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A NEMATODE-CAPTURING FUNGUS WITH ANASTOMOSING CLAMP-BEARING HYPHAE

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(WITH 4 FIGURES)

Under the genus *Nematoctonus* I have described earlier five nematode-destroying fungi whose hyphae are liberally beset with clamp-connections of the kind long known as being characteristic of some groups in the Basidiomycetes. Four of these fungi, namely *N. tylosporus* (**1**), *N. leiosporus* (**1**), *N. pachysporus* (**3**), and *N. leptosporus* (**3**), attack in a rather commonplace parasitic manner by sending a germ tube into the animal host from an externally adhering conidium. Necessarily the conidium in these parasites, and, indeed, in the generality of fungous parasites subsisting on free-living terricolous nematodes, must adhere very firmly, for otherwise it would almost certainly be dislodged as the animal continues to move briskly through materials of close texture during the period required for penetration of the integument and slow transfer of spore contents into the invading hyphal tip. In *N. tylosporus* and *N. leptosporus* the conidium secretes a minute mass of glutinous material at its apex while it is still supported on its sterigma. However in these two species, as also in *N. leiosporus* and *N. pachysporus,* the adhesive organ most usually found operating effectively is formed after the spore has become detached, the fallen conidium then regularly putting forth a short, erect or ascending outgrowth with a glandular tip, or terminal glandular cell, that secretes a sizable globule of adhesive material. In *N. haptocladus* (**4**), the fifth member of the genus to be named and described, similar adhesive outgrowths or adhesive organs are formed

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not only on fallen conidia, but also on the vegetative mycelium, usually being produced distally on prostrate hyphal branches as upcurving terminations. Rather often, especially when the proximal filamentous connection has been weakened through withdrawal of protoplasmic contents, the specialized hyphal termination is torn loose by a vigorous adhering eelworm, and then is carried away by the doomed animal much like a fallen conidium with glutinous outgrowth. Yet often, again, the hyphal connection withstands the struggles of the adhering eelworm, which consequently is held captive while undergoing invasion and, after death, expropriation of its fleshy substance. In view of the predacious manner of attack thus revealed, *N. haptocladus* offers an engaging parallelism with the few nematode-capturing phycomycetous forms found among the Zoopagaceae, as well as with the considerably more numerous nematode-capturing species that have been made known in the series of clampless predacious hyphomycetes.

Another species of *Nematoctonus* that attacks free-living terricolous eelworms both parasitically and predatorily came to light more recently in several maizemeal-agar cultures, which, after being overgrown with uncontaminated mycelium of *Pythium irregulare* Buism., had been further planted with pinches of decaying chess (*Bromus secalinus* L.) detritus taken from a handful of this material kindly gathered by Dr. W. J. Zaumeyer near Hermiston, Oregon, on August 20, 1947. The new *Nematoctonus* usually made its appearance ten to fifteen days after the addition of the decaying residues and in all instances obviously subsisted altogether on the many eelworms that soon had infested the cultures. Nearly all of the eelworms present belonged either to a somewhat robust species kindly identified by Dr. G. Steiner as *Panagrolaimus subelongatus* Cobb, or to a much more slender species determined as *Ditylenchus* sp. The two types of nematodes were utilized by the fungus without evident preference, though owing to its much greater abundance *P. subelongatus* was destroyed in larger numbers.

Unlike *Nematoctonus haptocladus,* which often is first observed developing in agar plate cultures at some distance from the decaying materials whence it originates, the Oregon fungus regularly begins its visible development in tracts bordering the planted detritus, and then spreads progressively into more remote areas.

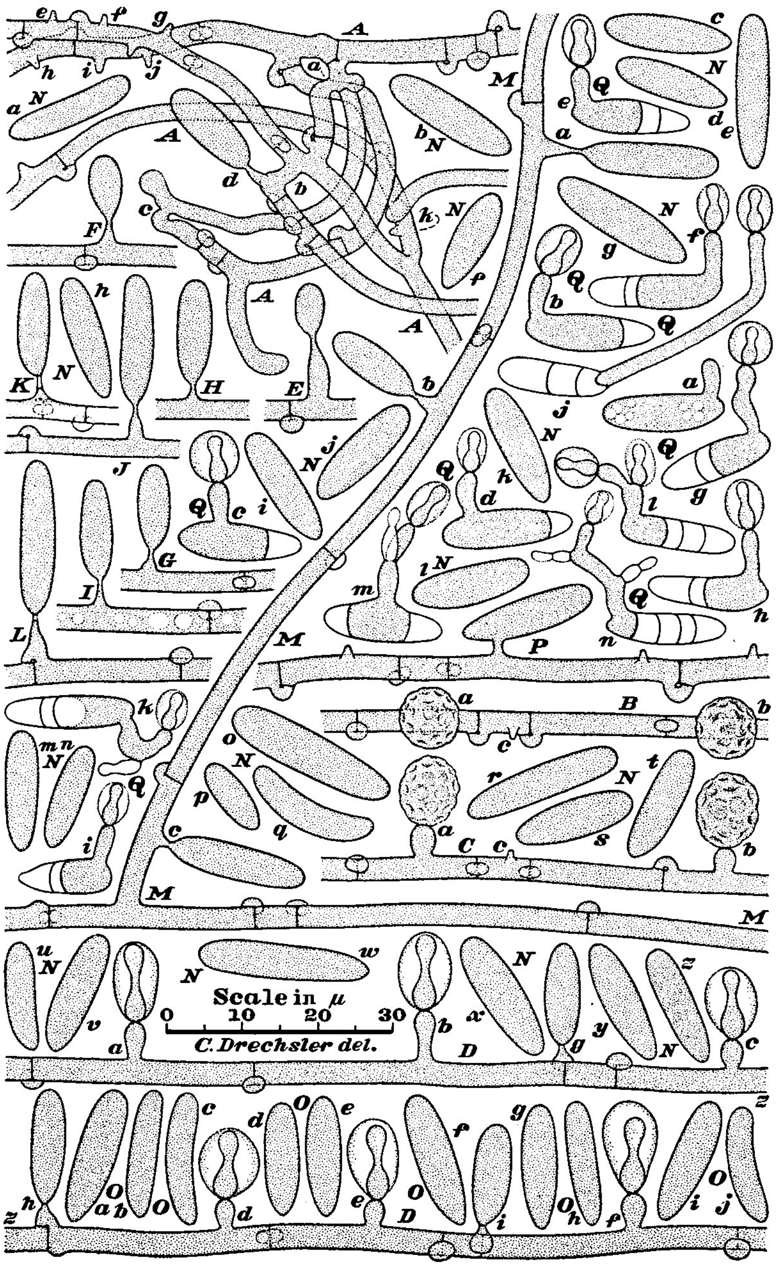

FIG. 1. *Nematoctonus concurrens.*

Nevertheless its ramifying mycelium (FIG. 1, *A*) greatly resembles that of *N. haptocladus* in general aspect, the constituent hyphae (FIG. 2, *A, a, b; B, a, b.* FIG. 3, *A; J, a, b; K, a–c.* FIG. 4, *A; B, a–c*) being filled while in their youthful condition with protoplasm of nearly homogeneous consistency. The longer filaments are little given to abrupt changes either in width or in direction. All mycelial elements except the shortest branches are studded with clamp-connections. For the most part the clamps are spaced at distances of 20 to 80 μ, but here and there they are wont to occur in more crowded arrangement with some intervals not exceeding 2 μ. Apparently no cross-walls other than those associated with clamp-connections are formed to serve as ordinary partitions between adjacent living undifferentiated vegetative hyphal segments. Hyphal fusions (FIG. 1, *A, a–c.* FIG. 2, *A, c, d; B, c, d.* FIG. 3, *A, a; I, a; J, c; K, d, e.* FIG. 4, *A, a–c; B, d*), which have not been observed either in *N. haptocladus* or in any of the four congeneric parasites, occur here in sufficient numbers to be immediately noticed, though scarcely with the frequency of anastomoses in the clampless nematode-capturing hyphomycetes.

The mycelium of the Oregon fungus, like that of *Nematoctonus haptocladus,* is furnished with predacious organs consisting individually of a globose adhesive body borne aloft 2 to 7 μ above the substratum on a short stalk rising vertically from a prostrate hypha. When examined microscopically from above, in their undisturbed posture and without any addition of water, they appear as projecting knobs with a pitted or irregularly indented surface (FIG. 1, *B, a, b;* FIG. 2, *A, e–o;* FIG. 4, *A, d*); their internal make-up and underlying hyphal connections being then only indistinctly visible or sometimes even wholly obscured. Viewed from the side in a dry mount the hyphal connections stand out clearly, but the internal make-up of the adhesive body still remains concealed (FIG. 1, *C, a, b*). The composition of the predacious organ is seen better in material that has been slightly moistened and with gentle pressure covered with a cover glass; the adhesive body in material thus mounted presenting a smoothly rounded profile, and revealing within it an elongated cell conspicuously narrowed in the equatorial region somewhat after the manner of an hour-glass (FIG. 1, *D, a–f.* FIG. 2, *B, e–o; C, a, b; D, a, b; E, a–c; F, a–c; G, a–f; H, a; I, a–c; J, a;*

K, a; L, a–c; M, a. FIG. 3, *A, b; B, a, b; C, a, b; D, a, b; E, a; F, a; G, a, b; H, a, b; I, b, c; J, d–f; K, f–h.* FIG. 4, *B, e–h; C, a*). A very distinct line of demarcation always separates the distally rounded protuberant stalk from the proximally rounded elongated cell. Although an abrupt junction of two rounded lobes might in itself be expected to offer much the appearance of a septum even where no septum exists, close examination of many predacious organs has inclined me strongly to the belief that a delimiting cross-wall is really present here—this cross-wall, of course, being an ordinary one, not associated with a clamp-connection.

Near its attachment to the stalk for a distance upward of about 1.5 μ, the peripheral wall of the elongated cell seems slightly thickened and has a somewhat dark indurated appearance. Beyond this more substantial collar-like part the envelope is uniformly thin, though yet of sufficient thickness to remain clearly visible throughout; the fungus thereby differing from *Nematoctonus haptocladus*, in which the membrane of the corresponding cell is so thin at the rounded distal end as to be virtually indiscernible. It may be presumed that whereas in *Nematoctonus haptocladus* the glutinous substance surrounding the cell is probably given out mainly from the very thin-walled apical region, exudation in the Oregon fungus may take place about equally from all portions of the membranous envelope above the indurated collar-like part. The glandular cell of the Oregon fungus is fully twice as long as that of *N. haptocladus*, and, in general, about half again as wide. Its narrower shape is accentuated in some degree by its more gradual and more extended median constriction. Its greater volume and dimensions are reflected in correspondingly greater volume and dimensions of the globule of adhesive material secreted by it; and its more elongate form seems associated with a noticeably greater tendency toward an elongated shape in the globule.

Some protuberant stalks after producing a glandular cell in the usual way will grow out laterally or obliquely at the tip and give rise on a short prolongation to a second glandular cell (FIG. 3, *J, g*). The process may be repeated again with the resulting development of a third glandular cell (FIG. 2, *H, b*). Such successive development, like the similar development noted earlier in *Nematoctonus haptocladus* as well as in *N. pachysporus,* is frequently preceded by

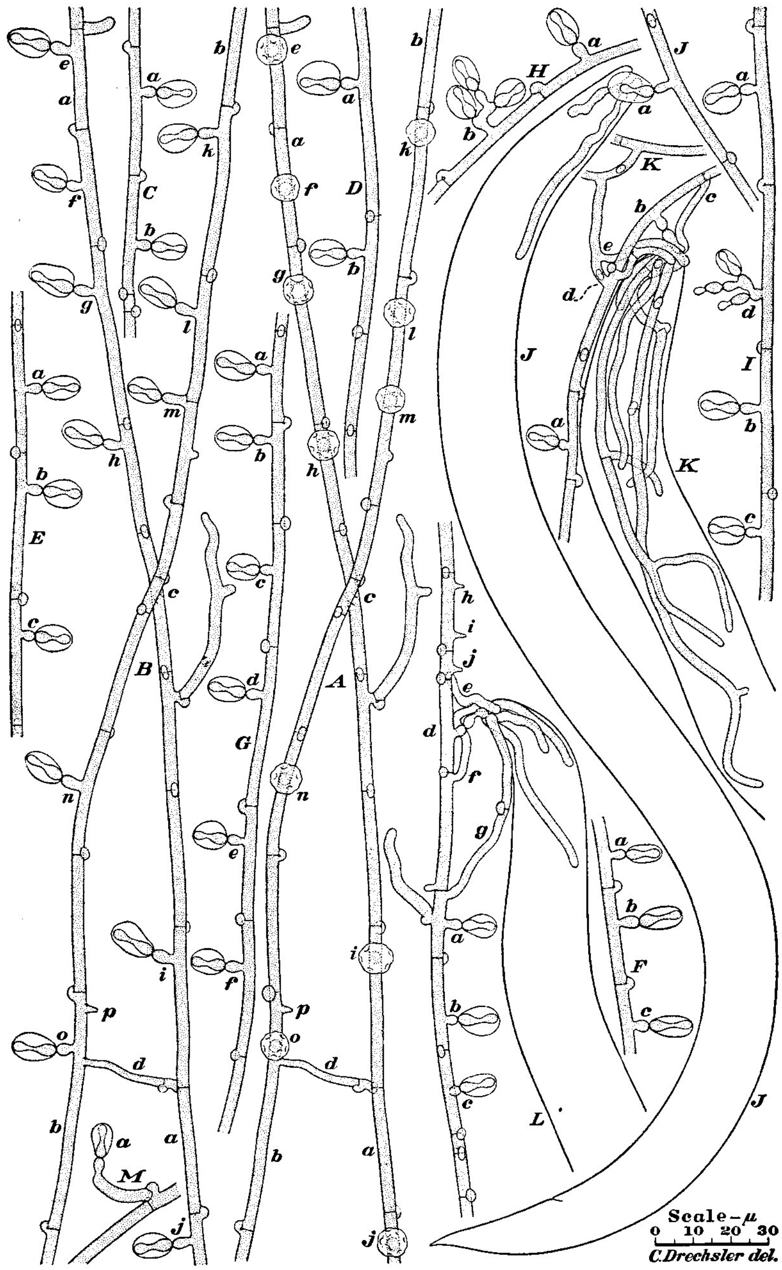

FIG. 2. *Nematoctonus concurrens.*

degeneration in the older glandular cells—this degeneration becoming manifest usually in withdrawal of protoplasmic contents from the distal lobe (FIG. 3, *J, h*), together sometimes with disappearance of the enveloping mass of adhesive material (FIG. 2, *I, d*). In instances where the distal lobe is found empty while the proximal lobe is still filled with protoplasm, the retaining wall present in the constriction consists of an ordinary partition not associated with a clamp-connection.

As the very short erect stalks supporting the glandular cells always arise from prostrate hyphae, never being borne on submerged or ascending mycelial filaments, the Oregon fungus, much like *Nematoctonus pachysporus,* is capable of capturing only nematodes moving on the surface of a culture. In its usually forward movement, the animal commonly strikes the raised adhesive globule with the anterior portion of its body, often, indeed, being found held directly by its head (FIG. 2, *J, a.* FIG. 3, *I, b, c; J, i; K, i.* FIG. 4, *B, i; D–G: a; H, a*); though attachment to adhesive organs also takes place farther backward (FIG. 4, *B, j, k*). Adhesion to a single predacious organ suffices, as a rule, for the capture of robust specimens of either *Panagrolaimus subelongatus* or *Ditylenchus* sp. After the struggles of the captive have diminished in violence, presumably from exhaustion, the glandular cell puts forth a narrow process which perforates the animal's integument, then immediately widens out and begins growing through the fleshy interior as an assimilative hypha (FIG. 3, *H, c;* FIG. 4, *D, a*). In many instances the assimilative hypha soon gives off a branch close to its origin (FIG. 2, *J, a;* FIG. 4, *H, a*), but often, again, it may attain a length of approximately 100 μ while remaining in a simple condition (FIG. 3, *I, b, c; J, i.* FIG. 4, *E–G: a*). Branching in assimilative hyphae frequently is accompanied, or perhaps rather closely followed, by the formation of clamp-connections (FIG. 2, *K, b;* FIG. 3, *K, i*).

Although a single predacious organ usually is altogether effective in holding fast a moderately robust eelworm, the struggling animal often brushes against other predacious organs, and thus becomes affixed in two (FIG. 3, *H, b, c; I, b, c*), three (FIG. 4, *B, i–k*), or more places. Since here, as in nematode-capturing fungi generally, each predacious organ operates rather independently of others, captives often incur multiple invasion by reason only of their multiple affixture (FIG. 3, *I, b, c*). In the Oregon fungus multiple infection further comes about very frequently through the curious development of accessory infective branches (FIG. 2, *K, c–e; L, e–g.* FIG. 3, *I, d; J, j–l; K, j–m.* FIG. 4, *B, l, m; C, c; D–G: b, c; H, c*). These branches arise usually at distances of 10 to 50 μ from a predacious organ that has newly captured a nematode. Very often they are put forth from the same hypha that bears the predacious organ (FIG. 2, *K, c, d; L, e–g.* FIG. 3, *J, l.* FIG. 4, *B, l; C, c; D, b, c*), but with about equal frequency they originate from neighboring hyphae, which in some instances have an observable connection with the predacious organ either from the ramification of the mycelium (FIG. 2, *K, e*) or from anastomosis of mycelial filaments (FIG. 3, *K, j–m*), but in other instances lack such connection (FIG. 3, *J, j, k;* FIG. 4, *B, m*). Often the growth of the accessory branches is from the beginning rather accurately directed toward the position where the struggling animal is held fast by the fungus (FIG. 3, *J, l;* FIG. 4, *D, b*), though often, again, their courses seem rather haphazard or even circuitous (FIG. 4, *B, j; D, c*). Despite some aberration they converge unmistakably as they elongate (FIG. 4, *E, b, c*), and after about an hour or perhaps two hours of growth they reach their goal, each bringing its tip against the animal's integument in immediate proximity to the adhering predacious organ (FIG. 4, *B, l, m; F, b, c*). On penetrating the integument the individual branch intrudes a prolongation which then extends itself autonomously through the fleshy interior as an assimilative hypha (FIG. 4, *C, c; F, b; G, b*) in fellowship with the assimilative hypha arising from the predacious organ.

Although in most cases the number of accessory infective branches associated with a predacious organ ranges from one to five, development of such branches in numbers from six to ten occurs rather often, and instances of development in numbers from eleven to fifteen come under observation at least occasionally. The convergence of multiple branches makes for an appearance strongly reminiscent of sexual reproductive apparatus in species of oomycetes where the oogonium is fertilized by plural antheridia. No development of accessory infective branches was recorded in my account of *Nematoctonus haptocladus* or in the descriptions of the four congeneric species, though until further observations are made the possibility is not to be dismissed that among these closely related forms similar development might occur on so small a scale as readily to escape detection. The accessory infective branches produced by the Oregon fungus offer some little resemblance to the supplementary connections formed in some clampless nematode-capturing hyphomycete species—my *Dactylella doedycoides* and my *D. heterospora* (2: 341–342) may be cited as examples—where the stalk supporting the predacious organ lacks sturdiness, owing mainly to its length, and consequently often suffers injury from the struggles of the prey. These supplementary connections, however, are commonly produced only singly and, as a rule, are intercalated between two fungus cells external to the animal. Unlike the accessory infective branches, they generally neither penetrate the animal's integument anew nor intrude an additional assimilative hyphal system; their function evidently being only to supply better communication between the external mycelium and the assimilative hyphae intruded by the predacious organ.

Since in most instances a captured specimen of *Panagrolaimus subelongatus* adheres to the predacious organ by its head, invasion of its body proceeds commonly from the head (FIG. 2, *J–L;* FIG. 3, *I–K;* FIG. 4, *D–G, H*) toward the tail. The angular relationships of the ramified mycelium in the posterior portion of a dead captive (FIG. 3, *L;* FIG. 4, *I, J*) suggest strongly that hyphal fusions must occur rather frequently among assimilative filaments, even though it is true that an appearance of hyphal fusion is often simulated here through the circumstance that many branches are extended in a direction opposite to the direction of growth of the parent filament. As a rule the protoplasm elaborated by the fungus from the contents of a relatively small eelworm is transferred to the external mycelium entirely through the adhesive organ and accessory infective branches. This is often true also where larger animals are concerned, if many accessory infective branches are present. However, in many instances where the eelworm is of large size and only a few accessory infective branches are present, a portion of the elaborated protoplasm is used in extending several hyphae—often about five or six—out from the posterior (FIG. 3, *L, a, b;* FIG. 4, *J*) and median portions of the animal. Obviously these erumpent hyphae belong with the

FIG. 3. *Nematoctonus concurrens.*

external mycelium, and therefore, after some elongation and branching, may put forth predacious organs and conidia.

In contrast to *Nematoctonus haptocladus,* which produces conidia only rather sparingly, the Oregon fungus usually shows abundant sporulation. Its prostrate mycelium gives rise to conidia haphazardly (FIG. 1, *A, d–k*), the longer procumbent hyphae often bearing them (FIG. 1, *D, g–i;* FIG. 2, *A, p; L, h–j*) interspersed among predacious organs. They originate as terminal swellings on tapering sterigmata (FIG. 1, *E, F*) and increase in size with continued accession of protoplasm from below (FIG. 1, *A, d; G–J*) until they become delimited from the slender supporting tip by a septum (FIG. 1, *K, L;* FIG. 4, *K*). On the ascending hyphae, which regularly are devoid of predacious organs, conidia are produced in the beginning at rather wide intervals (FIG. 1, *M, a–c;* FIG. 3, *M, a, b*), but seemingly more conidia are later put forth from intercalary positions, to provide eventually a bristling display (FIG. 4, *L, M*). Prostrate (FIG. 3, *K, b, c*) as well as aerial (FIG. 4, *N–P*) hyphae on which conidia have been produced at close intervals show in their denuded condition a conspicuously close arrangement also of clamp-connections.

Although slightly plumper and appreciably larger, the mature detached conidia of the Oregon fungus (FIG. 1, *N, a–z; O, a–j.* FIG. 3, *N–P: a–z.* FIG. 4, *Q, a–z*) most nearly resemble, among congeneric forms, those of *Nematoctonus haptocladus* with respect to size and shape. In my cultures they germinated less freely than the conidia of *N. haptocladus,* but their germinative development followed essentially the same course. The fallen spore would first send up a short erect outgrowth from a position usually near one of its ends, as simultaneously several clustered vacuoles came into view toward its other end (FIG. 1, *Q, a*). On the rounded tip of the spur-like outgrowth a glandular cell, noticeably smaller but otherwise similar to glandular cells of mycelial origin, was then produced while the farther end of the spore was emptied of protoplasmic contents with concomitant formation of one (FIG. 1, *Q, b–d*) or two (FIG. 1, *Q, e–i*) retaining walls. In one observed instance (FIG. 1, *Q, j*) the spore envelope was almost wholly emptied from production of a single glandular cell at the tip of a germinative outgrowth over 30 μ long—this being fully six times the usual length of the erect support. Ordinarily, however, about one-half to three-fifths of the protoplasm was left over, so that the conidium through further withdrawal of contents (FIG. 1, *Q, k*) and deposition frequently of a third retaining wall (FIG. 1, *Q, l*) was capable of giving rise to a second glandular cell on a short prolongation of the germinative outgrowth. Occasionally a conidium that had produced a second glandular cell on an outgrowth arising from a median position showed an empty segment at each end (FIG. 1, *Q, m*). Following the degeneration of the first two glandular cells produced by them some conidia extended their outgrowth again to form a third glandular cell (FIG. 1, *Q, n*), thereby emptying a fourth segment though yet retaining about one-fifth of their original protoplasmic contents—enough, presumably, to have made possible the formation later of a fourth glandular cell.

Each glandular cell produced on a germinative outgrowth soon secretes an enveloping globule of adhesive material which serves, whenever opportunity offers, to attach the conidium to some roving eelworm (FIG. 4, *H, b*). An animal that has been thus encumbered may continue to move about until it is disabled from progressive invasion by an assimilative hypha intruded by the adhering spore, but rather often before such disablement supervenes it encounters a predacious organ and is held fast (FIG. 4, *H, a*). In the latter event the glandular cell produced by the conidium may evoke development of accessory infective branches (FIG. 4, *H, c*) after the same manner as glandular cells of mycelial origin. As the very numerous conidia in my cultures gave rise to adhesive outgrowths only sparingly, the Oregon fungus displayed little of the strong capabilities for parasitic attack it assuredly should unfold under conditions favorable for germination of its spores. Owing to the enduringly sturdy attachment of its predacious organs, including those borne on lateral branches (FIG. 2, *M, a*; FIG. 3, *F, a*; *G, a, b*), it affords little scope for the simulation of parasitic attack usual in *Nematoctonus haptocladus,* where the attachment of predacious organs often becomes weakened early through evacuation of the proximal segments of the branches on which they are borne.

Occasionally a fallen conidium is found united to a neighboring mycelial filament by means of a short hyphal connection (FIG. 1, *P*). Manifestly such a fusion is of the same character as the hyphal

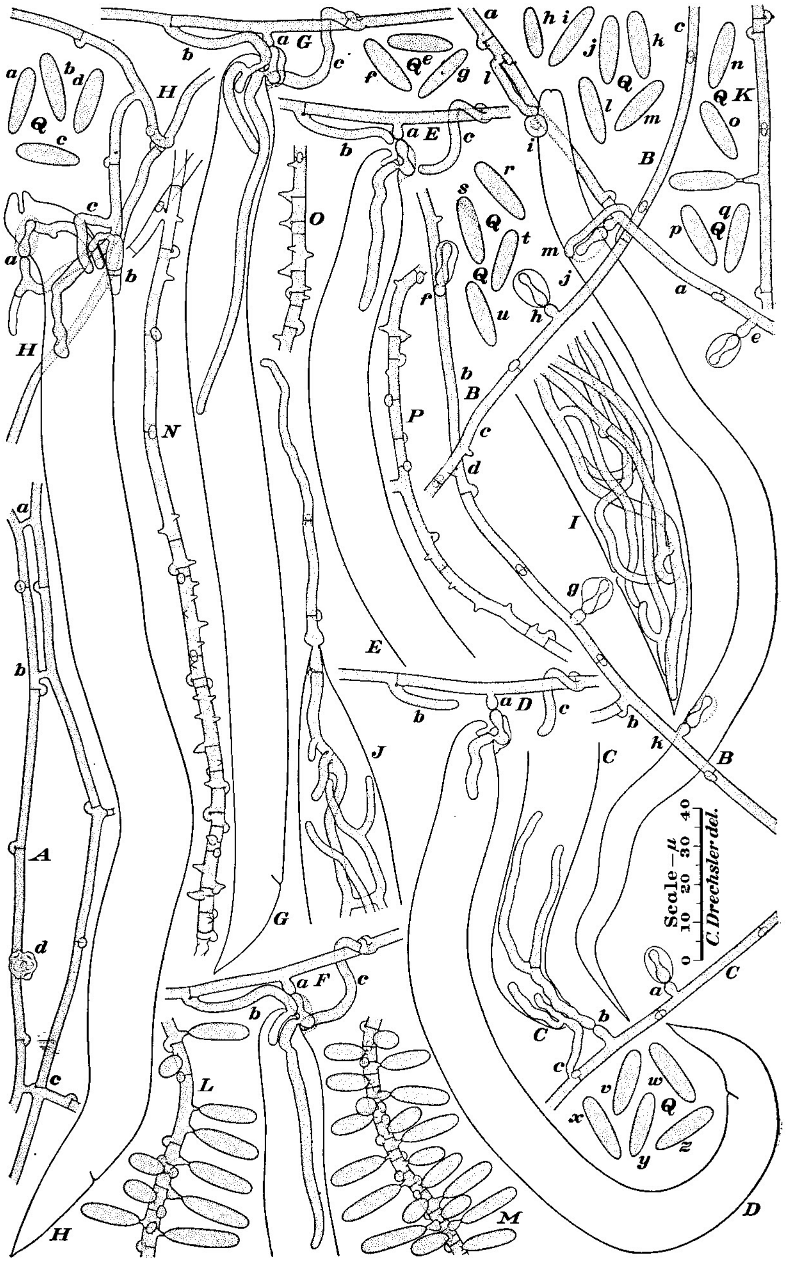

FIG. 4. *Nematoctonus concurrens.*

anastomoses so frequent in the fungus, and like these offers parallelism with the clampless nematode-capturing hyphomycetes. Since hyphal fusions serve to join numerous small mycelia into more extensive three-dimensional tracts, and in some basidiomycetes bring about nuclear relationships necessary for sexual development, the Oregon fungus would seem, perhaps somewhat more likely than the several congeneric forms previously described, to yield a basidial stage visible to the naked eye. In my cultures, however, no basidial stage ever came to light, nor was any reproductive apparatus ever found produced by the fungus apart from the conidial apparatus herein discussed. The fungus is therefore described in the genus *Nematoctonus,* and under a specific epithet having reference to the convergence of its accessory infective branches.

Nematoctonus concurrens sp. nov.

Mycelium tenellum, oculo nudo parum visibile, aliquid araneosum. Hyphae procumbentes incoloratae, filiformes, ramosae, in modum Hymenomycetum septato-nodosae, saepe inter se conjunctae, 2–3.5 μ crassae, cellulas glutinosas in apice columellarum atque conidia in apice sterigmatum gignentes; his columellis erectis, plerumque 3–7 μ altis, basi circa 2 μ crassis, sursum 2.4–3.7 μ crassis, apice rotundis; cellulis glutinosis harum 6–12 μ (saepius circa 10 μ) longis, 2.5–4 μ crassis, medio gradatim sed valde constrictis itaque ibi modo 0.8–1.5 μ crassis, primo nudis sed mox pila glutinis globosa vel ellipsoidea 6–12.5 μ longa, 4–8.5 μ crassa circumdatis, denique saepe ad vermiculum nematoideum inhaerentibus, itaque animal capientibus, cuticulam ejus perforantibus, quandoque tantummodo ipsis quandoque cum 1–15 ramulis adjunctis 10–50 μ longis hyphas assumentes incoloratas ramosas septato-nodosas intrudentibus quae carnem exhauriunt et interdum ramos mycelii extra emittunt. Hyphae ascendentes incoloratae, parce ramosae, septato-nodosae, 2–3.5 μ crassae, conidia in apice sterigmatum ferentes; sterigmatibus interdum ex nodis oriundis, 1.8–7 μ longis, basi 1.2–2.5 μ latis, sursum attenuatis, apice 0.6–0.8 μ latis. Conidia incolorata, cylindracea vel elongato-ellipsoidea, recta vel leniter curvata, sursum late rotundata deorsum similia vel leviter attenuata, plerumque 10–23 μ longa, 3.6–5.6 μ crassa, primo continua et protoplasmatis omnino repleta, post disjunctione ex apice columellae germinationis cellulam glutinosam ferentia, deinde quandoque identidem prope apicem columellae recrescentia 1 vel 2 alias cellulas glutinosas gignentia, denique in magna parte vel omnino inania et 1–4 septis intus divisa; cellulis glutinosis germinationis 4.5–6.5 μ longis, 2–2.5 μ crassis, medio constrictis, pila glutinis globosa vel ellipsoidea 4–7 μ longa 3.5–6.5 μ crassa mox vestitis.

Panagrolaimum subelongatum et *Ditylenchum* sp. capiens consumensque habitat in foliis caulibusque Bromi secalini putrescentibus prope Hermiston, Oregon.

Mycelium delicate, arachnoid, faintly visible to the naked eye. Prostrate hyphae colorless, filamentous, branched, 2 to 3.5 μ wide, studded with clamp-connections and often joined to one another by anastomosing connections, at variable intervals giving rise on protuberant outgrowths to glandular cells and producing conidia on the tips of sterigmata; the protuberant outgrowths regularly erect, mostly 3 to 7 μ high, about 2 μ wide at the base and 2.4 to 3.7 μ wide toward the rounded tip; the glandular cells here 6 to 12 μ (usually about 10 μ) long, 2.5 to 4 μ wide, gradually but strongly constricted at the middle and thus measuring only 0.8 to 1.5 μ in that region, at first naked but later always surrounded by a globose or ellipsoidal mass of glutinous material 6 to 12.5 μ long and 4 to 8.5 μ wide, therewith often adhering to a passing nematode, thus capturing the animal, and then, after perforating its cuticle, giving rise internally, sometimes alone and sometimes in association with 1 to 15 convergent accessory infective branches usually 10 to 50 μ long, to colorless, branched, clamp-bearing assimilative hyphae 2 to 3.5 μ wide, which permeate the fleshy body lengthwise, appropriating its substance, and in some instances eventually pushing branches out through the cuticle to elongate externally. Ascending hyphae studded with clamp connections, colorless, sparingly branched, 2 to 3.5 μ wide, bearing conidia on conical sterigmata usually 1.8 to 7 μ long, 1.2 to 2.5 μ wide at the base, and 0.6 to 0.8 μ wide at the tip. Conidia colorless, cylindrical or elongated ellipsoidal, straight or slightly curved, broadly rounded at the distal end, often rather similarly rounded at the basal end though sometimes slightly narrowed proximally, mostly 10 to 23 μ long and 3.6 to 5.6 μ wide, at first continuous and filled throughout with protoplasm, after abjunction producing a glandular cell on the tip of a germinative protuberant outgrowth, then frequently, following successive elongation of the outgrowth, giving rise to 1 or 2 additional glandular cells, thereby becoming largely or wholly emptied of protoplasm and concomitantly partitioned by 1 to 4 cross-walls; the glandular cells of germinative origin measuring usually 4.5 to 6.5 μ in length and 2 to 2.5 μ in width, soon becoming surrounded by a globose or elongated ellipsoidal mass of adhesive material commonly 4 to 7 μ long and 3.5 to 6.5 μ wide.

Capturing and consuming *Panagrolaimus subelongatus* and *Ditylenchus* sp., and besides often parasitizing them, it occurs in decaying leaves and stems of *Bromus secalinus* near Hermiston, Oregon.

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EXPLANATION OF FIGURES

FIG. 1. *Nematoctonus concurrens,* drawn to a uniform magnification with the aid of a camera lucida; × 1,000 throughout. *A,* Portion of clamp-bearing mycelium from surface of agar plate culture: *a–c,* anastomoses of hyphae; *d,* sterigma bearing a conidium with which it is still continuous; *e–k,* sterigmata from which the conidia have become detached. *B,* Portion of prostrate hypha as seen undisturbed in a dry preparation when viewed directly from above: *a, b,* globules of adhesive material showing irregular pitting of surface whereby the glandular cell and supporting stalk are concealed from view; *c,* denuded sterigma. *C,* Same portion of clamp-bearing prostrate hypha as seen in a dry preparation when viewed from side: *a, b,* globules of adhesive material whose pitted surface obscures the glandular cell within, each thereby offering a false appearance of having been formed terminally by the supporting stalk; *c,* denuded sterigma. *D,* Portion of clamp-bearing prostrate hypha (for lack of space drawn in two parts connecting at point *z*) as seen in a moist preparation under a cover glass: *a–f,* erect predacious organs, showing the erect spurs supporting aloft the hour-glass-shaped glandular cell surrounded by the globose mass of adhesive secretion; *g–i,* sterigmata, each bearing a conidium. *E, F,* Portions of clamp-bearing prostrate hypha, each with an erect sterigma terminating in a young growing conidium. *G–J,* Portions of clamp-bearing prostrate hypha (though no clamp is shown in *H*), each with an erect sterigma still continuous with the full grown or nearly full grown conidium surmounting it. *K, L,* Portions of clamp-bearing prostrate hypha, each with an erect sterigma on whose empty tip is borne a mature conidium. *M,* Portion of clamp-bearing prostrate hypha with the proximal portion of an ascending branch, which is likewise studded with clamp-connections and bears three conidia, *a–c,* all about fully grown though not yet delimited at the base. *N* (*a–z*), *O* (*a–j*), Detached mature conidia, showing usual variations in size and shape. *P,* Portions of prostrate hypha, beset with clamp-connections and denuded sterigmata, which has anastomosed with a detached conidium nearby. *Q,* Conidia showing various stages of germination: *a,* conidium with several small vacuoles and young germ tube; *b–d,* conidia, each with an empty segment at one end and bearing at the other end an erect spur that supports a glandular cell surrounded by a globule of adhesive material; *e–i,* conidia, each with two empty segments at one end and bearing near the other end an erect spur surmounted by a glandular cell which is surrounded by a globule of adhesive material; *j,*

conidium with envelope almost entirely emptied of protoplasm, and containing three partitions, its contents having been used in the production of an unusually long germ hypha whereon is supported an adhesive glandular cell; *k*, conidium with two empty segments at one end, and bearing at the other end a germ tube, which, after degeneration of the first adhesive glandular cell produced by it, continued growth to produce a second; *l*, conidium with three empty segments at one end, its remaining live segment being continuous with an erect germ tube whereon two glandular adhesive cells are supported; *m*, conidium with an empty segment at each end, its living median segment being continuous with a germ tube whereon two glandular adhesive cells have been formed, the older, proximal one having already degenerated; *n*, conidium with four empty segments, its remaining live segment being continuous with a germ tube that has formed three glandular adhesive cells successively, the older two, however, having now degenerated.

FIG. 2. *Nematoctonus concurrens*, drawn to a uniform magnification with the aid of a camera lucida; × 500 throughout. *A*, Portions of two main prostrate clamp-bearing hyphae, *a* and *b*, as seen from above, in a dry preparation not covered with a cover glass; *c*, short anastomosing connection joining the two main hyphae where they cross one another; *d*, longer anastomosing connection between the two main hyphae; *e–o*, globules of adhesive material with irregularly indented surface whereby is obscured the glandular cell within; *p*, denuded sterigma. *B*, Same two portions of mycelial hyphae *a* and *b* as seen in a moist preparation flattened down under a cover glass; the anastomosing connections *c* and *d* showing little change, but the predacious organs *e–o* here appearing in longitudinal profile; *p*, denuded sterigma. *C*, *D*, Portions of prostrate clamp-bearing hyphae as seen in a moist covered mount, each portion showing two predacious organs, *a* and *b*, in longitudinal profile. *E*, *F*, Portions of prostrate clamp-bearing hyphae as seen in a moist covered mount, each showing three predacious organs, *a–c*, in longitudinal profile. *G*, Portion of clamp-bearing prostrate hypha as seen in a moist covered mount; *a–f*, six predacious organs shown in longitudinal profile. *H*, Portion of clamp-bearing prostrate hypha as seen in a moist covered mount; showing in longitudinal profile two predacious organs, one, *a*, bearing a single adhesive cell, the other, *b*, bearing three adhesive cells. *I*, Portion of clamp-bearing prostrate hypha as seen in a moist covered mount; showing in longitudinal profile four predacious organs, of which three, *a–c*, have each a single glandular cell, while the other, *d*, bears two degenerate adhesive cells in addition to the one adhesive cell in a functional condition. *J*, Portion of clamp-bearing prostrate hypha with a predacious organ, *a*, that has intruded two growing assimilative hyphae into a captured specimen of *Panagrolaimus subelongatus*. *K*, Portion of clamp-bearing prostrate mycelium showing one predacious organ, *a*, in an inactive state, and another such organ, *b*, which after capture of a specimen of *P. subelongatus* has intruded an assimilative hypha into the animal; *c–e*, three convergent supplementary infective branches, each of which has intruded an assimilative prolongation into the captive. *L*, Portion of clamp-bearing prostrate hypha showing in longitudinal profile three inactive predacious organs, *a–c*, and a fourth predacious organ, *d*, which after capture of a specimen of *P. subelongatus* has intruded an assimilative hypha into the

animal; *e–g,* three convergent supplementary infective branches whereof two have each extended an assimilative prolongation into the captive; *h–j,* denuded sterigmata. *M,* Portion of prostrate hypha with a clamp-connection that has given off a short branch terminating in an erect predacious organ, *a.*

FIG. 3. *Nematoctonus concurrens,* drawn to a uniform magnification with the aid of a camera lucida; × 500 throughout. *A,* Portion of clamp-bearing prostrate mycelium as seen in a moist covered mount; *a,* anastomosis of two hyphae; *b,* predacious organ in longitudinal profile. *B, C,* Portions of clamp-bearing prostrate hyphae as seen in a moist covered mount, each showing two predacious organs, *a* and *b,* in longitudinal profile. *D,* Portion of clamp-bearing mycelium, showing two predacious organs, *a* and *b,* in longitudinal profile. *E, F,* Portions of clamp-bearing prostrate hyphae, each with a lateral branch terminating in an erect predacious organ, *a.* *G,* Long clamp-bearing hyphal branch as seen in a moist covered preparation; showing two predacious organs in longitudinal profile, one, *a,* being attached laterally, the other, *b,* being borne terminally. *H,* Portion of clamp-bearing prostrate hypha bearing a partly degenerated predacious organ, *a,* and two other predacious organs, *b* and *c,* that have been operative in capturing a small specimen of *Ditylenchus* sp.; from *c* a short assimilative hypha has begun invasion of the animal. *I,* Portion of prostrate clamp-bearing mycelium, showing two hyphae joined together by a short anastomosing connection, *a;* two predacious organs, *b* and *c,* after being operative in capturing a specimen of *Panagrolaimus subelongatus,* have each extended an assimilative hypha into the animal; two convergent supplementary infective branches, *d* and *e,* have begun growing toward the captive. *J,* Portion of clamp-bearing prostrate mycelium comprising a nearly simple hypha, *a,* and a ramified hyphal system, *b,* whereof two main branches are united by an anastomosing connection, *c;* of the five inactive predacious organs, *d–h,* shown arising from the mycelium in longitudinal profile, three (*d–f*) have a single glandular cell, one (*g*) has two adhesive cells, and the fifth (*h*) has three adhesive cells, the lowermost one having in part degenerated; the predacious organ *i,* having been operative in the capture of a specimen of *P. subelongatus,* has sent an assimilative hypha into the animal; of the three convergent supplementary infective branches present, *j–l,* one likewise has intruded an assimilative hypha. *K,* Portion of clamp-bearing prostrate mycelium comprising three hyphae, *a–c,* joined together by the anastomosing connections *d* and *e; f–h,* inactive predacious organs, each having a single glandular cell; *i,* predacious organ that has been operative in capturing a specimen of *P. subelongatus,* and has intruded a branching assimilative hypha into the animal; *j–m,* convergent supplementary infective branches that have reached the animal and, with the exception of *k,* have each intruded an assimilative prolongation into it; numerous denuded sterigmata are shown on hypha *b,* and a few on hypha *c.* *L,* Posterior portion of a dead captured specimen of *P. subelongatus,* showing presence of clamps on assimilative hyphae, and external prolongation of two branches *a* and *b* that have broken out through the animal's integument. *M,* Portion of clamp-bearing ascending hypha with two sterigmata bearing the conidia *a* and *b.* *N–P,* Detached mature conidia, *a–z,* showing usual variations in size and shape.

FIG. 4. *Nematoctonus concurrens*, drawn to a uniform magnification with the aid of a camera lucida; × 500 throughout. *A*, Two clamp-bearing prostrate hyphae joined together by three short anastomosing connections, *a–c*; *d*, a predacious organ as seen in a dry uncovered mount. *B*, Portion of prostrate mycelium including three clamp-bearing hyphae, *a–c*, two of which are joined together by a short anastomosing connection, *d*; besides four predacious organs in an inactive state, *e–h*, there are present three predacious organs, *i–k*, that have operated in the capture of a specimen of *Ditylenchus* sp.; the two active organs *i* and *j* having invited development of the two convergent supplementary infective branches *l* and *m*, respectively. *C*, Portion of clamp-bearing prostrate hypha with one inactive predacious organ, *a*, and with another predacious organ, *b*, which after effecting the capture of a specimen of *Panagrolaimus subelongatus* has extended a branched assimilative hypha into the animal; a supplementary infective branch, *c*, besides has extended an assimilative prolongation into the captive. *D*, Portion of prostrate clamp-bearing hypha with a predacious organ, *a*, that after having effected capture of a specimen of *P. subelongatus* has sent a short assimilative hypha into the animal; two convergent supplementary infective branches, *b* and *c*, have begun growing toward the captured eelworm. *E*, Same hypha and captured nematode twenty minutes later; showing continued growth of the intruded assimilative hypha, and also further growth of the two convergent branches toward the place where the animal is affixed to the fungus. *F*, Same hypha and captured nematode one hour later than in *E*; showing further growth of the assimilative hypha extended from the predacious organ, and the intrusion nearby of an assimilative hypha from the convergent branch *b*; the convergent branch *c* has elongated only a little. *G*, Same hypha and captured nematode one hour later than in *F*; showing additional growth of the assimilative hypha first intruded and both growth and branching of the assimilative hypha coming from convergent branch *b*; as the convergent branch *c* has not elongated further, it has not yet penetrated into the animal. *H*, Portion of clamp-bearing prostrate mycelium with a predacious organ, *a*, which after being operative in capture of a specimen of *P. subelongatus* has extended an assimilative hypha into the animal; another assimilative hypha was at the same time intruded nearby from a predacious organ borne on a conidium, *b*, which consequently is empty of protoplasm; a supplementary infective branch, *c*, meanwhile grew to the place where the predacious organ from the conidium had penetrated into the captive. *I*, Posterior portion of dead captured specimen of *P. subelongatus*, showing branching and anastomoses of assimilative hyphae. *J*, Posterior portion of a dead captured specimen of *P. subelongatus* showing branching of assimilative hyphae, and prolongation externally of a filament that broke out through the integument at the tip of the animal's tail. *K*, Portion of prostrate clamp-bearing hypha with a sterigma bearing a mature conidium. *L, M*, Portions of strongly ascending aerial hyphae, showing origin of conidia at close intervals and close arrangement of clamp-connections. *N–P*, Portions of ascending clamp-bearing hyphae showing denuded sterigmata and rather closely spaced clamp-connections. *Q*, Random assortment of detached conidia, *a–z*, showing usual variations in size and shape.