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A NEMATODE-DESTROYING HYPHOMYCETE FORMING PARALLEL MULTISEPTATE HYALINE CONIDIA IN CIRCULAR ARRANGEMENT[1]

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ABSTRACT

In several Petri plate cultures that had been inoculated with decaying plant detritus from central Maryland, a fungus developed which attacks nematodes by extending a rather wide infection-tube either from an adhesive hyphal protuberance, or, more often, from a subglobose adhesive cell produced terminally on its elongate-ellipsoid pluriseptate hyaline conidia. A number (sometimes three) of these conidia are borne simultaneously in peripheral positions on the broadly rounded tip of the colorless condiophore, and are directed upward, parallel to the conidiophore axis. From the segment immediately below its adhesive cell, each conidium puts forth laterally a flexible unicellular tubular appendage that grows downward approximately to the level of the spore attachment. The fungus is described as *Haptocara latirostrum* gen. n., sp. n. Although presumably belonging in the Moniliaceae, it shows no close kinship with the numerous interrelated clampless Hyphomycetes that have been made known as subsisting through capture of nematodes.

AN UNUSUALLY DISTINCTIVE nematode-destroying fungus came to light in several maize-meal-agar plate cultures into which had been pressed small quantities of decaying plant remains gathered along a weedy roadside about 0.5 km south of the National Agricultural Library near Beltsville, Maryland, on 28 May 1969. In the several cultures the fungus developed only sparingly. From an initial growth in the decaying material it usually became distributed very sparsely over an area of 1–2 cm^2 of adjacent agar substratum during the first 20 days following inoculation. Thereafter it made no further attacks on eelworms, though living animals apparently conspecific with those consumed earlier still remained available in moderate abundance. The scanty vegetative development was accompanied by even scantier development of conidiophores and conidia; so that the material found suitable for study included only about 90 invaded nematodes, less than 40 detached conidia, 3 or 4 denuded conidiophores, and one conidiophore active in producing conidia. Since the fungus, nevertheless, revealed pronounced departures in mycelial as well as in reproductive habit, it appears to merit recognition as type of a separate genus in the Moniliaceae. A generic term compounded of two words meaning "to fasten upon" and "head," respectively, together with an epithet derived from words meaning "wide" and "beak," may be helpful in recalling important features of the asexual spores formed by the species.

DIAGNOSIS—**Haptocara** Drechsler, gen. n.—Hyphae assumentes incoloratae, septatae, intra animalia minuta evolutae, simplices vel aliquantum ramosae, interdum ramulos longiores extra promittentes. Hyphae fertiles incoloratae, ascendentes, continuae vel parce septatae, circum apicem pluria parallela conidia prorsus emittentes. Conidia incolorata, elongato-ellipsoidea, pluriseptata, interdum brachio filiformi descendente praedita. Typus: *Haptocara latirostrum.*

Haptocara **latirostrum** Drechsler, sp. n. (Fig. 1–21)—Hyphae assumentes vulgo singulatim intra vermiculos nematoideos in longitudinem crescentes, interdum simplices sed saepius brevibus crassis ramulis sparsim praeditae, vulgo 150–400 μm longae, in cellulis globosis vel elongato-ellipsoideis vel dolioformibus vel cylindraceis, plerumque 4–25 μm longis et 4–13 μm latis, consistentes. Mycelium exterius vulgo exiguum, interdum in summa materia subjacente hic illis cellulis tenacibus subglobosis plerumque 5–7 μm latis praeditum. Hyphae fertiles ascendentes vel acclives, plerumque 40–80 μm longae, 6.5–9 μm latae, nonulla (3) parallela conidia in margine apicis late rotundatis (itaque in superficie declivi) simul prorsum ferentes. Conidia incolorata, in trunco et brachio et bulla tenaci consistentia; trunco (parte inferiore) elongato-ellipsoideo, plerumque 24–38 μm longo, 9–11 μm lato, 2–4-septato; brachio a latere ex supera cellula trunci emisso, primo unicellulari postea saepius vacuo, filiformi, plerumque 24–34 μm longo, circa 2 μm lato; bulla tenaci ex apice trunci emissa, unicellulari, elongato-ellipsoidea vel globosa, plerumque 8–9.5 μm longa, 6–7 μm lata, glutinosa, itaque ad vermiculum nematoideum commode inhaerente, mox tubulum germinationis 2–3.5 μm latum in animal intrudente.

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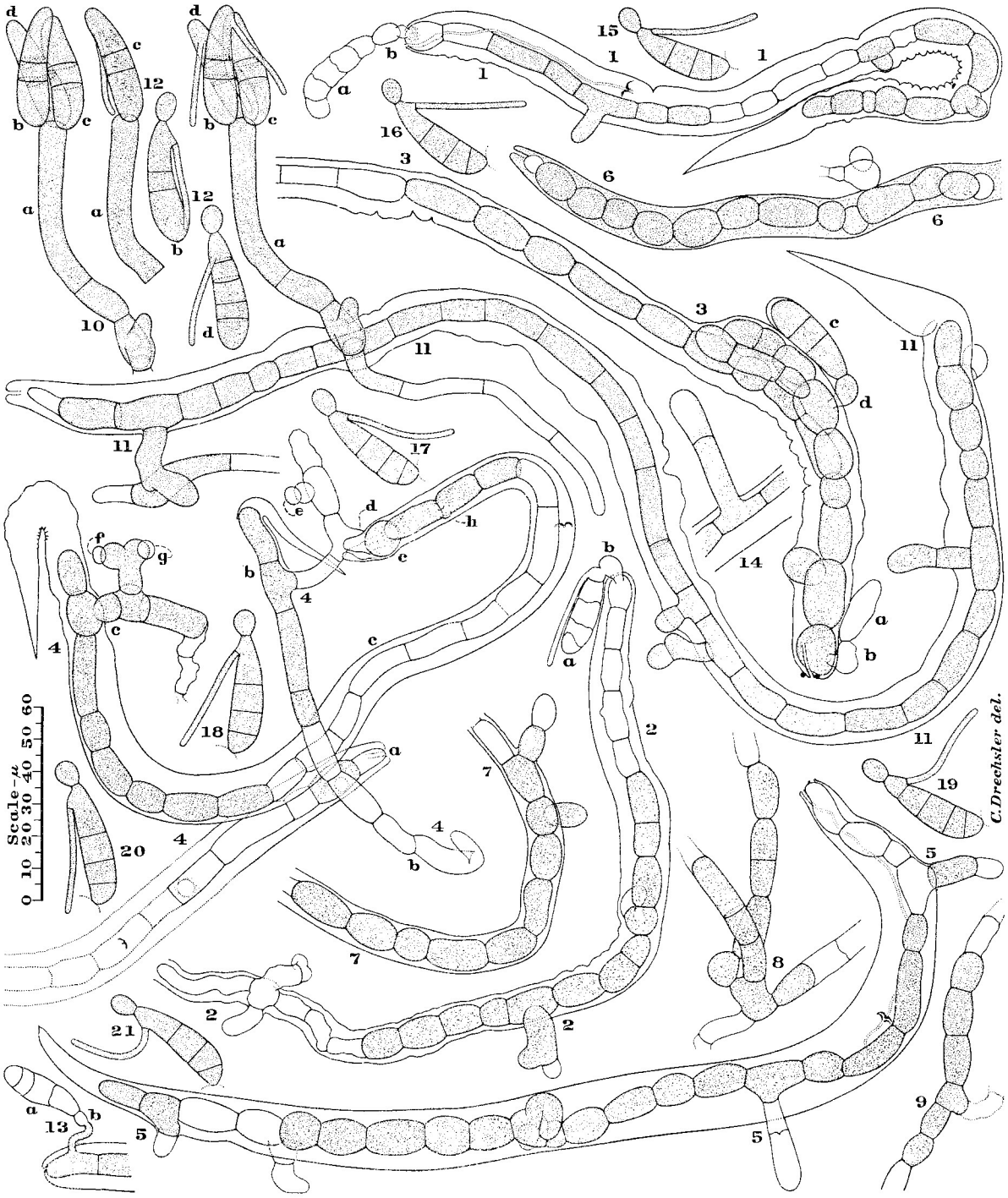

Fig. 1–21. *Haptocara latirostrum* as found developed in maize-meal-agar plate cultures 20 to 54 days old. All × 500. **1, 2.** Empty conidial envelopes, each comprising the membranes of a 4-septate trunk, a, together with the wall of a capitate cell, b, affixed to the head of a nematode integument; from the capitate cell an infection tube penetrated into the animal and extended a stout assimilative hypha lengthwise through the fleshy interior. **3.** Empty conidial envelope consisting of the peripheral membrane of the trunk, a, devoid of visible septa, though partitioned off from the wall of the capitate cell, b, which being affixed to the head of a nematode, intruded an infection tube to produce a long assimilative hypha within the animal; a second conidium, composed of a 2-septate trunk, c, and a capitate adhesive cell, d, is affixed to the animal backward 75 μm from the head, where it intruded an infection tube and produced a short supplementary assimilative hypha. **4.** Remains of three nematodes, a–c, that succumbed

Vermiculos nematoideos interficiens habitat in reliquis plantarum putrescentibus prope Beltsville, Maryland. Typus: Figurae 1–21.

GENERAL DESCRIPTION—In contrast to the numerous predacious hyphomycetes that usually extend several assimilative hyphae lengthwise through the body of a well developed eelworm, *H. latirostrum* commonly produces only one main endozoic hypha, whether the invaded animal is slender or stout (Fig. 1–14). The single endozoic filament is between two and three times wider than the plural hyphae of the more familiar nematode-capturing mucedinaceous species figured at the same magnification in other papers (Drechsler 1937, 1950). As can be seen in instances where the empty membrane of the infecting conidium remained affixed to the head of the dead invaded animal (Fig. 1–3, 13), the broad proximal end of the assimilative hypha is attached to, and evidently originated from, the tip of an infection-tube often three times wider than the corresponding tube in fungi of the genera *Arthrobotrys* Corda (1839), *Dactylella* Grove (1884) and *Dactylium* Nees (1816, 1817). In scattered specimens where two empty conidial envelopes were found attached to the animal's head, the adhesive cell of each spore usually bore an infection tube, but generally only one of the tubes was prolonged into an endozoic hypha. Yet now and then an empty spore (Fig. 3a, b) attached to an eelworm's head, was supplemented some distance behind by a second affixed conidium (Fig. 3c, d), the infection tube of which gave rise to a short additional hypha. The distinction between a massive infection-bladder and narrower endozoic hyphal segments, which was first made known by Zopf (1888) in the well illustrated accounts of his *Monosporidium repens* and *Arthrobotrys oligospora* Fres., is not clearly recognizable in the fungus under consideration.

Capture of nematodes by *H. latirostrum* (Fig. 4a–c) would seem restricted usually to rather small tracts of mycelium on which were borne several adhesive cells not widely separated from one another. Consequently, the few animals that were caught succumbed fairly close together, their bodies becoming intermingled in confused disorder. Owing presumably to injury sustained from the struggles of the captive, an adhesive cell, in fulfilling its function, often became difficult to recognize with certainty, though the position of the hyphal spur (Fig. 4d) on which it was supported, together with the position of the proximal segment of the endozoic filament, indicated where the animal must have been affixed. Mostly the adhesive cells (Fig. 4e–g) were produced flush on the surface of the substratum, under which the hyphal spurs and protuberances bearing them were securely imbedded.

While the single endozoic hyphae of *H. latirostrum* were assimilating the fleshy contents of eelworms invaded by them, they apparently used little of their protoplasmic material for any external development. The few short branches they often extended at nearly right angles usually did not exceed 25–30 μm in length, and some of them even stopped growing when still too short to erupt through the host cuticle. Obviously, the assimilative hyphae of the fungus employ their materials chiefly to augment their own growth. Unlike the endozoic filaments in most species of *Arthrobotrys*, *Dactylella* and *Dactylium*, they did not function as haustoria, constantly transferring newly elaborated protoplasm backward through the infection tube into the external parent mycelium. Instead, from the outset, they each developed as a main unit of vegetative mycelium. Upon completion of the expropriation of digestible material within an invaded eelworm the hyphae attained their greatest bulk; whereas, the slenderer assimilative filaments of the familiar predacious hyphomycetes usually are then emptied of their last remnants of protoplasm, and

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close together, owing to their capture by means of adhesive cells on hyphal protuberances; one such protuberance, d, operated in capture of nematode c; an adhesive cell, e, is shown in an empty state; two others, f–g, likewise appear devoid of contents; h, lateral tubular clamplike connection between two large hyphal segments. **5–7.** Assimilative hyphae formed within nematodes no longer visibly attached to an empty infective body, whether conidium or hyphal protuberance. **8, 9.** Hyphae in a culture 54 days old, in which integuments of infected eelworms had disappeared. **10.** Conidiophore, a, supporting three immature conidia, b–d, each with two septa that delimit a definitive middle segment. **11.** The same conidiophore, a, drawn three hours later, when the hyphal appendage extended downward from the distal portion of each conidium, b–d, had nearly attained its definitive length; the assimilative hypha from which the conidiophore originated is shown within the cuticle of the host eelworm. **12.** Same conidiophore, a, and its conidia, b–d, but drawn eight hours later than Figure 10, when conidia b and d had become detached and had each burgeoned forth terminally a capitate adhesive cell; further, conidium d had formed two additional cross-walls, with the septum dividing the distal cell being inserted, as usual, below the attachment of the appendage. **13.** Penetration into head of nematode by an unusually long infection tube extended from a conidium that earlier must have been affixed by its capitate adhesive cell. **14.** A denuded conidiophore. **15–21.** Detached mature conidia, showing attachment of flexible hyphal appendage on adaxial side of spore; for easier recognition of the basal delimiting wall, the earlier outline of adjacent portions of conidiophore membrane is shown by dotted lines.

the distal portions of their tubular membranes begin to vanish from sight.

In my several plate cultures stored at temperatures near 25 C., the stout hyphae of *H. latirostrum* slowly deteriorated during the six months following their development. Their living segments gradually diminished in number as all protoplasmic contents disappeared from one cell after another. Eventually, when the surviving segments were found present only singly or in very short chains, and the host integuments had become invisible (Fig. 8, 9), the fungus could no longer be distinguished with certainty amid the varied mixture of alien microorganisms. Owing possibly to the presence of these microorganisms, the addition, now and then, of small quantities of distilled water, aroused no growth in the hyphal segments that appeared still filled with living protoplasm.

The sequence of events occurring in asexual reproduction of *H. latirostrum* was observed conveniently in a conidiophore (Fig. 10–12: a), which, together with a slab of subjacent agar, was mounted successfully under a cover-glass without seriously disturbing positional relations or impeding continued spore development. Three conidia that arose from peripheral positions on the broadly rounded distal end of the supporting hypha grew forward simultaneously until the trunk of each attained its definitive size and became divided by two cross-walls into a short middle cell and two longer end cells (Fig. 10b–d). From an adaxial position about 5 μm below the tip of each trunk, a tubular appendage then grew downward until it extended nearly to, or slightly below, the level of the conidial attachment (Fig. 11b–d). Thereupon the distal trunk segment in two of the spores each put forth an apical bud which expanded steadily to form the capitate adhesive cell (Fig. 12b, d). In one of the spores a final step in development soon followed with the insertion of two additional cross-walls, whereby the two long end cells of the trunk were each divided into two segments approximately equal in size to the median segment (Fig. 12d). When, as occasionally happened, neither of the two additional cross-walls was formed, the biseptate conidium appeared not inferior to other spores in its capability for infecting eelworms (Fig. 3c). The lower of the two additional cross-walls was generally formed much more consistently than the upper one (Fig. 15–21).

The trunk of the conidium of *H. latirostrum* always presented a convex longitudinal profile on the abaxial side directed away from the axis of the supporting conidiophore. On the adaxial side turned toward the conidiophore its longitudinal profile was nearly straight, though modified distally by a protuberance bearing the appendage. Near the proximal end the adaxial profile merged with the delimiting septum as seen edgewise. Since detached conidia (Fig. 15–21) consistently showed the delimiting septum as forming the lower portion of the adaxial profile, it seems evident that the spores are regularly borne, as set forth in Fig. 11, at the periphery of a bluntly rounded hyphal tip, where the apical membrane slopes rather steeply downward. Detachment of a mature conidium left behind no wartlike protuberance, no spur, no pedicel, no conspicuous scar or other easily recognizable mark in the vacated area. A denuded conidiophore (Fig. 14) appeared usually so nearly featureless that no clear indication was provided as to whether it had produced only a single group of spores, or perhaps had given rise to successive groups.

DISCUSSION—Although the filamentous appendage attached to the conidium of *H. latirostrum* possibly serves the fungus usefully under natural conditions, it showed no recognizably helpful qualities in the several cultures available for study. Since in many instances the empty conidial membrane found affixed to an invaded eelworm was devoid of any slender tubular part (Fig. 1a, 3a, 13a), there is reason to believe that before the animal succumbed to infection its violent movements resulted in loss or destruction of the appendage. At all events, the spore appendage must be considered a highly distinctive feature of *H. latirostrum*, owing especially to its growth downward from its subterminal origin on the adaxial side of the segment immediately below the adhesive cell. Consisting of a tubular filament of virtually uniform width, it differs markedly from the tapering appendages often borne singly or plurally on conidia of many nematode-capturing fungi referable to the genera *Dactylella* and *Dactylium*. In originating from the distal spore segment rather than from the basal segment, it differs notably from the droopy swordlike appendage often present on conidia of *Mycocentrospora acertina* (Hartig) Deighton (1972), a parasite occasionally very destructive to various economic plants (Neergaard and Newhall, 1951).

Haptocara latirostrum may hitherto have remained unknown less because of any real scarcity in nature than because its development in agar plate cultures is usually too scanty to arrest attention. The parasite was observed to spread only a short distance from the plant detritus used for inoculation; its failure to become more widely extended being due, presumably, to very rapid disablement of eelworms after they have been penetrated individually by the unusually wide germ hypha protruded from the adhesive cell of the affixed conidium. For the most part, the few conidiophores, all produced while the substratum is still moderately fresh, may escape notice, since under low magnification the several conidia borne

terminally are, as a rule, crowded together too closely to be recognized as a group of spores. Following a brief period of parasitic development and of meager sporulation, the fungus often appeared to become completely inactive, though in the same cultures the destruction of nematodes by other fungi—whether by members of the Zoopagales, or of the clamp-bearing genus *Nematoctonus* Drechsler (1941), or of the familiar series of predacious hyphomycetes—usually continued unabated.

The early inactivation of *H. latirostrum* recalls the similar behavior of many species of *Conidiobolus* and *Basidiobolus* when exposed to microbial contamination in agar plate cultures. This similar behavior is sustained by morphological resemblances between the assimilative hyphae of the fungi under consideration—resemblance with respect to outward form, to septation, and to texture of protoplasmic contents. Besides, the conidia of *H. latirostrum* likewise show general parallelism in outward form and septation with many elongated secondary conidia of *B. haptosporus* (Drechsler 1947, Fig. 22) that have undergone internal division into sporangiospores. However, the adhesive cell borne terminally on conidia of *H. latirostrum* is entirely filled with living protoplasm, whereas the apical knob on strobiliform secondary conidia of *B. haptosporus* shows a subspherical mass of lifeless yellow adhesive material surrounding a slender glandular core. Naturally, the difference in structure implies a difference of utility. The apical knob on the elongated secondary conidium of *B. haptosporus* fulfills its function by merely attaching the spore to a roving arthropod. Contrastingly, in *H. latirostrum* the adhesive cell serves not only in affixing the conidium to a host eelworm, but also in thrusting an infection tube into the animal.

The facile migration of all cellular contents from an affixed conidium of *H. latirostrum* outward through the infection tube into the body of the hapless eelworm would seem to confirm the presence of pores in the conidial cross-walls, and the fungus appears definitely estranged from the Entomophthorales through its manner of spore germination. Although occasionally the trunk of an empty affixed conidial envelope is devoid of transverse septa (Fig. 3a), much more often it reveals a full complement of three or four cross-walls (Fig. 1a, 2a, 13a). Since the conidium of *H. latirostrum* has so far been seen to behave solely as a unitary infective spore, never as a sporangium, the fungus is held properly referable to the Moniliales. Its pronounced departures with respect to the character of its endozoic mycelium, as well as to the peripheral attachment, oblique basal delimitation, and parallel orientation of its conidia, appear adverse to any very close kinship with the main series of clampless predacious fungi most familiarly exemplified in *Arthrobotrys oligospora*.

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