rotifers would, of course, hardly be possible without considerable intake of nutrients. Dearth of protoplasmic content might be expected likewise to determine a parasitic manner of attack for the zoospores ascribed to *Zoophagus insidians* Somm., should these really belong to Sommerstorff's species or, for that matter, to any other aquatic rotifer-capturing phycomycete. With respect to their manner of attack it would presumably make little difference whether the zoospores came into being through the *Pythium*-like development attributed to *Z. insidians* by Arnaudow (**1**) and Valkanov (**17**), or through the somewhat chytridial development described by Gicklhorn (**16**).

Although the clamp-bearing Colorado fungus was examined in some quantity, with the possibility of encountering basidial development being always kept in mind, it has so far been found to reproduce only by conidia. It is therefore described as a species of *Nematoctonus;* the specific name proposed for it, compounded of 2 words meaning "to fasten" and "branch," respectively, being intended to signalize its predaceous character.

Nematoctonus haptocladus sp. nov.

Hyphae assumentes incoloratae, plus minusve ramosae, plerumque 1.8–3.0 μ crassae, rarius usque 4.5 μ latescentes, in modum Hymenomycetum septato-nodosae, intra vermiculum nematoideum viventum crescentes, post mortem animalis hyphas ex magna parte procumbentes aut ascendentes extra emittentes. Hyphae procumbentes septato-nodosae, plerumque 1.8–3.0 μ crassae, rarius usque 4.5 μ latescentes, ramos plerumque 20–75 μ longos expandentes qui prope apicem abrupte in aerum se flectunt, quoque ita columellam erectam vel ascendentem 2–8 μ altam porrigente; columella corpus bilobum medio constrictum 3.5–5.5 μ longum, 2–3 μ crassum ferente; corpore bilobo mox guttula glutinosa globosa vel ellipsoidea 4–6 μ longa 3.5–5.5 μ crassa circumdato, denique saepe ad vermiculum nematoideum inhaerente, animal capiente. Hyphae ascendentes incoloratae, parvulum ramosae, mediocriter septato-nodosae, saepe circa 500 μ longae, 1.5–2.5 μ crassae. Conidia incolorata, cylindricea vel elongato-ellipsoidea, recta vel leniter curvata, sursum rotundata, deorsum saepe parve attenuata, plerumque 11–18 μ longa, 3.3–4.5 μ crassa, erecta, in apice sterigmatis vulgo 2.5–4.5 μ longi, .8–1.2 μ crassi, raro ex hyphis procumbentibus crebrius ex hyphis ascendentibus oriunda; primo continua, protoplasmatis omnino repleta, post disjunctione saepe in parte inferiore evacuata et 1–2 septis instructa, denique ex apice hypham germinationis erectam 2–8 μ altam porrigentia quae corpus glutinosum fert.

Vermiculos nematoideos diversos praecipue *Panagrolaimum* capiens consumensque etiam eadem animalia soluta necans habitat in foliis plantarum (*Cucumeris sativi, Elaeagni angustifoliae,* specierum *Syringae, Populi, Tamaricis*) putrescentibus prope Greeley, Colorado.

Assimilative hyphae colorless, more or less branched, mostly 1.8 to 3.0 μ in diameter, here and there widening to 4.5 μ, bearing clamp-connections, developing within living nematodes, after death of invaded animal putting forth prostrate and ascending external hyphae. Prostrate hyphae mostly 1.8 to 3.0 μ in diameter, here and there widening to 4.5 μ, provided with clamp-connections, ramifying at rather wide angles, the outspread branches, mostly

20 to 75 μ long, bending abruptly upward into the air to project as erect or ascending stalks 2 to 8 μ high; each stalk bearing a transversely constricted bilobate body 3.5 to 5.5 μ long and 2 to 3 μ wide; the bilobate body soon becoming surrounded by a globose or ellipsoidal droplet of glutinous substance, 4 to 6 μ long and 3.5 to 5.5 μ wide, then often adhering to a nematode and capturing it. Ascending hyphae colorless, meagerly branched, provided moderately with clamp-connections, often about 500 μ long and 1.5 to 2.5 μ wide. Conidia colorless, cylindrical or elongate-ellipsoidal, straight or slightly curved, broadly rounded at the tip, often tapering slightly toward the base, measuring mostly 11 to 18 μ in length and 3.3 to 4.5 μ in greatest width, borne erect on sterigmata, commonly 2.5 to 4.5 μ long and .8 to 1.2 μ wide, that arise sparingly from prostrate hyphae and in closer arrangement from ascending hyphae; the spores at first continuous and filled with protoplasm throughout, but after disarticulation regularly becoming evacuated proximally and partitioned proximally by 1 or 2 septa in extending from the apex an erect or ascending germ hypha, mostly 2 to 8 μ long, whereon an adhesive body is borne terminally.

Capturing and consuming various nematodes (especially *Panagrolaimus* sp.) and also destroying these animals in free condition, it occurs in decaying plant (*Cucumis sativus, Elaeagnus angustifolia, Syringa* sp., *Populus* sp., *Tamarix* sp.) leaves near Greeley, Colorado.

As was set forth in a recent paper (**15**: p. 3) elaboration of adhesive material in easily visible masses previous to encounter with prey has not been noted among the predaceous Zoopagaceae, and among the clampless predaceous hyphomycetes has been noted only in *Arthrobotrys entomopaga* Drechsl., a species primarily adapted for capture of springtails, though occasionally also capturing nematodes (**14**). The statement then made to the effect that no fungus specially adapted for capture of eelworms secretes adhesive material in visible quantities beforehand (**15**: p. 3, lines 9–13), now requires modification limiting its application to the 2 main predaceous groups. Indeed, the anticipative secretory behavior wherein *Nematoctonus haptocladus* differs so markedly from the many nematode-capturing fungi taxonomically alien to it, is present likewise in the congeneric predaceous Hawaiian species which "utilizes erect hyphal processes bearing droplets of adhesive mucus at the tip" (**12**: p. 780, lines 33–35).

LITERATURE CITED

1. **Arnaudow, N.** Zur Morphologie und Biologie von *Zoophagus insidians* Sommerstorff. Jahrb. Univ. Sofia **15–16**: 1–32. 1921.
2. ——. Ein neuer Rädertiere (Rotatoria) fangender Pilz (*Sommerstorffia spinosa* nov. gen., nov. sp.). Flora **116**: 109–113. 1923.
3. **Drechsler, C.** *Pedilospora dactylopaga* n. sp., a fungus capturing and consuming testaceous rhizopods. Jour. Washington Acad. Sci. **24**: 395–402. 1934.
4. ——. Some conidial phycomycetes destructive to terricolous *Amoebae*. Mycologia **27**: 6–40. 1935.
5. ——. Some non-catenulate conidial phycomycetes preying on terricolous. *Amoebae*. Mycologia **27**: 176–205. 1935.
6. ——. New conidial phycomycetes destructive to terricolous *Amoebae*. Mycologia **28**: 363–389. 1936.
7. ——. A *Fusarium*-like species of *Dactylella* capturing and consuming testaceous rhizopods. Jour. Washington Acad. Sci. **26**: 397–404. 1936.
8. ——. Some hyphomycetes that prey on free-living terricolous nematodes. Mycologia **29**: 447–552. 1937.
9. ——. New Zoopagaceae capturing and consuming soil *Amoebae*. Mycologia **30**: 137–157. 1938.
10. ——. A few new Zoöpagaceae destructive to large soil rhizopods. Mycologia **31**: 128–153. 1939.
11. ——. Three new hyphomycetes preying on free-living terricolous nematodes. Mycologia **32**: 448–470. 1940.
12. ——. Some hyphomycetes parasitic on free-living terricolous nemotodes. Phytopathology **31**: 773–802. 1941.
13. ——. Two new basidiomycetous fungi parasitic on nematodes. Jour. Washington Acad. Sci. **33**: 183–189. 1943.
14. ——. A species of *Arthrobotrys* that captures springtails. Mycologia **36**: 382–399. 1944.
15. ——. Several additional phycomycetes subsisting on nematodes and *Amoebae*. Mycologia **37**: 1–31. 1945.
16. **Gicklhorn, J.** Studien an *Zoophagus insidians* Som., einem Tiere fangenden Pilz. Glasn. Soc. Sci. Nat. Croate **34**: 198–229. 1922.
17. **Valkanov, A.** Nachtrag zu meiner Arbeit über rotatorienbefallende Pilze. Arch. Protistenk. **78**: 485–496. 1932.
18. **Woronin, M.** *Sphaeria Lemaneae, Sordaria coprophila, fimiseda, Arthrobotrys oligospora*. *In* Bary, A. de, & M. Woronin, Beitr. Morph. Physiol. Pilze. III. Abhandl. Senckenbergische naturf. Ges. **7**: 325–360. 1870.

EXPLANATION OF FIGURES

FIG. 1. *Nematoctonus haptocladus;* adhesive bodies, about 34 in number, borne aloft on the upcurved tips of prostrate branches coming from the assimilative mycelium in a nematode, *A* (*Panagrolaimus* sp.), that has become nearly invisible owing to expropriation of contents. A second nematode, *B*, of the same species is shown attached to two of the adhesive bodies. Unretouched photomicrograph, × 300.

FIG. 2. *Nematoctonus haptocladus;* drawn to a uniform magnification with the aid of a camera lucida, from a moist preparation covered with a cover glass; × 1000 throughout. *A*, Branching hyphae extended under the surface of an agar culture from a specimen of *Panagrolaimus* sp. that had succumbed in a submerged position. *B*, Ramifying prostrate hyphal system with 5 predaceous branches bearing aloft the adhesive bodies *a–e*; the ramifying system having developed terminally on a hypha that came from a submerged eelworm to the surface of the culture. *C*, Terminal portion of a prostrate hypha with a single predaceous branch bearing aloft the adhesive body *a*. *D*, Portion of prostrate mycelium with a predaceous branch holding aloft the adhesive body *a*; one of the 3 clamp-connections present is shown empty of contents and only faintly visible. *E*, *F*, Predaceous branches, each bearing aloft an adhesive body, *a*; through evacuation of protoplasm, the living part of each branch has been reduced to a structure not differing much in shape, size, and function from a conidium that has put forth an adhesive germ hypha. *G*, Predaceous branch arising directly from an assimilative hypha, and terminating in the adhesive body *a*. *H*, Predaceous branch that has given rise successively to 3 adhesive bodies, *a*, *b*, *c*. *I*, Prostrate ramifying filament with 4 predaceous branches bearing aloft the 4 adhesive bodies *a–d*; a young conidium, *e*, is found arising from a clamp-connection, and 2 fully formed conidia, *f*, *g*, are shown attached, the latter arising from a clamp. *J*, Prostrate branch, in large part evacuated, terminating in an adhesive body, *a*, and bearing a conidium, *b*, on a sterigma arising from a clamp. *K*, Conidium borne on an empty sterigma arising from a clamp. *L*, Newly detached conidia, *a–w*, showing variations in size and shape. *M–O*, Disarticulated conidia, each of which has become evacuated proximally in putting forth a germ hypha with an adhesive body. *P*, *Q*, Detached conidia of similar development, but in which 2 septa were laid down during evacuation of the proximal part.

FIG. 3. *Nematoctonus haptocladus;* drawn to a uniform magnification with the aid of a camera lucida, from a moist preparation covered with a cover glass; × 1000 throughout. *A*, Portion of body of a nematode, referable to *Panagrolaimus* sp., that is occupied by assimilative mycelium; one of the assimilative filaments having put forth a prostrate ramifying system with 6 predaceous branches, whereon are borne 7 adhesive bodies, *a–g*. *B*, Prostrate ramifying system with 2 predaceous branches that after producing the adhesive bodies, *a* and *b*, respectively, have continued growth. *C*, Portion of prostrate ramifying system with a predaceous branch terminating in the adhesive body *a*. *D*, Somewhat extensive prostrate ramifying system, whose predaceous branches bear aloft the 10 adhesive bodies *a–j*; a conidium, *k*, is shown attached to a sterigma arising from a clamp-connection. *E*, Portion

of prostrate hyphal system showing 2 conidia, *a* and *b*, borne on empty sterigmata. *F*, Newly disarticulated conidia, *a–r*, showing variations in size and shape.

FIG. 4. *Nematoctonus haptocladus;* drawn to a uniform magnification with the aid of a camera lucida, from a moist preparation covered with a cover glass; × 1000 throughout. *A*, Posterior portion of a dead specimen of *Panagrolaimus* sp. occupied by assimilative mycelium of which terminal parts have become evacuated in supplying material for production of external hyphae; one of the 2 external hyphae shown has produced 2 adhesive bodies, *a* and *b*. *B*, Branched ascending hypha bearing 3 conidia, *a–c;* owing to lack of space the hypha is shown in parts whose proper continuity is indicated by means of the alphabetical sequence *n–s*; *n–q* being a proximal element that bears distally the branches *q–o* and *q–s*. *C*, Portion of specimen of *Panagrolaimus* sp. occupied by assimilative filaments, one of which has put forth an ascending branched hypha whereon are borne 6 mature conidia, *a–f*, and a very young, growing conidium, *g*; from lack of space the hypha is shown in parts whose proper continuity is indicated by the letters *x*, *y*, *z*. *D*, Portion of ascending filament showing a conidium in half-grown state. *E*, Portion of ascending filament showing a conidium almost full-grown but still continuous with the sterigma; the latter arising from a clamp-connection.

FIG. 5. *Nematoctonus haptocladus;* external growth made in 48 hours from the same individual eelworm shown in figure 1, *B*; approximately 30 predaceous branches, each with an adhesive body, being recognizable; a single conidium, also present, not being recognizable; unretouched photomicrograph, × 300. After the photograph shown in figure 1 had been taken the culture was flooded with water for a few minutes, completely obliterating all the prostrate hyphae and adhesive bodies derived from nematode *A* of that figure; so that all the prostrate hyphae and adhesive bodies visible in the later photograph were necessarily produced during the intervening 2 days.

FIG. 6. *Nematoctonus haptocladus;* portion of colony-like group of nematodes mostly referable to *Panagrolaimus* sp.; showing, in addition to scattered predaceous branches, 2 conidia, *a* and *b*, arising from prostrate filaments; unretouched photomicrograph, × 400.

FIG. 7. *Nematoctonus haptocladus;* drawn to a uniform magnification with the aid of a camera lucida, from a moist preparation covered with a cover glass; × 500 throughout. *A*, Prostrate ramifying hyphal system with 4 adhesive branches, *a–d*, on one of which, *a*, a specimen of *Panagrolaimus* sp. has been captured; slight movement of the animal from time to time showed it was still alive, though invaded by an assimilative hypha over 10 μ long. *B*, Small specimen of *Paraphelenchus pseudoparietinus* 48 hours after being captured by adhesion to 2 predaceous branches, *a* and *b*; both predaceous branches are still attached to the parent hypha, though their mycelial connection has become indiscernible owing to evacuation of intercalary hyphal parts. *C*, Specimen of *Panagrolaimus* sp. still capable of slight movement, but manifestly close to death, owing to hyphal invasion from 6 adhering predaceous branches, *a–f*; all the predaceous branches had been torn from their attachments to mycelium, and the animal was succumbing in a free condition.