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A NEMATODE-CAPTURING PHYCOMYCETE WITH DISTALLY ADHESIVE BRANCHES AND PROXIMALLY IMBEDDED FUSIFORM CONIDIA[1]

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ABSTRACT

DRECHSLER, CHARLES. (U.S.D.A., Plant Industry Sta., Beltsville, Md.) A nematode-capturing phycomycete with distally adhesive branches and proximally imbedded fusiform conidia. Amer. Jour. Bot. 49(10): 1089–1095. Illus. 1962.—A fungus newly described as *Acaulopage* **pectospora,** 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 branches. After effecting capture, the knob grows out at its apex and produces a clavate or dolioform appressorium 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 200μ long and 11μ wide. Each conidium is connected with a subsurface hypha by an isthmus about 1μ 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 submerse elongated "gemmae" of *Zoophagus tentaclum* 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 wad 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 aseptate mycelium nourished manifestly through capture of nematodes. While in the dimensions and angular relations of its main hyphae the fungus closely resembled the several nematode-capturing phycomycetes I described earlier (Drechsler, 1935, 1936, 1941, 1945, 1957) under the binomials *Stylopage hadra, S. leiohypha, Cystopage lateralis, C. intercalaris* and *C. cladospora,* it differed conspicuously from these species as well as from *S. grandis* Duddington (1955) 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 cephalic 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 aseptate mycelium in one culture continued for at least 71 days to capture eelworms in scattered positions, though owing apparently to serious attack by a chytridiaceous parasite it produced only 3 conidia during this period. In the other culture, the aseptate mycelium continued its capture of eelworms until after only 20 days the *Bunonema* had been virtually exterminated by the more efficiently predacious *Dactylella gephyropaga* Drechsler (1937). Fortunately, as no parasite here interfered with reproduction, the shorter period sufficed for the development of more than 60 conidia. The conidial phycomycete thereby revealed would seem best referable to the Zoopagaceae, and accordingly is described as a new member of the most suitable genus in that family.

ACAULOPAGE **pectospora** sp. nov.[2] (Fig. 1–46) —Mycelium colorless, moderately branched, composed of hyphae 2.3–7.8μ (mostly 2.5–5μ) wide,

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[2] Mycelium incoloratum, mediocriter ramosum; hyphis 2.3–7.8 μ (plerumque 2.5–5 μ) crassis, saepe ex magna parte 2–4 μ sub superficie materiae insessae procurrentibus et hic illic similiter immersos ramos vulgo 10–25 μ longos 2.5–3 μ crassos emittentibus—his hyphis etiam ramis prope apicem ascendentibus denique capitulum glutinosum in superficie proferentibus; capitulis glutinosis circa 2.5 μ crassis, ad vermiculos nematoideos inhaerentibus, animalia ita capientibus, mox apice excrescentibus tum appressorium clavatum vel dolioformem plerumque 7–25 μ longum 5–10 μ latum gignentibus et tuber debilitantem in captivum intrudentibus; tuberibus debilitantibus plerumque 4–8 μ crassis, hyphas assumentes 2.2–3.2 μ latas quae carnem exhauriunt intus evolventibus; conidiis incoloratis, solitariis, erectis, in aerem assurgentibus sed parte inferiore plerumque 17–28 μ longa in materiam insessam firme insitis, anguste fusiformibus, vulgo 180–240 μ longis, medio 7–14 μ latis, utrimque valde attenuatis, sursum in filum 2 μ latum vel tubulum inanum 7–52 μ longum abeuntibus, deorsum aliquid cornuatis, basi 1–2 μ latis, ibi quandoque plus minusve (saepius in parte infima 1–20 μ longa) inanitis, interdum stipula 5–12 μ longa 1–1.3 μ lata praeditis.

Vermiculos nematoideos speciei *Bunonematis* capiens consumensque habitat in musco prope Highlands, North Carolina. Typus: Fig. 1–46.

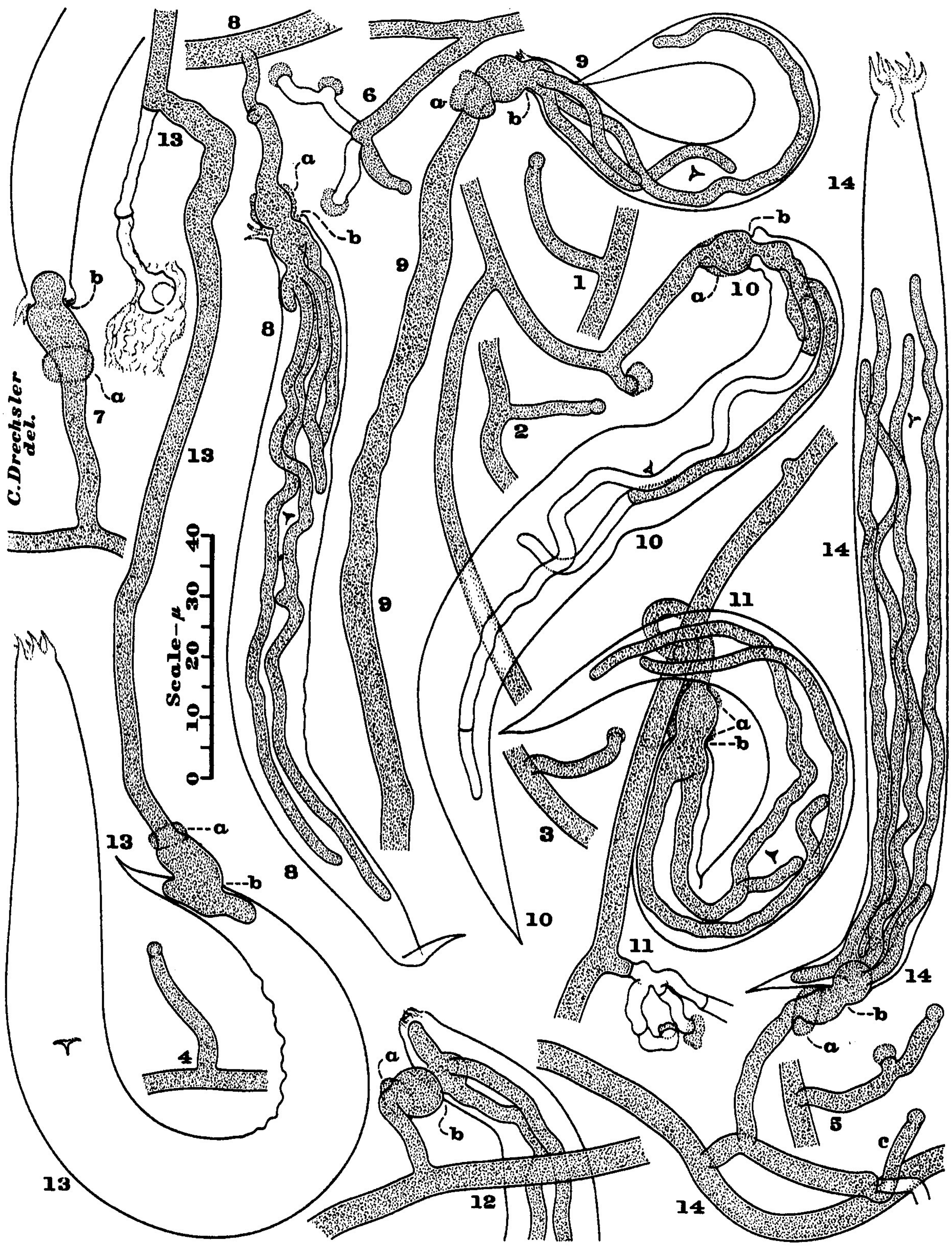

Fig. 1–14. *Acaulopage pectospora* in maize-meal-agar plate cultures; ×1000.—Fig. 1–4. Portions of hyphae each bearing a branch with a terminal upcurved adhesive knob.—Fig. 5. Hyphal branch that after forming 1 adhesive knob grew out subterminally to produce another.—Fig. 6. Hyphal branch showing 3 old 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 wide, often adhering to a nematode (*Bunonema* sp.) and thereby capturing it, then growing out at the tip in producing a clavate or dolioform 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 adhesion, such capability in *Acaulopage pectospora* is restricted to the meagerly differentiated knobs at the tips of many hyphal elements (Fig. 1–6, 14c, 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 *Nemotoctonus haptocladus* and *N. campylosporus*. 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 eelworm, often secrete a quantity of clear viscous material, which soon becomes more easily visible in taking on a yellowish coloration. After a knob has been surmounted by a deposit of adhesive material (Fig. 5, 15c) 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 *Acaulopage 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 hyphomycetes. 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. 7–14:b; 18–21:b; 23–25:b) 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 *Stylopage hadra* in a position between a predacious hypha and a captured eelworm, the robust appressorium of *Acaulopage pectospora* would seem without parallel among other known nematode-capturing fungi. It may serve helpfully in excluding bacterial in-

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sorium and intruded infection-bulb; a, mass of yellowish adhesive material; b, front of captured *Bunonema*.—Fig. 8–11. Predacious branches, each with an appressorium from which a frontally adhering *Bunonema* has been invaded first by an infection-bulb and then more extensively by 2–4 assimilative hyphae; a, mass of yellowish adhesive material; b, front of captured *Bunonema*.—Fig. 12. Portion of long hypha bearing a short predacious branch with a haustorium affixed laterally to a captured *Bunonema* about 7 μ from its frontal profile, whence the animal has been invaded by an infection-bulb and assimilative hyphae; a, mass of adhesive material; b, affixture of haustorium to integument.—Fig. 13. Axial hypha that after expropriating a captured eelworm has extended a longish predacious branch from which was broadly invaded a *Bunonema* about 10 μ forward from the tip of its tail; a, mass of adhesive material; b, breach in animal's cuticle.—Fig. 14. Portion of mycelium showing a predacious branch from which a *Bunonema* adhering laterally about 15 μ from the tip of its tail has been invaded by 5 assimilative hyphae that are still growing toward the captive's head; a, mass of adhesive material; b, breach in animal's cuticle; c, new predacious branch.

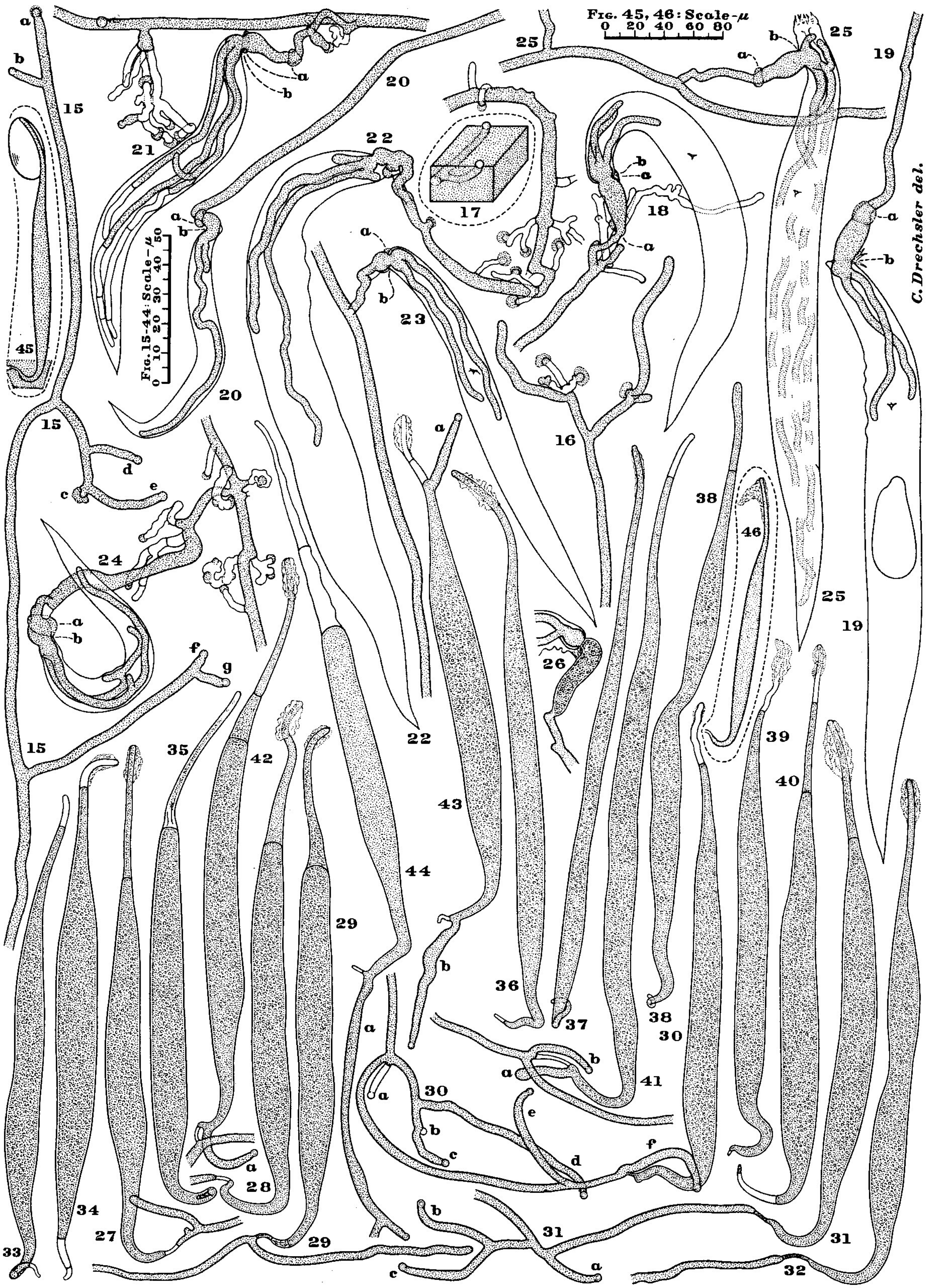
Fig. 45, 46: Scale-μ
0 20 40 60 80
Fig. 15-44: Scale-μ
0 10 20 30 40 50
C. Drechsler del.

vasion of the fleshy interior after the animal's outer covering has been rather widely breached. Although when the firm cuticle of a nematode has been penetrated after the more usual manner by an infection tube only 1–1.3 μ wide, bacteria are effectively excluded because the tube continues to occupy the hole snugly, it appears probable that if the soft frontal parts 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 infective 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 eelworm 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 evacuated 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 chytridiaceous parasite (Fig. 26). As *Acaulopage pectospora*, like other predacious phycomycetes, lacks the capacity for hyphal anastomosis so conspicuous among the clampless nematode-capturing hyphomycetes, 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 from asexual reproduction. Such hyphae cannot readily achieve asexual reproduction by themselves, owing to the frequently small dimensions of the captured eelworms 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 phycomycete he held to be identical with *Zoophagus insidians* Sommerstorff (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. tentaclum*. 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

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, ×500; Fig. 45–46 drawn from undisturbed uncovered living material, ×250.—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 3 μ 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 eelworm.—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 eelworm.—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, breach in animal's integument.—Fig. 26. Appressorium occupied by a chytridiaceous 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 substratum 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 substratum 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 (πηκτός, σπορά) 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 protoplasm 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, 43) that become 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 protoplasm 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 eelworms of that genus may be present only in rather small number.

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 swarmspores. 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 viscous 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 protoplasm in the conidia of *Acaulopage pectospora* is of somewhat granular texture, whereas that in the conidia of congeneric species subsisting by capture of protozoans appears nearly homogeneous. Moderately granular texture is usual also in the protoplasm filling the asexual spores of nematode-capturing species of *Stylopage* and *Cystopage*, while the asexual spores of the protozoan-capturing members of these genera contain nearly homogeneous protoplasm. Since the nematode-capturing fungi here concerned are of necessity considerably coarser than their protozoan-capturing congeners and produce correspondingly larger asexual spores, the difference in protoplasmic texture may well have sufficient explanation in the dimensional inequality of the conidia or of the chlamydospores. Although assignment of the several nematode-capturing phycomycetes to *Stylopage* and *Cystopage* 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 aseptate mycelium that captures eelworms by lateral adhesion after the manner familiar, for example, in *S. hadra* and *C. intercalaris*.

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