A NEMATODE-CAPTURING PHYCOMYCETE WITH DISTALLY ADHESIVE BRANCHES AND PROXIMALLY IMBEDDED FUSIFORM CONIDIA

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ABSTRACT

DRECHSLER, CHARLES. (U.S.D.A., Plant Industry Sta., Beltsville, Md.) A nematode-capturing phycymycete with distally adhesive branches and proximally imbedded fusiform conidia. Amer. Jour. Bot. 49(10): 1089-1095. Illus. 1962.—A fungus newly described as Acaulopez pectinosa, though some uncertainty remains as to its taxonomic relation, captures nematodes (Bunonema sp.) by means of small sticky knobs disposed on the surface of the substratum, where they are supported on upcurved tips of continuous subsurface hyphae and of short subsurface hyphal branchess. After effecting capture, the knob grows out at its apex and produces a clavate or dolioform apressorium together with an infection-bulb broadly intruded into the animal. From the infection-bulb assimilative hyphae are extended lengthwise through the fleshy interior. Asexual reproduction ensues through development of solitary, colorless, slenderly fusiform conidia, gradually but markedly tapered toward both ends, mostly about 200 μ long and 11 μ wide. Each conidium is connected with a subsurface hypha by an isthmus about 1 μ wide. While its cornuate proximal end is securely imbedded in the substratum, the conidium for about seven-eights of its length extends erectly into the air, thereby contrasting with the submere elongated “gemmae” of Zoophagus tentaculium and of some other robust rotifer-capturing fungi that have been referred to Z. insidians.

Two Petri plates of maize-meal-agar on each of which had been placed a wa containing leaves, stems and rhizoids removed from a tuft of moss from western North Carolina, 14 days later showed rather meager development of a fungus with an asperate mycelium nourished manifestly through capture of nematodes. While in the dimensions and angular relations of its main hyphae the fungus closely resembled the several nemato-capturing phycymycetes I described earlier (Drechsler, 1935, 1936, 1941, 1945, 1957) under the binomials Stylopago hadra, S. letohypha, Cystopago lateralis, C. intercalaris and C. cladospora, it differed conspicuously from these species as well as from S. grandis Duddington (1953) in adhering to prey only by the tips of its hyphae and hyphal branches. Although several other nematode species were present in much greater abundance, the mycelium limited its predacious activity to a relatively scarce eelworm which from its distinctive sculpture and characteristic cephial appendages was readily recognized as belonging to the genus Bunonema. To encourage multiplication of the animal, which moved about rather sluggishly and only on the surface, the 2 plate cultures were moistened sparingly from time to time by means of an atomizer. The asperate mycelium in one culture continued for at least 71 days to capture eelworms in scattered positions, though owing apparently to serious attack by a chytridaceous parasite it produced only 3 conidia during this period. In the other culture, the asperate mycelium continued its capture of eelworms until after only 20 days the Bunonema had been virtually exterminated by the more efficiently predacious Dactylella sephyrropaga Drechsler (1937). Fortunately, as no parasite here interfered with reproduction, the shorter period sufficed for the development of more than 60 conidia. The conidial phycymycete here revealed would seem best referable to the Zoopagaceae, and accordingly is described as a new member of the most suitable genus in that family.

ACAPULOPE pectinosa sp. nov. —Mycelium colorless, moderately branched, composed of hyphae 2.3–7.8 μ (mostly 2.5–5 μ) wide,

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2 Mycelium incolorum, medio etiam tum griseo-leuco-rameo; hyphis 2.3–7.8 μ (plerumque 2.5–5 μ) crassius, sepe ex magna parte 2–4 μ sub superficie materie incarnata; hyphis 2.5–3 μ crassius emittentibus—his hyphis etiam ramis propre apicem ascendentibus demunque capitulis gluminois in superficie procerentibus; capitulis gluminois circa 2.5 μ crassis, ad vernicosos nematoideos inhaerentibus, animalia ita capientibus, mox apice excrescentibus tum appressorum clavatum vel dolioformem plerumque 7–25 μ longum, 5–10 μ latum gigantibus et tuber debilitantibus in capitum intrudentibus; tuberibus debilitantibus plerumque 4–8 μ crassis, hyphis assumptis 2.2–3.2 μ latas quae carnem exhaerent intus evolventibus; condis incoloratis, solitaris, erectis, in serem agglomerantibus et parte inferiores plerumque 17–28 μ longa in materiam inseam firmam intactis, anguste fusiformibus, vulgo 180–240 μ longis, medio 7–14 μ latis, utrinque vaide attenuatis, sursum in filum 2 μ latum vel tubulum inanum 7–32 μ longum aequulum, deorsum aliquid cornutum, basi 1–3 μ latum, ibi quandoque plus minusve (sepius in parte infima 1–20 μ longa) inanis, interdum stipula 5–12 μ longa 1–3 μ lata praelvulis.

Vermiculce nematoideos speciei Bunonemalis capsus consumenque habitat in musico prope Highlands, North Carolina. Typus: Fig. 1–46.
Fig. 1-14. *Acaulopage pectospora* in maize-meal-agar plate cultures; X1000.—Fig. 1-4. Portions of hyphae each bearing a branch with a terminal upcurved adhesive knob.—Fig. 5. Hyphal branch that after forming 1 adhesive knob grew out subterminally to produce another.—Fig. 6. Hyphal branch showing 3 old adhesive knobs borne on empty secondary branches and a fourth adhesive knob on a new secondary branch.—Fig. 7. Predacious branch with widening appres-
which often in large part lie 2–4 μ under the surface of the occupied material, where at intervals they give off predacious branches commonly 10–25 μ long and 2.5–3 μ wide—the hyphae and branches in many instances ascending distally to terminate on the surface in an adhesive knob; the adhesive knobs at first about 2.5 μ, often adhering to a nematode (Bunonema sp.) and thereby capturing it, then growing out at the tip in producing a clavate or doliiform appressorium 7–25 μ long and 5–10 μ wide, together with a broadly intruded globose infection-bulb, 4–8 μ thick, from which assimilative hyphae, often 2.2–3.2 μ wide, are extended lengthwise through the captive; conidia colorless, solitary, ascending erectly into the air though imbedded proximally for a distance of 17–28 μ, rather slenderly spindle-shaped, usually 180–240 μ long, 7–14 μ in greatest width, tapering upward to a diameter of 2 μ and downward to a diameter of 1.2 μ, sometimes devoid of living protoplasm at the tip for a distance of 7–52 μ and at the base for a distance of 1–20 μ, connected proximally with a subsurface hypha by an isthmus often 5–12 μ long and 1–1.3 μ wide.

Although in most predacious members of the Zoopagaceae virtually all portions of the mycelium seem about equally capable of holding prey through adherence, such capability in Acuolopage pectospora is restricted to the meagerly differentiated knobs at the tips of many hyphal elements (Fig. 1–6, 14e, 15a-g, 17, 30a-f, 31a-c, 41b, 42a, 43a-b, 44a). With respect to their terminal position, the knobs resemble the adhesive cells used in capturing nematodes by 2 clamp-bearing fungi I described (Drechsler, 1946, 1954) as Neฌotocutum haptopodellus and N. camblysporos. Unlike those cells, however, the knobs are not delimited basally by a cross-wall, and for some time usually show no accumulation of adhesive substance. Later, the knobs, apparently even without being active in capture of an edlworm, often secrete a quantity of clear viscid material, which soon becomes more easily visible in taking on a yellowish coloration. After a knob has been surrounded by a deposit of adhesive material (Fig. 5, 15e) for some time, its supporting hyphal branch may extend a lateral prolongation and produce a new knob (Fig. 15e). Eventually an inactive knob, together with a portion of the adjacent hyphal element, is evacuated of protoplasmic contents. From a position below the emptied tubular membrane a new predacious branch (Fig. 6, 14c, 16) is often extended.

In maize-meal-agar plate cultures the predacious branches of Acuolopage pectospora, as also the axial hyphae on which they are borne, lie submerged for the most part at a rather uniform depth of approximately 3 μ below the surface (Fig. 17), but near the tip they curve upward, so that the distal hemisphere of the terminal knob protrudes above the surface. The sparse array of slightly protruding knobs looks much less formidable than the abundant apparatus employed in capture of nematodes by many members of the clampless series of predacious hyphomyctetes. It appears likely that the success of the knobs in holding specimens of Bunonema is due largely to their special capability for fastening on to the soft, protruding, intricately appendaged head characteristic of these animals. About four-fifths of all captives are affixed frontally (Fig. 7–11, 18–24), the others being affixed laterally, most often near the head (Fig. 12, 25) or near the tail (Fig. 13, 14). Judging from the few relevant examples that came under observation, a newly captured struggling nematode is held attached to the glandular tip of the predacious branch by a cushion-like layer of colorless adhesive material 2–3 μ thick. In later stages this material is usually found in its original position, then being most often present, wholly or largely, in a somewhat massive yellowish ring (Fig. 7a, 9a, 10a, 12a, 13a, 14a, 19a, 20a, 21a, 24a, 25a) surrounding the junction between the predacious branch and its wider prolongation, or appressorium, which is distally in contact with the animal (Fig. 7–11b; 18–21b; 23–25b) and communicates broadly with an infection-bulb within. Less often in advanced stages the adhesive material forms a yellowish layer (Fig. 8a, 11a) encasing the appressorium, or is distributed, wholly or partly, in irregular lumps (Fig. 18a, 21a, 23a) attached basally or distally to the appressorium.

Except for the globose lateral protuberance that is formed now and then by Stylopague hadra in a position between a predacious hypha and a captured edlworm, the robust appressorium of Acuolopage pectospora would seem without parallel among other known nematode-capturing fungi. It may serve helpfully in excluding bacterial in-

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...and a new predacious branch.
vasion of the fleshy interior after the animal's outer covering has been rather widely breached. Although the wet cuticle of a nematode has been penetrated after the more usual manner by an infection tube only 1.3 μ wide, bacteria are effectively excluded because the tube continues to occupy the hole snugly, it appears probable that if the soft frontals of a Bunonema specimen were penetrated so narrowly the struggles of the invaded animal might cause fissures through which alien microorganisms could enter. At all events, the fungus invades the frontal region broadly, pushing aside the stoma and forming an infection-bulb that in many instances tightly plugs the tubular forward end of the body integument, thereby strengthening the barrier to bacterial invasion furnished in the closely applied appressorium. Broad penetration, it is true, takes place not only in instances of frontal invasion but also in instances where the fungus breaches the captive's firm cuticle near the head (Fig. 25) or near the tail (Fig. 13, 14). Wherever the appressorium incurs early injury, presumably from the struggles of the captive, a new infectious branch is usually extended laterally from below the injured parts (Fig. 22–24) to invade the animal either at (Fig. 23b, 24b) or near (Fig. 22) the earlier place of attack.

After a captured celworm has become motionless, assimilative hyphae about equal in width to the narrower filaments of the external mycelium grow from the infection-bulb lengthwise through the fleshy interior. They are only rather indistinctly visible amid musculature and organs during the earlier stages in the expropriation of the captive. In relatively large captives, indeed, they are then discernible only here and there (Fig. 25). Later, when the animal's contents have mostly been absorbed by them (Fig. 8, 9, 11) they can be seen without difficulty. Afterwards they become progressively evaginated through gradual withdrawal of protoplasm, first from their distal and later from their proximal portions (Fig. 10, 21), until at last only their tubular membranes are left within the evanescent cuticle. In one of the Petri-plate cultures, serious interference with the outward movement of protoplasm ensued in the numerous instances where the appressorium, before fulfilling its function as an outlet, was destroyed internally by a chytridaceous parasite (Fig. 26). As Acaulopage pectospora, like other predacious phycomyctes, lacks the capacity for hyphal anastomosis so conspicuous among the clamped nematode-capturing hyphomyctes, the assimilative hyphae that become separated from the external mycelium through destruction of the appressorium cannot become reunited with it, and therefore, cannot supply it with materials for asexual reproduction. Such hyphae cannot readily achieve asexual reproduction by themselves, owing to the frequently small dimensions of the captured celworms and the unusually large size of the asexual spores.

In their large size and elongated shape, the conidia (Fig. 27–46) of Acaulopage pectospora resemble somewhat the "gemmae" that Arnaudow (1925) found produced by an aquatic rotifer-capturing phycymycte he held to be identical with Zoophagus insulans Sommerstoff (1911). They show general similarity also to the "gemmae or conidia" formed by a less robust rotifer-capturing species described by Karling (1936) as Z. tentaculum. Apparently the conidia of A. pectospora taper more strongly toward both ends than the reproductive bodies figured by Arnaudow and by Karling. With respect to posture, they reveal adaptation to terrestrial rather than to aquatic conditions. When a Petri-plate culture

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Fig. 15–46. Acaulopage pectospora in maize-meal-agar plate cultures: Fig. 15–44 drawn from living material in a wet mount under a cover glass, X500; Fig. 45–46 drawn from undisturbed uncovered living material, X150. —Fig. 15. Portion of young mycelium with 7 adhesive knobs, a–g. —Fig. 16. Portion of mycelium showing 4 adhesive knobs including 3 old ones borne on empty branches.—Fig. 17. Terminal portion of branched hypha in agar block, showing filaments submerged about 3μ below surface but with terminal adhesive knobs projecting slightly.—Fig. 18–21. Portions of mycelium, each showing a predacious branch with an appressorium affixed to the front of a Bunonema invaded by assimilative hyphae; a, mass of adhesive material; b, front of captured celworm.—Fig. 22–24. Portions of mycelium, each showing a specimen of Bunonema that after being captured through frontal adhesion was invaded not from the primary branch but from a secondary branch or appressorium given off some little distance below; a, mass of adhesive material; b, front of celworm.—Fig. 25. Portion of mycelium showing a specimen of Bunonema which after being captured through lateral adhesion near its head was broadly penetrated and extensively invaded by assimilative hyphae that are visible only here and there in the fleshy interior; a, mass of adhesive material; b, branch in animal's integument.—Fig. 26. Appressorium occupied by a chytridaceous parasite.—Fig. 27–32. Full-grown conidia, each showing narrow attachment to the parent hypha; an adjoining portion of mycelium in Fig. 30 shows 2 empty knobs, a–b, as well as 4 young predacious branches c–f; an adjoining portion of mycelium in Fig. 31 shows 3 adhesive knobs, a–c.—Fig. 33–40. Detached conidia showing usual variations in size and shape.—Fig. 41. Attached conidium that has put forth a short germ tube, a, at its proximal end; b, predacious branch given off by the parent hypha.—Fig. 42. Attached conidium with a predacious germ hypha, a, arising from its basal end.—Fig. 43. Detached conidium with 1 predacious germ hypha, a, at its distal end, and another, b, at its basal end.—Fig. 44. Detached conidium with a penultimate segment that became emptied in supplying protoplasmic materials for the production of a germ hypha, a, which after forming 1 adhesive knob continued growth repeatedly in forming others.—Fig. 45. Full-grown or nearly full-grown conidium imbedded proximally in agar substrate and at the narrow distal end bearing an extruded droplet.—Fig. 46. The same conidium after the droplet had evaporated and left a delicate pennant-like film.
is examined microscopically under a dry objective immediately after the lid has been removed, they are commonly found extending erectly into the air, though in many instances the filamentous tip may be bent over from the weight of an adhering droplet of clear liquid (Fig. 45). The tall conidia are prevented from toppling by being imbedded proximally in the agar sub- stratum for a distance usually varying from one-tenth to one-eighth of their total length—a distinctive positional relationship that suggested for the fungus an epithet compounded of 2 words (πετος, σπορέ) meaning "stuck in" and "seed," respectively. Very commonly the imbedded portion of a conidium does not pass straight downward into the substratum but gradually curves sideways in a plane oblique to the main axis of the spore. Withdrawal of proplasm from a proximal portion of the conidium is somewhat less usual and generally less extensive than withdrawal of contents from the filamentous distal portion. Apart from empty tubular segments (Fig. 33, 34, 40, 41) that became walled off consequent to withdrawal of contents, some distal segments are found walled off presumably because of internal degeneration (Fig. 27-29, 31, 38, 40). It appears probable, however, that degeneration of proplasm in situ is an abnormal event resulting from some unfavorable condition—possibly oxygen deficiency—that ensues when a conidium is flattened down on moist agar under a cover glass. Similar degeneration is seen when immature aerial conidia and immature aerial conidial chains of other zoopagaceous fungi are examined microscopically in wet, covered mounts.

Being imbedded proximally, the conidia of Acaulopage pectospora sometimes germinate while still in an erect posture by putting forth a short germ tube (Fig. 41a) laterally or obliquely from a position immediately adjacent to its narrow base. Often such a germ tube forms an upcurved adhesive knob and thus becomes a predacious element (Fig. 42a). Conidia that have toppled may germinate by extending 1 predacious germ hypha from its distal end (Fig. 43a) and another from its basal end (Fig. 43b). Owing to the large size of the conidia, a germ hypha (Fig. 44a) may repeatedly grow out below one adhesive knob to form another in a farther position, and thus may develop into a predacious system extensive enough to intercept specimens of Bunonema even though ecdysones of that genus may be present only in rather small numbers.

No reproductive bodies other than elongated fusiform conidia were formed by Acaulopage pectospora in my 2 cultures of the fungus or in any material removed from them. Whenever slabs excised from either culture were examined microscopically in a wet mount under a cover glass they were irrigated with fresh distilled water at intervals of 15-20 min. The frequent irrigation was intended not only to reduce any ill effect resulting from the moderate bacterial contamination that was present but also to encourage zoospore formation, should the fungus be readily capable of such reproduction. In none of the preparations did A. pectospora show any development of swarmpores. The tendency of its conidia to degenerate in wet mounts suggested that the fungus was little fitted for a submerse existence and probably little given to a manner of reproduction suitable especially for an aquatic environment.

It remains uncertain whether the extrusion of liquid distally from conidia of Acaulopage pectospora—a feature unusual among the Zoopagaceae—is of moment in the ecology of the fungus, or like the extrusion of droplets from sporangiophores of many members of the Mucorales represents merely an incident of growth. The liquid would seem to contain some viscus substance in solution, for after being permitted to evaporate it leaves behind a delicate wrinkled film which often extends away from the filamentous tip of the conidium like a pennant (Fig. 46). In wet mounts the film usually is disposed more symmetrically around the filamentous tip (Fig. 27-29, 31, 32, 34, 36, 37, 39, 40, 42, 43) but in many instances is only rather indistinctly visible.

The proplasm in the conidia of Acaulopage pectospora is of somewhat granular texture, whereas that in the conidia of congenerics species subsisting by capture of protozoans appears nearly homogeneous. Moderately granular texture is usual also in the proplasm filling the asexual spores of nematode-capturing species of Stylopagace and Cystopagace, while the asexual spores of the protozoan-capturing members of these genera contain nearly homogeneous proplasm. Since the nematode-capturing fungi here concerned are of necessity considerably coarser than their protozoan-capturing congeners and produce corresponding larger asexual spores, the difference in proplasmic texture may well have sufficient explanation in the dimensional inequality of the conidia or of the chlamydospores. Although assignment of the several nematode-capturing phycomyetes to Stylopagace and Cystopagace was based mainly on general parallelism with respect to mycelial morphology, predacious habit, and asexual reproduction, it received noteworthy confirmation through the discovery of unmistakably zoopagaceous sexual apparatus in a fungus (Drechsler, 1945) similarly having a robust asetate mycelium that captures ecdysones by lateral adhesion after the manner familiar, for example, in S. hadra and C. intercalaris.

LITERATURE CITED


