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THREE ZOÖPAGACEOUS FUNGI THAT CAPTURE AND CONSUME SOIL-INHABITING RHIZOPODS

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(WITH 8 FIGURES)

Three fungi, all subsisting by capture of terricolous rhizopods, are described herein as new species of the Zoöpagaceae. Two of the new forms can be set forth in their asexual and sexual reproductive phases as well as their vegetative stage; though the details of morphology whereby they differ from forms previously made known appear of rather commonplace character. Their prey, like the prey of most predaceous members of the family, and, indeed, like the host animals of most parasitic members, consists of amoebae of the familiar pelliculate type developing abundantly in agar plate cultures planted with partly decayed vegetable materials. Although the third form can be presented only in its vegetative and asexual reproductive stages, the vegetative stage here offers marked departure in its predaceous relationship to a non-pelliculate, frequently reticulate rhizopod, while the asexual reproductive phase is given distinctiveness by the unusual design of the curiously topknotted conidia.

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A RHABDOSPORA-LIKE SPECIES OF STYLOPAGE SUBSISTING ON AMOEBA VERRUCOSA

A maizemeal-agar plate culture which, after being permeated with mycelium of *Pythium ultimum* Trow, had been further planted with a small quantity of partly decomposed friable barley (*Hordeum vulgare* L.) straw collected near Greeley, Colorado, early in October, 1945, showed after 20 days dozens of large amoebae congregated in areas adjacent to the superadded material. On microscopical examination under low magnification the clustered animals gave much the same appearance as had been noted earlier in the groups of large amoebae captured by my *Zoöpage phanera* (**3**: 26–30) and more recently again in the assemblages of robust individuals of *Amoeba terricola* Greeff (*sensu strictiore*) taken captive by my *Acaulopage marantica* (**8**: 143–149). Under higher magnification the captured animals (FIG. 1, *A–F; G, a, b; H*), which commonly measured 50 to 100 μ across, were each found to be surrounded by a clearly visible, firm pellicle, in part delicately rippled and in part disposed more smoothly about broadly protruding pseudopodia. In the colorless, rather dispersedly granular sarcode could readily be distinguished a single somewhat prolate ellipsoidal nucleus measuring commonly 17 to 23 μ in length and 14 to 19 μ in width. As the nucleus showed always a slightly darker globose central body, mostly 7.5 to 10.5 μ in diameter, within the clear outer layer, the animal was immediately recognized as *Amoeba verrucosa* Ehrenb.—as the same widespread soil-inhabiting rhizopod that previously has been found attacked endoparasitically by *Cochlonema megalosomum* Drechsl. (**8**: 128–137), *C. symplocum* Drechsl. (**9**: 258–266), and *C. agamum* Drechsl. (**12**: 120–133). Although this rhizopod has further been reported as subject to destruction by the predaceous hyphomycete *Dactylella tylopaga* Drechsl. (**4**), it has not hitherto been found captured by any member of the Zoöpagaceae.

In the areas where capture of *Amoeba verrucosa* was just beginning to become noticeable from a grouped arrangement of relatively few individuals, the animals were often held through adhesion to only a single meagerly branching mycelial filament (FIG. 1, *A*), mostly 1.4 to 3 μ wide, whose phycomycetous character was

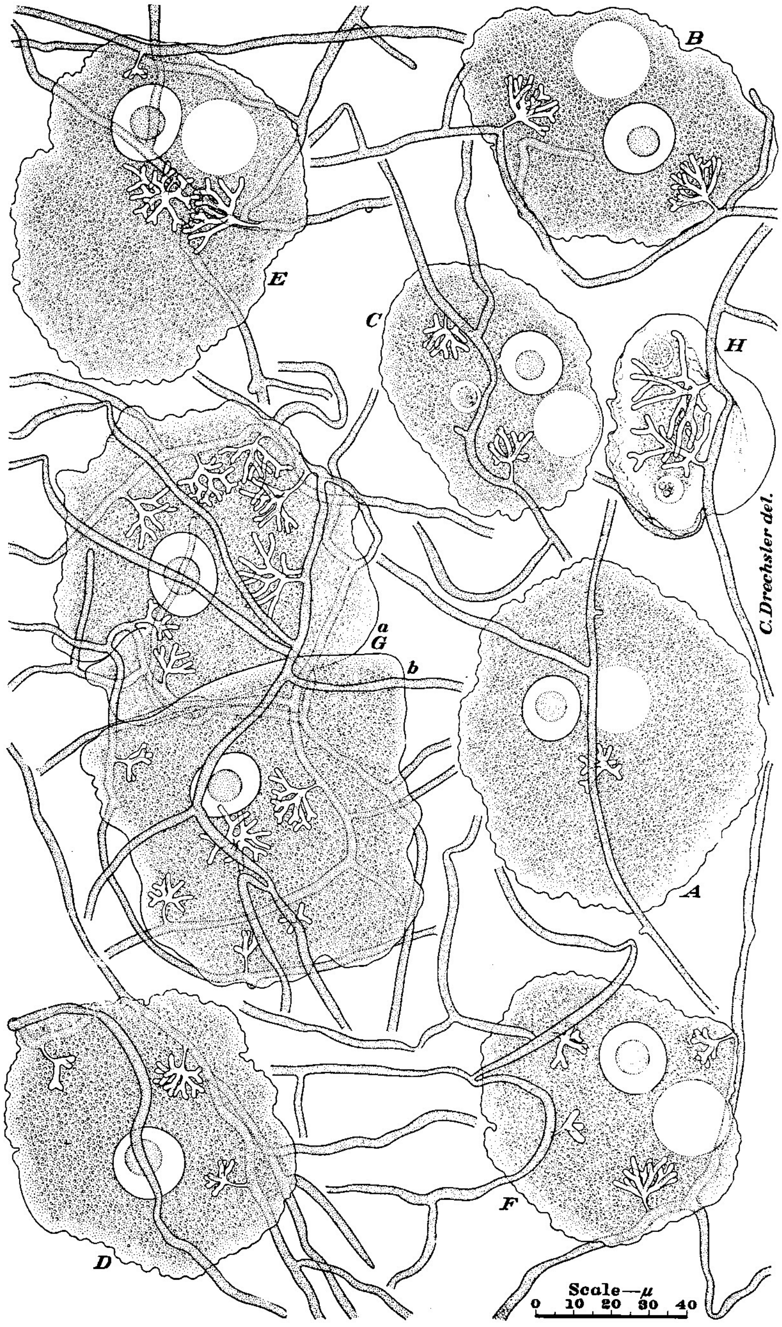

FIG. 1. *Stylopage rhabdoides.*

shown clearly in a lack of all intercalary cross-walls. After an animal had been taken, branches were evidently put forth more abundantly from the adhering portions of filament than from adjoining portions; so that the captive became increasingly invested with hyphal elements (FIG. 1, *B–D*). As the rhizopod usually continued long to wallow about by extending pseudopodia now in one direction now in another, it was not surprising that the investing hyphae were soon found to pursue markedly irregular courses. Yet even where the animal's struggles seemed less resolute the new hyphae that were put forth locally appeared likewise much given to capricious turns and to rather pronounced haphazard variations in width. Similar haphazard irregularity in the elongation of enveloping branches was observable also in instances where the rhizopod was captured by two (FIG. 1, *E, F*) or more (FIG. 1, *G, a, b*) separate hyphae, as often happened where the fungus had been present for some time and had thus been able beforehand to extend mycelial filaments more copiously. Consequently in areas where many captives had become unhappily congregated in readily noticeable groups, the animals, whether single or huddled in pairs (FIG. 1, *G, a, b*), were nearly always found intricately enveloped, above and below, in a confusion of promiscuously branching hyphae.

Usually at a rather early stage in the envelopment of the captured animal, a narrow process, or sometimes two narrow processes, would be extended through its pellicle from the adhering filament or filaments. On attaining a length of several microns each of the processes would widen abruptly at the tip and then would branch dichotomously at close intervals to form a pedicellate haustorium with short divaricate assimilative branches. Further envelopment of large animals usually brought intrusion of additional haustoria, so that in the end six or seven such organs were commonly found present (FIG. 1, *G, a, b*), and in more than a few instances as many as ten or twelve. The progressive expropriation of materials by these haustoria did not immediately have any noticeable effect on the sarcode, or on the nucleus, or on the operation of the contractile vacuole. It was not until the animal's protoplasmic contents had been largely depleted that the nucleus degenerated visibly and that the contractile vacuole ceased to operate.

Sometimes when the last remnants of degenerating protoplasm lay beyond reach of the haustoria many of the assimilative branches most favorably situated would elongate at a relatively late stage (FIG. 1, *H*) to bring about thorough expropriation. In any case, when all granular residues had vanished, the contents of the haustoria themselves were withdrawn backward into the parent mycelium, leaving only the collapsed empty pellicle as evidence of the completed predaceous action.

Near the groups of captured animals the Colorado fungus gave rise on prostrate hyphae to erect conidiophores (FIG. 2, *A–E: a*) which at a height of 25 to 50 μ tapered rather markedly before they widened again in elongating further to form the single terminal conidium (FIG. 2, *A–E: b*). Sometimes the conidiophore (FIG. 2, *E, a*) growing out distally into a young conidium (FIG. 2, *E, b*) extended a lateral branch (FIG. 2, *E, c*) which soon began to form distally a second young conidium (FIG. 2, *E, d*). Occasionally the erect hypha (FIG. 2, *F, a*) would fail to produce a conidium at its tip, but instead gave rise to a lateral branch (FIG. 2, *F, b*) that subsequently was found producing a young conidium (FIG. 2, *F, c*). When definitive size was attained, two cross-walls were laid down close together in the narrow isthmus to separate each functional conidiophorous hyphal element (FIG. 2, *H, a; I, a–c*) from the conidium (FIG. 2, *H, b; I, d–f*). No instance of a conidiophore growing from below its delimited distal end to form a second conidium on a newly prolonged tip came to light in the fungus preying on *Amoeba verrucosa*. Absence of such successive development, and lesser length of the conidiophore—this dimension here did not usually exceed 50 μ—would seem to represent features distinguishing the fungus from my *Stylopage rhabdospora* (**5**: 374–377; **12**: 138–140), in which production of plural conidia on a successively elongated conidiophore has often been observed, and in which the conidiophores, even without taking any increments into account, have frequently been found measuring between 50 and 100 μ in height. With respect to shape the conidia (FIG. 2, *J, a–z*) closely resemble those of *S. rhabdospora,* and though they have been found of appreciably larger size the dimensional difference is not sufficiently pronounced to merit much emphasis.

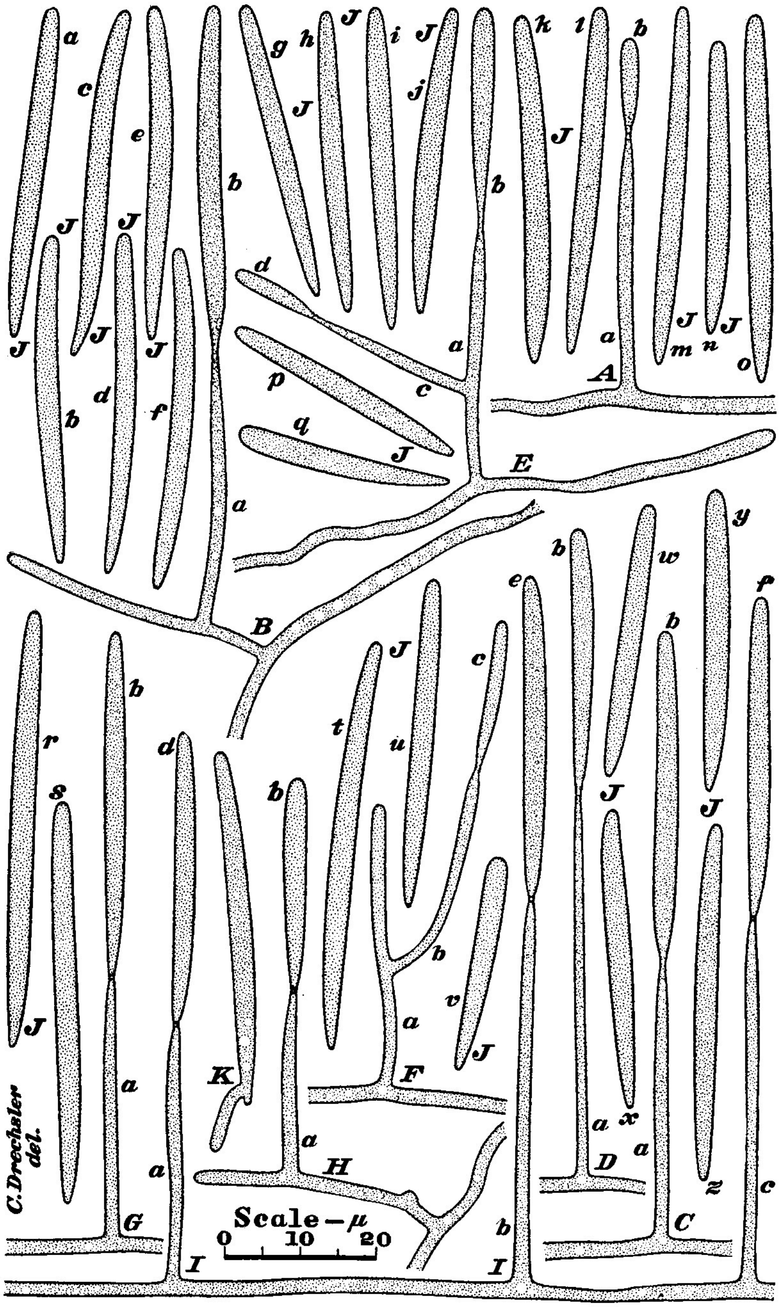

FIG. 2. *Stylopage rhabdoides.*

In nearly all areas occupied by it the fungus predaceous on *Amoeba verrucosa* showed moderately abundant sexual reproduction. Now and then instances were found where two neighboring mycelial filaments (FIG. 3, *A, a, b*) had evidently given rise to a pair of zygophoric branches (FIG. 3, *A, c, d*) which, after making contact with each other distally, became united at the tip (FIG. 3, *A, u*); a septum having meanwhile been laid down in each branch about 15 to 25 μ from the tip to delimit the conjugating parts as gametangia. Much more often, however, one of the two conjugating elements was supplied from a germinating conidium (FIG. 3, *B–J: a*) while the other was supplied from a mycelial hypha (FIG. 3, *B–J: b; D, c; H, c*). Most commonly the conidium germinated from one of its ends (FIG. 2, *K*). Sometimes the cross-wall delimiting the gametangium was laid down within the conidium itself, so that a small portion of the asexual spore was included in the conjugating cell (FIG. 3, *B, c; E, c; G, c*). In other instances the delimiting wall of the gametangium was laid down at the base of the germ-tube flush with the conidial wall (FIG. 3, *D, d, e; F, c; H, e*). Frequently, again, the septum was intercalated in the germ-tube, whether within a few microns from the base (FIG. 3, *C, c; E, d; H, d; J, c*) or, perhaps, 10 to 25 μ above it (FIG. 3, *I, c*). Although the opposing gametangium borne on a branch from a mycelial hypha sometimes included nearly the entire branch (FIG. 3, *E, f*), more often the delimiting septum here was found 5 to 25 μ above the branch origin (FIG. 3, *B, d; C, d; D, f; F, d; H, g; J, d*) and not infrequently it would set off the sexual cell from a stalk more than 25 μ (FIG. 3, *E, e; G, d; H, h*) or even more than 50 μ (FIG. 3, *D, g; I, d*) in length. Some conidia participated in the development of two zygospores by giving rise to two germ tubes that each produced a gametangium. In such instances the two germ-tubes came from opposite ends of the spore (FIG. 3, *D, d, e*), or, again, one of the two came from an end position (FIG. 3, *E, c; H, d*) while the other came from a more nearly median position (FIG. 3, *E, d; H, e*). Often the two gametangia borne on the germ-tubes conjugated with gametangia from separate mycelial hyphae (FIG. 3, *D, b, c; H, b, c*), but rather frequently, also, they conjugated with gametangia supplied from the same mycelial filament (FIG. 3, *E, b*).

In one observed instance a gametangium (FIG. 3, *E, c*) supplied by a conidium became united with two sexual branches (FIG. 3, *E, e, g*) supplied from the same mycelial filament. Occasionally a conidium that had already supplied two gametangia (FIG. 3, *H, d, e*) on separate germ-tubes was found putting forth a third germ-tube (FIG. 3, *H, f*).

Following fusion of the paired gametangia one of them—more usually the one contributed from the mycelial filament—soon began to swell out, commonly at a distance of about 5 μ from the union, to form a lateral intercalary globose excrescence (FIG. 3, *D, g; E, e; H, g, h; I, d; J, d*). When this excrescence attained a diameter of about 10 μ, and had received the entire protoplasmic content of both gametangia, it gave rise endogenously to the zygospore proper. At maturity the membrane of the globose part enveloped somewhat loosely the boldly verrucose, thick-walled, distinctly yellowish sexual spore (FIG. 3, *K–U*). Internally the ripe zygospore often seemed to have the unitary organization familiar among oöspores, its coarsely granular material apparently surrounding a single reserve globule and single refringent body (FIG. 3, *K, N, O, R, S, T, U*). At other times, however, two or three homogeneous reserve globules seemed present, usually without any clearly discernible refringent body (FIG. 3, *L, M, P, Q*).

The fungus manifestly is most closely related to *Stylopage rhabdospora*. In the vegetative stage it appears separated from that species by reason of its coarser mycelial hyphae and its utilization of a different *Amoeba* as prey. Though not wholly unknown in the Zoöpagaceae, utilization of more than one species of rhizopod is so exceptional among members of the family that it cannot be assumed for any member without unmistakable evidence. In view of the differences shown in its vegetative stage and in its conidiophores, there seems somewhat more reason for holding the fungus to be distinct from *S. rhabdospora* than for regarding it as being the same. It is therefore described as new under a specific epithet meaning "rod-like," which may perhaps serve helpfully in signalizing its conidial shape and in recalling the species most closely related to it.

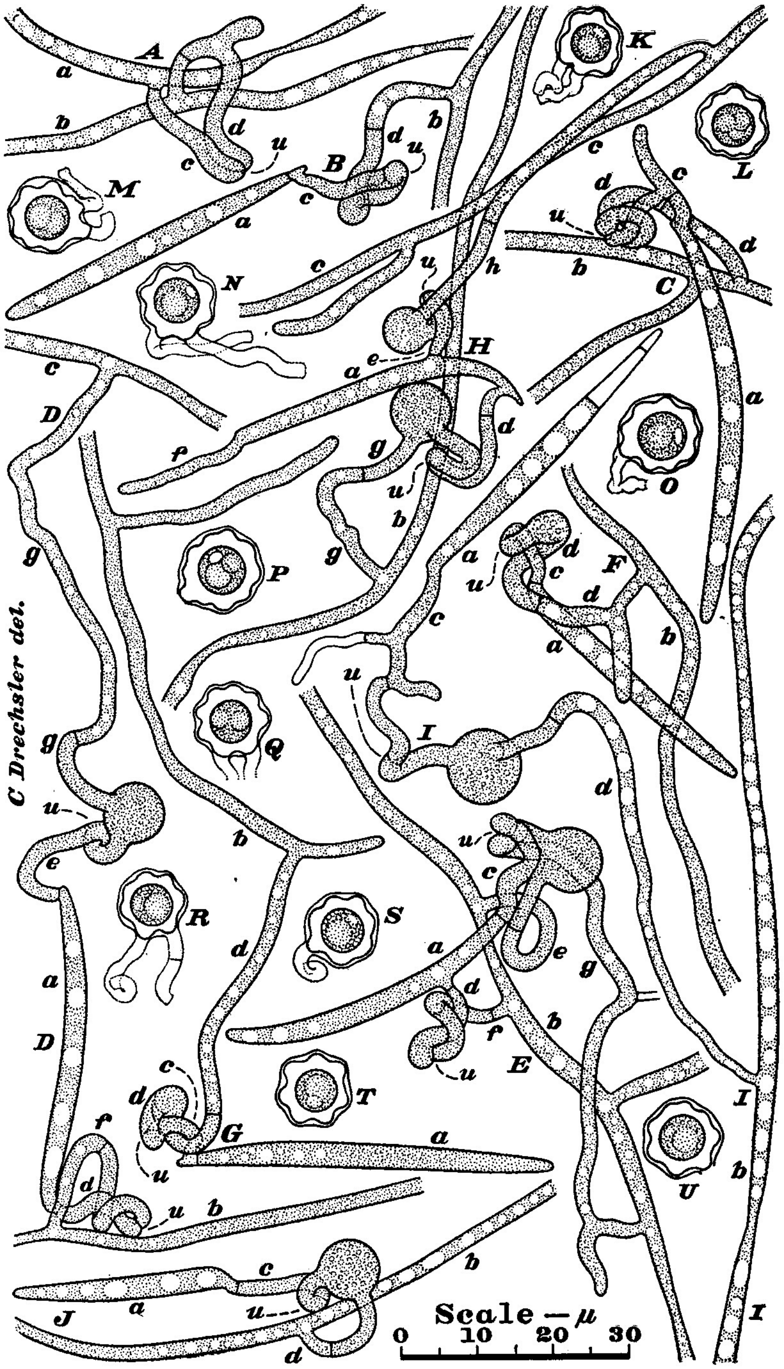

FIG. 3. *Stylopage rhabdoides.*

Stylopage rhabdoides sp. nov.

Mycelium effusum; hyphis continuis, incoloratis, filiformibus, parce ramosis, fere 1.4–3 μ crassis, ad animalia minuta extense inhaerentibus, saepe ea contorte implicantibus, pelliculam eorum perforantibus, haustoria intus evolventibus quae protoplasma exhauriunt; haustorio pedicellato, pedicello vulgo 3–7 μ longo, 0.5–1.5 μ crasso, apice abrupte latescente, saepius bis vel quater repetite bifurco, ita usque 16 ramulos divaricatos 5–18 μ longos et 1–2.5 μ crassos ferente. Hyphae fertiles incoloratae, erectae, simplices vel interdum parce ramosae, vulgo 20–50 μ altae, 1.4–2 μ crassae, sursum leniter attenuatae, apice unicum conidium gignentes; conidiis incoloratis, elongato-cylindraceis, saepe sursum leniter attenuatis et abrupte rotundatis, deorsum plus attenuatis, itaque basi acutiusculis, plerumque 25–57 μ longis, 2.7–3.5 μ crassis. Hyphae zygosporiferae saepius 15–85 μ longae, 1.5–3 μ crassae, vulgo 10–27 μ infra apicem septo divisae, ambae rarenter ex duabus hyphis mycelii exeuntes sed saepissime altera ex hypha mycelii altera ex conidio germinanti oriunda; duabus cellulis terminalibus (gametangiis) saepe plus minusve irregulariter flexuosis, interdum inter se circumplicantibus, apice inter se conjungentibus; zygosporangio circa 5 μ ab junctione oriundo, primum levi, sphaeroideo, vulgo 9–11 μ crasso, maturitate membrana ejus circa zygosporam laxe collapsa; zygospora aliquantum flavida, globosa, circa 8–10 μ crassa, in maturitate membrana valde verrucosa, cellulam viventem sphaeralem 5–6.5 μ crassam circumdante.

Amoebam verrucosam capiens consumensque habitat in stramento (foliis acère caulibusque) *Hordei vulgaris* putrescenti prope Greeley, Colorado.

Mycelium spreading; vegetative hyphae colorless, filamentous, sparingly branched, mostly 1.4–3 μ wide, adhering to and often extensively enwrapping minute animals, penetrating the pellicle of each captive and intruding haustoria to appropriate the protoplasmic contents; haustoria pedicellate, the pedicel usually 3–7 μ long, 0.5–1.5 μ wide, abruptly enlarging distally and bifurcating often 2 to 4 times in succession at wide angles, thus bearing commonly 4 to 16 assimilative branches 1–2.5 μ wide and in combined length of successive parts measuring 5–18 μ. Conidiophores simple or occasionally sparingly branched, colorless, 20–50 μ high, 1.4–2 μ wide, tapering gradually toward the apex whereon a single conidium is borne; conidia colorless, elongated-cylindrical, tapering slightly toward the abruptly rounded tip and rather pronouncedly toward the somewhat more pointed basal end, mostly 25–57 μ long and 2.7–3.5 μ wide. Zygophoric hyphae mostly 15–85 μ long and 1.5–3 μ wide, both occasionally rising from 2 mycelial filaments, but much more often one of a pair arising from a mycelial filament and the other from a germinating conidium, each in any case partitioning off a terminal cell 10–27 μ long; the paired terminal cells often more or less irregularly flexuous and sometimes intertwined, conjugating apically. Zygosporangium formed about 5 μ from the union and mostly in the gametangium supplied from the mycelium, at first smoothly subspherical and commonly 9–11 μ in diameter, its membrane at maturity collapsing loosely about the zygospore; the latter distinctly yellowish, subspherical, boldly verrucose, 8–10 μ in diameter, its thick wall surrounding a living cell 5–6.5 μ in diameter.

Capturing and consuming *Amoeba verrucosa* it occurs in decaying straw (stems, leaves, and chaff) of *Hordeum vulgare* near Greeley, Colorado.

A SLENDER-SPORED ACAULOPAGE PREYING ON TWO SPECIES OF AMOEBA

Several maizemeal-agar plate cultures which after being permeated with mycelium of *Pythium ultimum* had been further planted with small quantities of deciduous leaf mold collected near Mercer, Wisconsin, on November 14, 1945, showed in ten days a somewhat extensive development of an aseptate mycelium composed of hyphae about 1.5 μ wide that were active in capturing amoebae belonging manifestly to two separate species. The captured animals referable to one species (FIG. 4, *A, a; B*) often measured about 35 μ across when they were drawn into a rounded shape. The delicate and frequently rather minutely rippled pellicle here surrounded finely granular protoplasm together with a single globose or prolate ellipsoidal nucleus, commonly 8 to 9.5 μ long and 6 to 8 μ wide, in which about twelve slightly darker oblate ellipsoidal bodies could be distinguished in scattered positions close under the peripheral membrane. Unquestionably these captives were referable to the same species of *Amoeba* that previously had been found captured habitually by my *Zoöpage thamnospira* (**7**: 141–144) and my *Acaulopage tetraceros* (**10**: 289–291). The other animals serving as prey measured commonly 30 to 35 μ across when drawn into a rounded form (FIG. 4, *C, a, b; D; E; F*). They similarly were surrounded by a thin firm pellicle, and their protoplasm, too, was of finely granular, hyaline character; but the single globose or prolate ellipsoidal nucleus they contained, which often measured 4.3 to 8 μ in length and 4 to 7 μ in width, had its darker material collected in a globose central body, 2.2 to 3 μ in diameter, that frequently offered a homogeneous appearance (FIG. 4, *C, a, b*) but frequently, again, revealed a vacuole or lacuna of variable size (FIG. 4, *D, F*). While for purposes of identification this type of nuclear organization is less distinctive than might be desired, occurring evidently among many species of *Amoeba,* large and small, it nevertheless separates decisively any animal that embodies it from animals whose darker nuclear material (chromatin) is present in plural peripheral bodies.

Individuals of both species of *Amoeba* were held securely through adhesion to the aseptate hyphae. Usually the captive was invaded by only a single haustorium (FIG. 4, *A, a, b; B; C, b; E; F*), though occasionally two haustoria were intruded (FIG. 4, *C, a*). The assimilative organs were of the pedicellate type, consisting of a usually slender pedicel together with divaricate absorptive branches approximately equal in width to the mycelial hyphae. In some instances the pedicel seemed wider than is usual for this structure (FIG. 4, *C, b*) and in others appeared, besides, somewhat shortened (FIG. 4, *E*). The captured animals of both species remained alive, stubbornly operating their contractile vacuoles until most of their protoplasmic material was expropriated. When ultimately death came, the nucleus degenerated; its degenerating substance and all granular remnants of cytoplasm then being assimilated by the fungus. Subsequently the contents of the haustorium were withdrawn backward into the parent hypha, leaving only the empty evanescent envelope of the absorptive apparatus within the equally evanescent pellicle of the rhizopod.

Thus amply nourished from abundant prey the fungus gave rise freely to asexual reproductive apparatus consisting of long, slender conidia (FIG. 5, *A, a–g; B–D*) borne erectly on short sterigmata projecting upward from procumbent hyphae (FIG. 5, *A–D; E, a–i; F, a–g*). In some instances a conidium was found delimited from its sterigma by a basal septum while protoplasm still filled the young spore throughout its length (FIG. 5, *B*). Conidia filled with protoplasm from base to tip were often found detached (FIG. 5, *G, a–c*) after being subjected to the disturbance unavoidable in covering material with a cover glass. In undisturbed cultures the conidia, after being delimited at the base, usually remained attached while a distal portion, including from one-tenth to one-fifth of the length of spore, was evacuated of contents; so that, as

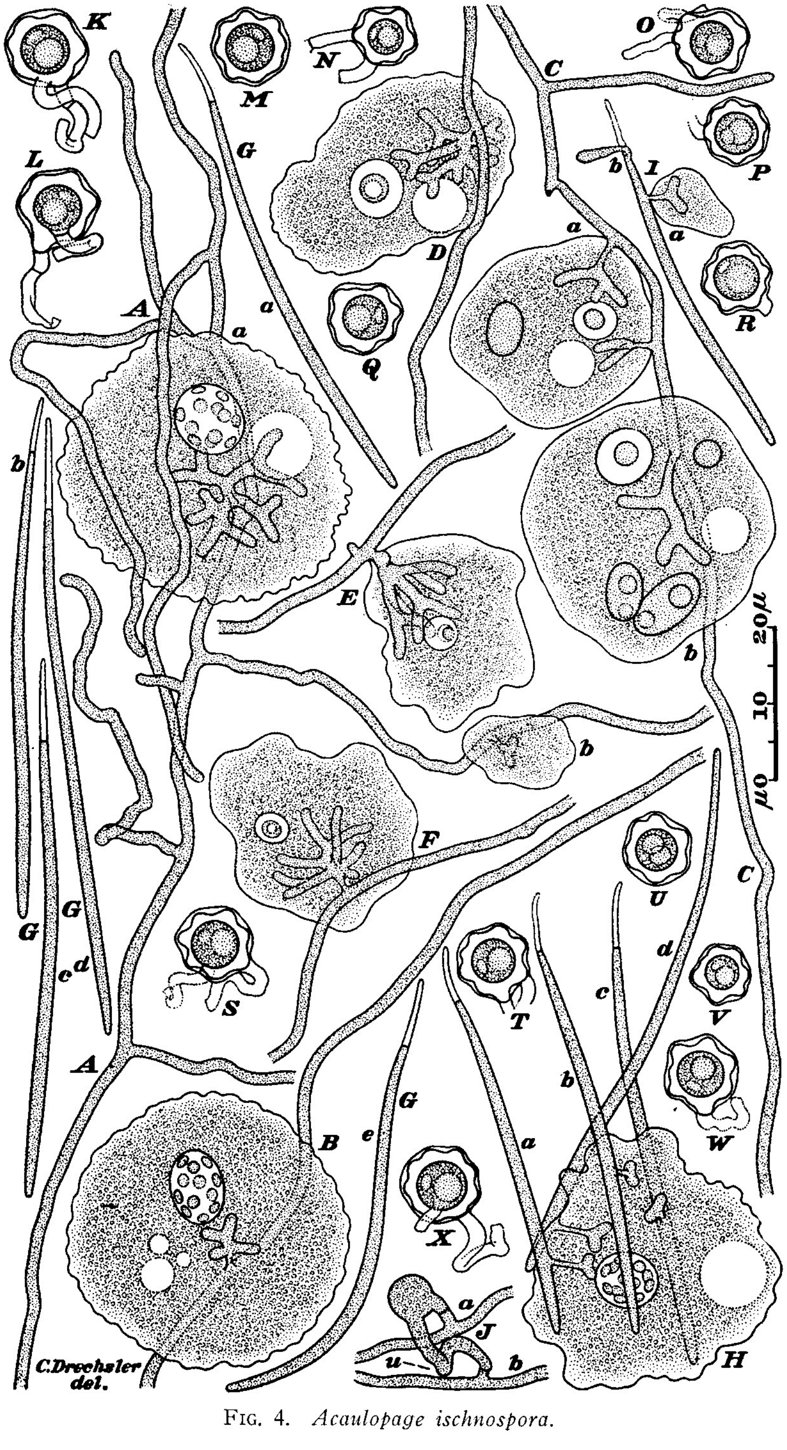

FIG. 4. *Acaulopage ischnospora.*

a rule, spores that had become detached spontaneously bore an empty portion of tubular envelope as an apical appendage (FIG. 4, *G, a–e;* FIG. 5, *H, a–p*). Whether they bore an empty appendage (FIG. 4, *H, a–c*) or were filled with protoplasm throughout (FIG. 4, *H, d*), detached conidia were readily capable of infecting a susceptible amoeba by adhering to its pellicle and then invading its sarcode with a haustorium. Usually animals attacked in such commonplace parasitic manner, especially when they were of good size, continued in their locomotion for some time, carrying the spores along with them. However, when a conidium intruded a haustorium into a smaller adhering amoeba measuring perhaps only about 10 μ across (FIG. 4, *I, a*)—a nucleus could not usually be distinguished in these undersized specimens—the animal's locomotion was arrested no less decisively than when capture was effected by a mycelial filament (FIG. 4, *A, b*). As might be expected, capture and invasion of an amoeba by a conidium did not prevent the conidium from putting forth a vegetative germ-tube (FIG. 4, *I, b*).

Usually after asexual reproduction had been proceeding for some time the fungus also produced sexual apparatus in readily noticeable quantity. As in *Stylopage rhabdoides* and many other zoöpagaceous forms, zygospore development took place only sparingly before conidia were formed; for here, too, zygophoric branches from mycelial hyphae (FIG. 4, *J, a, b;* FIG. 5, *I, a, b*) only occasionally would pair and conjugate with others of similar origin. Once a tract of substratum became bestrewn with detached conidia, however, more spirited conjugation ensued between sexual branches arising from mycelium filaments (FIG. 5, *I–M: a*) on the one hand, and sexual branches arising as germ-tubes from conidia (FIG. 5, *I, c; J–M: b*) on the other. Owing to the slenderness and frequently rather irregular course of the conjugating hyphal elements the cross-walls delimiting the gametangia were often not clearly discernible; and the place of union between the gametangia often remained uncertain for similar reasons. Where both delimiting septa (FIG. 5, *M, c, d*) and the apical union (FIG. 5, *M, u*) were clearly revealed, the globose enlargement destined for the formation of the zygospore was more often found developing in the gametangium on the branch contributed by the my-

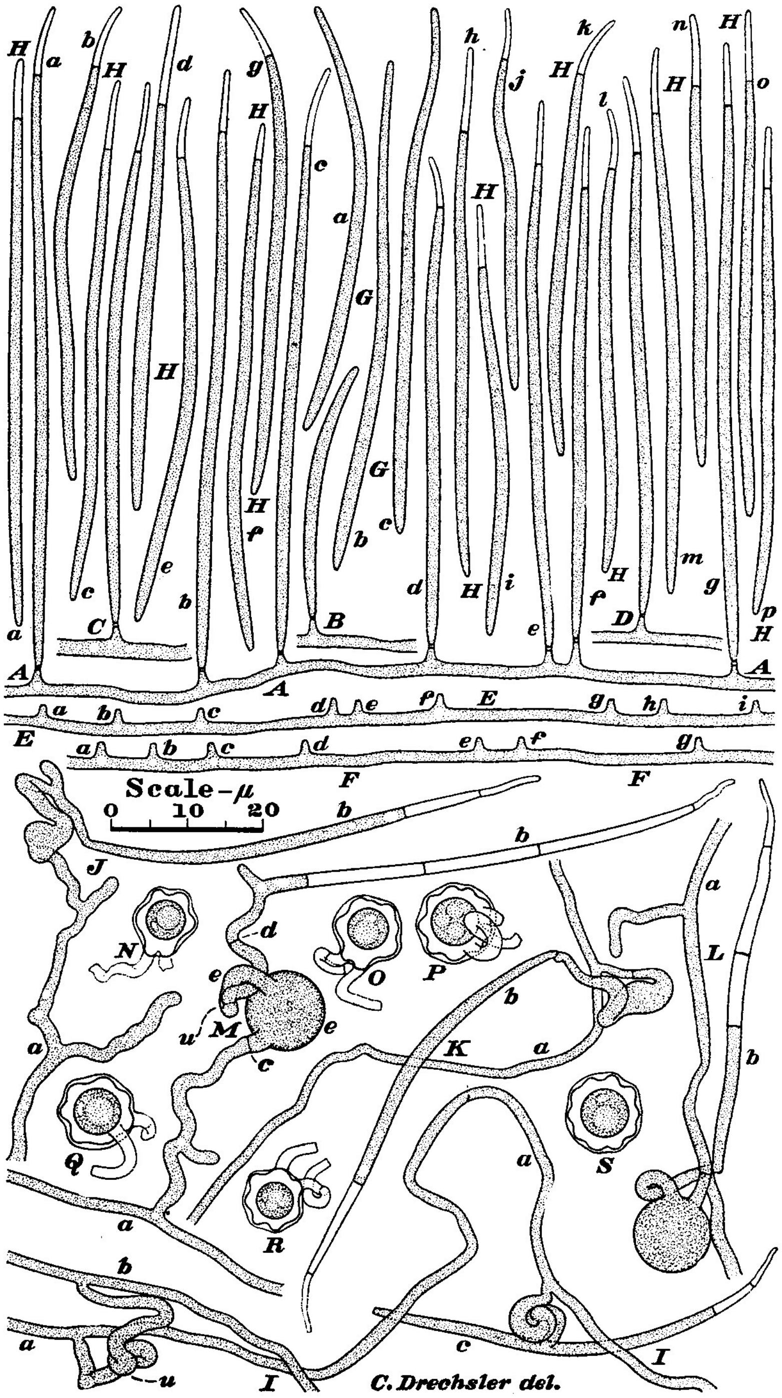

FIG. 5. *Acaulopage ischnospora.*

celial hypha (FIG. 5, *M, e*) than in the gametangium borne on the germ hypha. As in many related species the progressive evacuation of the conidium entailed in the growth of the zygosporangium was marked by deposition of two to four successive retaining walls within the conidial envelope (FIG. 5, *J–M: b*). When the sexual apparatus reached maturity (FIG. 4, *K–W;* FIG. 5, *N–S*) the membrane of the globose zygosporangium was found collapsed somewhat loosely about a pronouncedly verrucose, thick-walled, yellowish zygospore that showed an internal organization rather similar to the unitary organization familiar in the oöspores of many oömycetes—their granular protoplasm being disposed in a parietal layer surrounding a homogeneous central reserve globule.

In the genus *Acaulopage* to which it manifestly belongs, the fungus would seem to be distinguished from previously described species more especially by the unusual length and slenderness of its distally appendaged conidia. It is therefore presented as new under a specific epithet compounded in part of a word meaning both "thin" and "withered."

Acaulopage ischnospora sp. nov.

Mycelium effusum; hyphis continuis, incoloratis, filiformibus, parce ramosis, plerumque 1–2 μ crassis, ad animalia minuta inhaerentibus, pelliculam eorum perforantibus, haustorium (quandoque 2 haustoria) intus evolventibus quod protoplasma exhaurit; haustorio pedicellato, pedicello fere 2–6 μ longo, 0.5–1 μ crasso, apice abrupte latescente, semel vel quater repetite bifurco, ita 2–12 ramulos divaricatos 2–12 μ longos 1–2 μ crassos ferente. Conidia incolorata, ex sterigmatibus erectis, plerumque 1.5–4 μ altis, basi 1–1.5 μ crassis, sursum attenuatis, apice 0.5–0.7 μ crassis, inter se 3–25 μ distantibus oriunda, vulgo in partibus duabus constantia: pars supera vacua, 4–13 μ longa, basi 0.8–1.2 μ crassa, sursum leniter attenuata, saepius plus minusve marcida vel collapsa; pars infera protoplasmatis repleta, filiformis, utroque parvulum attenuata, plerumque 50–80 μ longa, 1.6–2 μ crassa. Hyphae zygosporiferae irregulariter flexuosae, quandoque inter se circumplicantes, ambae rarenter ex duabus hyphis mycelii exeuntes sed saepissime altera ex hypha mycelii altera ex conidio germinanti oriunda. Zygosporangia primo levia, sphaeroidea, plerumque 8–11 μ crassa, membrana eorum in maturitate circa zygosporam laxe collapsa; zygospora aliquantum flavida, globosa, 7–10 μ crassa, valde verrucosa, membrana ejus 1–2 μ crassa cellulam viventem sphaeralem 4.3–6.5 μ crassam stricte circumdante.

Amoebas duarum specierum 20–40 μ latas capiens consumensque habitat in foliis arborum (*Betulae, Aceris, Ulmi*) putrescentibus prope Mercer, Wisconsin.

Mycelium spreading; vegetative hyphae continuous, colorless, filamentous, sparingly branched, 1–2 μ (mostly about 1.5 μ) wide, adhering to minute animals, penetrating the pellicle of each animal thus captured, and intruding a haustorium (sometimes 2 haustoria) to appropriate the protoplasmic contents; haustoria pedicellate, the pedicel usually 2–6 μ long, 0.5–1 μ wide, abruptly enlarging and bifurcating successively 1 to 4 times and thus bearing 2 to 12 divergent assimilative branches 2–12 μ long and 1–2 μ wide. Sterigmata arising abruptly from procumbent hyphae at intervals frequently of 3–25 μ, commonly 1.5–4 μ high, 1–1.5 μ wide at the base, tapering upward to a width of 0.5–0.7 μ at the tip whereon is borne erectly a single conidium. Conidia colorless, usually composed of two parts: an upper empty membranous part generally 4–13 μ long, 0.8–1.2 μ wide proximally, gradually tapering upward, often more or less collapsed; and a lower filamentous living part tapering slightly toward both ends, commonly 50–80 μ long and 1.6–2 μ wide. Zygophoric hyphae often irregularly flexuous, sometimes winding about one another in some measure, both of them occasionally arising from separate mycelial filaments, but much more frequently only one arising from a mycelial filament, the other being supplied from a germinating conidium; zygosporangium at first smoothly subspherical and measuring 8–11 μ in diameter, but its membrane at maturity collapsing loosely about the zygospore; the latter yellowish, subspherical, 7–10 μ in diameter, boldly verrucose, having a wall 1–2 μ thick that closely surrounds a spherical living cell 4.3–6.5 μ in diameter.

Capturing and consuming two species of *Amoeba* commonly 20–40 μ in width, it occurs in decaying leaves of deciduous trees (*Betula, Acer, Ulmus*) near Mercer, Wisconsin.

AN ACAULOPAGE DESTRUCTIVE TO A RETICULATE RHIZOPOD

Several soft maizemeal-agar plate cultures which when well overgrown by *Pythium ultimum* had been further planted with small quantities of ash (*Fraxinus* sp.) leaves collected near Greeley, Colorado, early in October, 1945, showed after 35 days numerous ovoid bodies distributed sparsely over much of the agar surface, each curiously ornamented at its apex with a small tuft-like empty appendage. When the younger ovoid bodies, in which the appendage was still filled with protoplasm (FIG. 6, *A, a*), were examined closely they could often be seen attached basally to a hyphal branch that led backward to a scanty aseptate my-

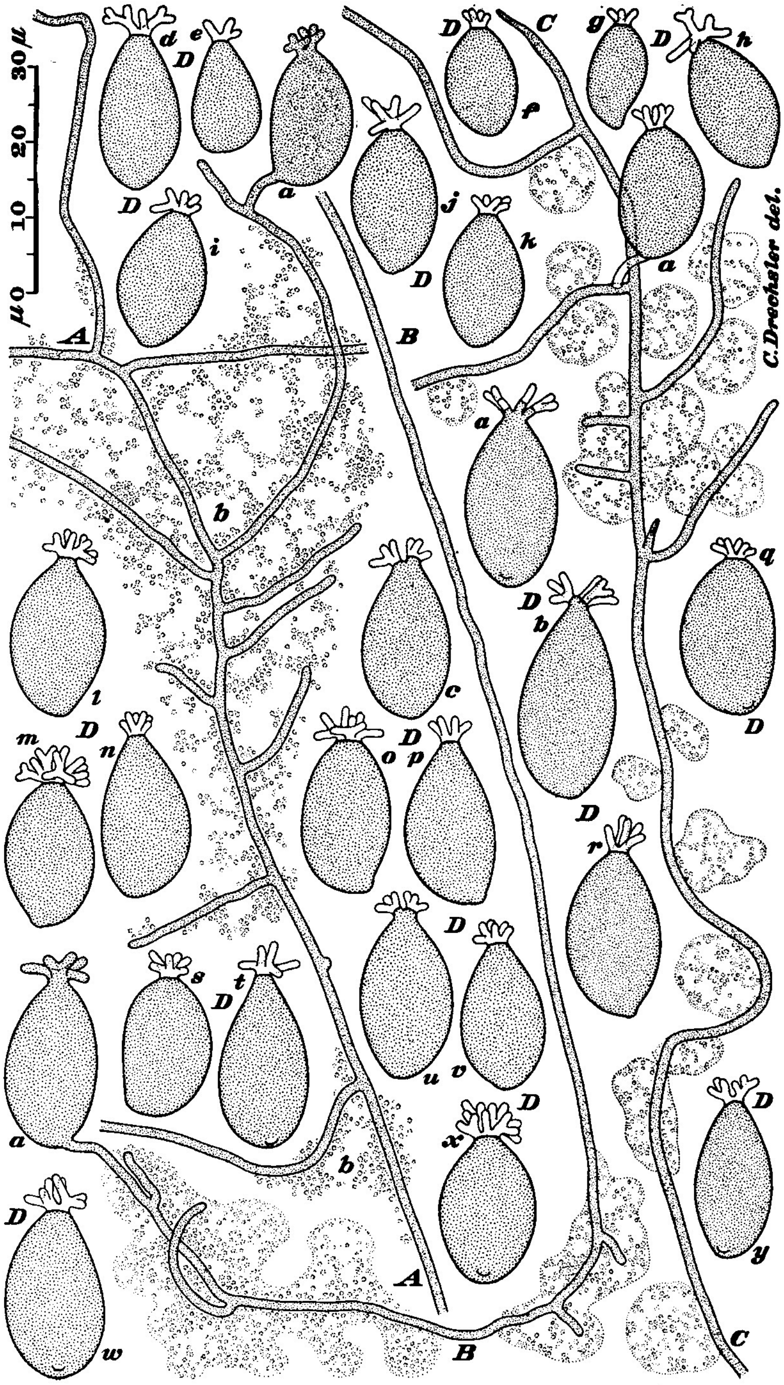

FIG. 6. *Acaulopage crobylospora.*

celium composed of filaments mostly about 1.3 µ wide. In following the longer hyphae through the soft agar substratum, branching was generally encountered at rather long intervals, but here and there, over stretches often 50 to 100 µ or more in length, branches were given off in closer arrangement. As a rule the regions of such more copious ramification had an untidy appearance, owing to the presence of promiscuously scattered deposits of loose granular material (FIG. 6, *A, b*). On continued exploration an instance came to light wherein a ramifying mycelial tract (FIG. 7, *A*) was surrounded not with the usual messy deposits, but with an extensive mass of living protoplasm that kept on changing its shape continually through protrusion and retraction of pseudopodia. Nearby, in addition, several smaller protoplasmic masses, all having finely granular consistency like the main mass, from which they had evidently become separated, were found in irregular alignment along the hyphae. The smaller masses, together with the large mass, were invaded with short, frequently somewhat curved branches (FIG. 7, *A, a–n*) presumably functional as haustoria despite their meager outward differentiation. A few minute spurs (FIG. 7, *A, o, p*) about 2.5 µ long and 0.6 µ wide, that were found projecting from one of the longer branches, offered a little the appearance of adhesive organs, though it was not evident that they helped in holding fast the protozoan. As other modifications seemed lacking, it could only be presumed that escape of the animal was prevented by adhesiveness of the mycelial filaments themselves.

The captured protozoan was not surrounded by any pellicle—at least not by any pellicle thick enough to be clearly visible under the microscope. Its irregular shape and lack of integument gave ground for the suspicion that the untidy deposits of granular material could well have come from the disintegration of similar animals—a suspicion soon amply confirmed through the discovery of protoplasmic masses showing transitional stages of granular disorganization (FIG. 6, *B, C;* FIG. 7, *B–E*). Owing to the nearly normal condition of the actively struggling captive it was without difficulty recognized as being conspecific with numerous protozoans still at liberty in the culture. For the most part these protozoans were submerged in the soft agar, where they appeared as

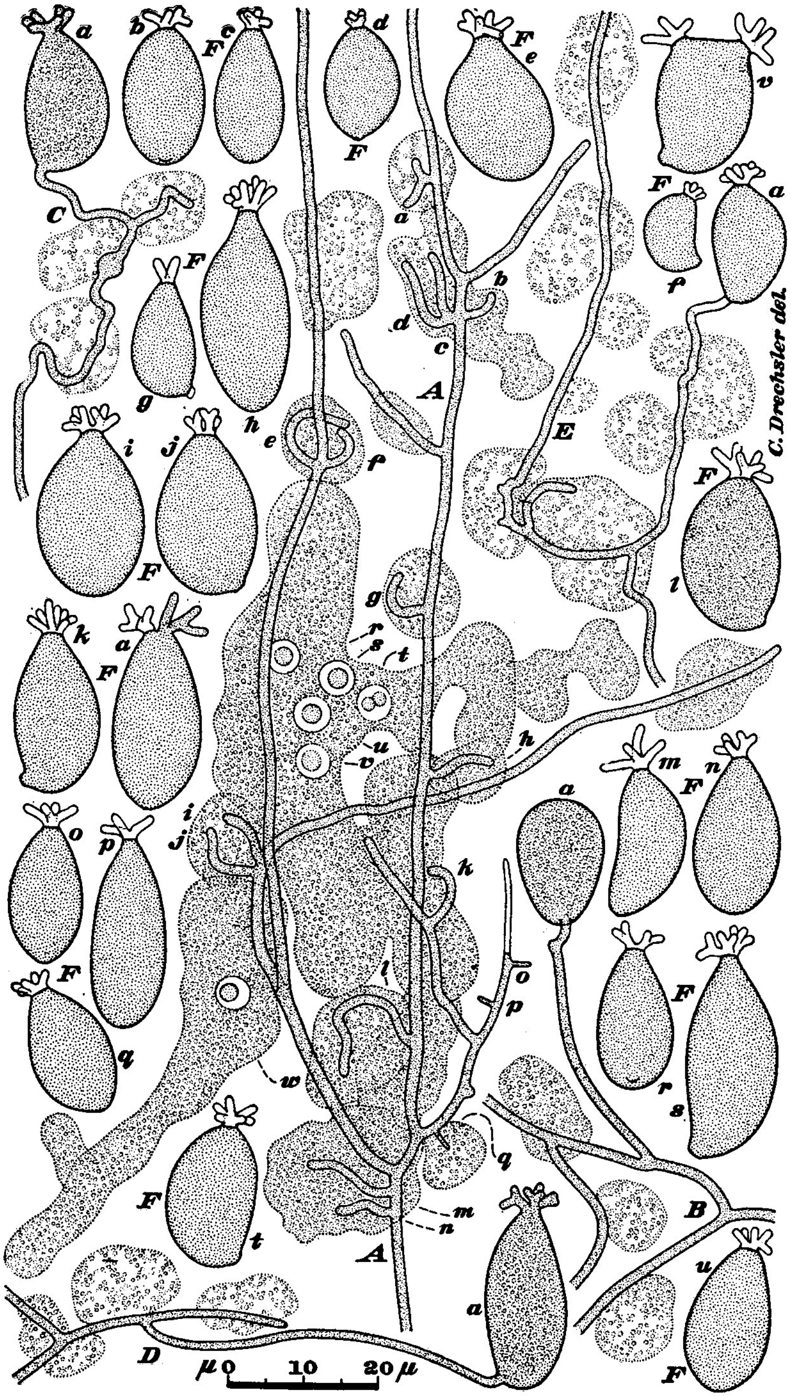

FIG. 7. *Acaulopage crobylospora.*

three-dimensional networks measuring 50 μ to 1 mm. across, and composed largely of anastomosing protoplasmic strands 2 to 6 μ wide. At the periphery of the networks new strands were protruded rather briskly, and these, on anastomosing with one another, would form additional meshes; though simultaneously other meshes nearby might disappear through retraction of protoplasmic branches. As the multiple pseudopodial activity was not usually well coördinated the locomotion of the whole animal appeared rather slow, but nevertheless was fast enough for the species to spread throughout the culture. On the surface of the agar substratum the protoplasm seemed more inclined to collect in a thin sheet from which irregular arms would extend out, freely anastomosing here and there, to enclose lacunae of variable shape and extent. At the base of the pseudopodia the animal showed very little of the strongly acuminate modification illustrated in Leidy's (**15**: pl. 47, FIGS. 5–12; pl. 48), Penard's (**16**: 549, FIGS. 1–4), Cash's (**2**: pl. 8, FIGS. 3, 4), and Kudo's (**14**: 293, FIG. 134, e) figures of the reticulate *Biomyxa vagans* Leidy—a modification that Calkins (**1**: 350) cited as a distinguishing character of the genus *Biomyxa* in his key of the subclass Proteomyxa under the class Rhizopoda. The animal seems to fit better the description of *Leptomyxa reticulata* Goodey (**13**), a proteomyxan rhizopod originally described from soft agar plate cultures that had been inoculated with soil. It would appear to conform to the characterization of the genus *Leptomyxa* with respect to multinuclear condition; for in captured specimens plural nuclei (FIG. 7, *A*, *r–w*), measuring commonly 4.4 to 5 μ in diameter and containing individually a slightly darker central body 2.3 to 2.8 μ wide, seemed recognizable. In newly captured specimens, further, as also in free animals, multiple contractile vacuoles were distributed at varying intervals. The colorless, highly transparent character, and finely granular, almost homogeneous consistency of its protoplasm readily distinguished the animal from *Penardia mutabilis* Cash (**2**: 90–91), as well as from other colored genera compiled in the Proteomyxa.

In initiating asexual reproduction, hyphal branches little differentiated from other mycelial elements gave rise terminally to swellings that at first were of subspherical shape. After some time, however, further enlargement took place mainly by elongation vertically into the air (FIG. 7, *B, a*), so that the swelling soon came to consist of an egg-shaped body with its long axis often nearly perpendicular to the supporting filament, its broadly rounded basal end resting in the agar, and its narrower end extended erectly into the air (FIG. 6, *A, a; B, a;* FIG. 7, *C, a; D, a*); the ovoid shape being conspicuously modified through apical prolongation of the body into a tuft of divergent processes having individually about the same width as the mycelial hyphae. Thereupon, as the protoplasm was withdrawn from the supporting hyphal branch and a basal retaining wall was laid down, the ovoid body became delimited as a conidium (FIG. 6, *C, a;* FIG. 7, *E, a*). Meanwhile the contents also of the distal processes were withdrawn backward, and a retaining wall was formed to delimit the living conidial cell from the empty membranous topknot. In some instances where the apical branches were relatively long—5 μ being approximately their greatest length (FIG. 6, *D, a;* FIG. 7, *F, a*)—a cross-wall might be laid down in them to mark an intermediate stage in their evacuation. Now and then some of the branches would become evacuated while others still retained their contents (FIG. 7, *F, a*); and occasionally, again, the protoplasmic mass would be left extending slightly into the proximal portion of the topknot, so that plural retaining walls were needed to delimit two or more tubular elements separately (FIG. 6, *D, b, c*). Where a single retaining wall delimited the living cell distally in the usual manner (FIG. 6, *D, d–y;* FIG. 7, *E, b–u*) considerable diversity in the appearance of the membranous topknot, nevertheless, came about from differences in the number, length, and divergence of its constituent branches. In a few instances conidia of unusual width at the distal end were found ornamented with two well-separated tufts (FIG. 7, *F, v*).

Although the fungus is here described primarily from cultures prepared with Colorado material, its conidia have come under observation repeatedly for more than a decade in cultures planted with leaf mold and other kinds of decomposing vegetable detritus originating from different localities in Maryland, Virginia, Delaware, New York, Maine, and Wisconsin. However, owing to usually rather early evanescence of the branches bearing them, their connection with a predaceous mycelium was not ascertained previously. A mistaken inference as to their probable identity was drawn from their fortuitous resemblance to frequently intermixed conidia produced by an apparently undescribed species of *Rhopalomyces* that often developed in the same soft agar plate cultures; the error being encouraged not merely by general similarity in size and shape, but also by the circumstance that the *Rhopalomyces* spores had their thin outer membrane extended emptily at either end. Yet the loosely protruding membrane of the *Rhopalomyces* spore was never seen disposed in a tuft; so that the predaceous fungus may conveniently be described under a specific epithet having reference to its curiously topknotted conidia.

Acaulopage crobylospora sp. nov.

Mycelium sparsum; hyphis filiformibus, incoloratis, primum continuis, plerumque parce ramosis, 1–1.8 μ (vulgo circa 1.3 μ) crassis, animalia minuta impedientibus, deinde ramulos assumentes fere 5–25 μ longos in eadem intrudentibus qui protoplasma magnam partem exhauriunt. Conidia in superficie materiae animalia ambientis sparsim oriunda, ex cellula viventi et crista vacua constantia: cellula viventi incolorata vel aliquantulum fumida, ovoidea, 10.5–27 μ longa, 6.8–14.3 μ crassa; crista vacua in 2–15 tubulis 1–5 μ longis 0.8–1.3 μ crassis consistens, saepius ad instar arbusculae divaricata.

Speciem *Leptomyxae* (forsitan *Leptomyxam reticulatam*) impediens necansque habitat in foliis *Fraxini* proper Greeley, Colorado, atque in humo silvarum et aliis materiis plantarum putrescentibus prope Beltsville, Maryland, et prope Georgetown, Delaware, et prope Webster, New York, et prope Presque Isle, Maine, et prope Butternut, Wisconsin, et in Arlington, Virginia.

Mycelium scanty; vegetative hyphae filamentous, colorless, at first continuous, for the most part only meagerly branched, measuring 1–1.8 μ (commonly about 1.3 μ) in width, holding minute animals and intruding into them assimilative branches usually 5–25 μ long which largely appropriate the protoplasmic contents. Conidia formed sparsely on the surface of the material surrounding the animals, colorless or slightly smoky, their single living cell usually of ovoid shape, mostly 10.5–27 μ long and 6.8–14.3 μ wide, bearing on its apex a frequently bush-like branching crest consisting of 2 to 15 empty membranous tubules 1–5 μ long and 0.8–1.3 μ wide.

Capturing and destroying *Leptomyxa* sp. (perhaps *Leptomyxa reticulata*) it occurs in decaying leaves of *Fraxinus* sp. near Greeley, Colorado, and also in deciduous leaf mold and other decaying plant materials near Beltsville, Maryland, near Georgetown, Delaware, near Webster, New York, near Presque Isle, Maine, near Butternut, Wisconsin, and in Arlington, Virginia.

DESTRUCTION OF A RETICULOCYTE RHIZOPOD BY A PREDACEOUS HYPHOMYCETE

In a culture abundantly infested with the reticulate rhizopod habitually taken as prey by *Acaulopage crobylospora,* this animal was found being captured and destroyed by a septate mycelium belonging presumably to a hyphomycete of the predaceous series most familiarly exemplified in *Arthrobotrys oligospora* Fres. On the longer filaments of this mycelium (FIG. 8, *A, B*) were borne here and there irregularly ramifying lateral branches. These branches were found surrounded by the same untidy granular deposits habitually associated with *A. crobylospora,* and they manifestly represented special assimilative elements despite their meager outward differentiation. Although the septate mycelium, with its constituent hyphae measuring about 3 μ in width, was appreciably coarser than the continuous mycelium of the zoöpagaceous form, it yet bore

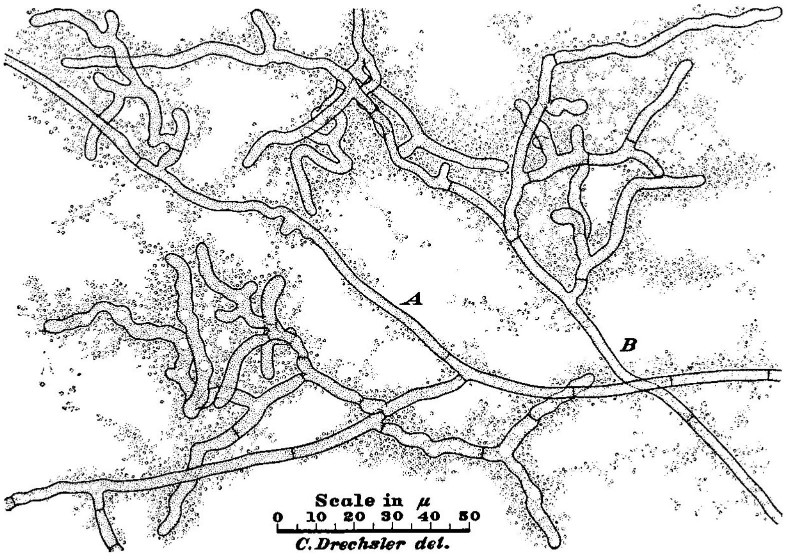

FIG. 8. Mycelium of a hyphomycete.

a striking resemblance to the latter—a resemblance obviously deriving from similarity in biological relationship to the same peculiar rhizopod. Unfortunately no reproductive bodies of any kind were produced whereby the specific identity of the septate mycelium might have been determined. A possibility worthy of consideration is that this mycelium might have belonged to one of the several described species, including notably *Dactylella atractoides* Drechsl. (**11**: 357–360), *Dactylella heptameres* Drechsl. (**11**: 352–354), *Dactylella rhombospora* Grove (**6**: 539–540), *Dactylella rhopalota* Drechsl. (**11**: 354–357), *Dactylella tenuis* Drechsl. (**6**: 538–539), and *Dactylaria pulchra* Linder (**11**: 349–352) which, though obviously referable taxonomically to the predaceous series of hyphomycetes, have not hitherto been observed in any important biological relationship to animals. At the time the species mentioned were tried out in cultures infested with nematodes and rhizopods of various kinds, the appearances usual in the destruction of non-pelliculate proteomyxan rhizopods were unknown to me, and therefore would very probably have been disregarded had they been present.

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EXPLANATION OF FIGURES

FIG. 1. *Stylopage rhabdoides;* drawn to a uniform magnification with the aid of a camera lucida; × 500 throughout. *A,* Specimen of *Amoeba verrucosa* captured through adhesion to a meagerly branched mycelial filament from which a single haustorium has been intruded. *B, C,* Specimens of *A. verrucosa,* each captured through adhesion to a branched hypha from which two haustoria have been intruded. *D,* Specimen of *A. verrucosa* captured through adhesion to a branching hypha somewhat extensively enwrapping it; three haustoria have been intruded into the animal. *E,* Specimen of *A. verrucosa* held captive through rather extensive adhesion of mycelial hyphae; from these hyphae three haustoria have been intruded into the animal. *F,* Specimen of *A. verrucosa* captured through somewhat extensive adhesion to two branched hyphae, from each of which two haustoria have been intruded. *G,* Two specimens of *A. verrucosa, a* and *b,* huddled together and extensively enwrapped by hyphal elements belonging to three branching systems; seven haustoria have been intruded into *a,* six into *b.* *H,* Small specimen of *A. verrucosa* which after being captured through adhesion to a mycelial hypha, and subsequently being almost completely expropriated of its protoplasmic content by two rangy haustoria intruded into it, has succumbed to death.

FIG. 2. *Stylopage rhabdoides;* asexual reproductive apparatus drawn to a uniform magnification with the aid of a camera lucida; × 1000 throughout. *A–D,* Portions of prostrate hyphae from each of which has arisen an erect conidiophore, *a,* continuous at its narrowed distal end with a young conidium, *b.* *E,* Prostrate hypha from which has arisen an erect conidiophore, *a,* which is still continuous with the young conidium, *b,* being formed distally on it; from *a* has been extended a lateral branch, *c,* which is continuous with the young conidium, *d.* *F,* Portion of prostrate mycelial filament from which has arisen an erect hypha, *a,* that has given off a branch, *b,* which is still continuous with the young conidium, *c,* being formed terminally on it. *G, H,* Portions of prostrate hyphae, each with an erect conidiophore, *a,* that has become delimited from the conidium, *b,* borne at its tip. *I,* Portion of prostrate hypha from which have arisen three conidiophores, *a–c,* each delimited distally from the single conidium, *d–f,* borne terminally on it. *J,* Random assortment

of detached conidia, *a–z,* showing usual variations in size and shape. *K,* Conidium germinating.

FIG. 3. *Stylopage rhabdoides;* sexual reproductive apparatus drawn to uniform magnification with the aid of a camera lucida; × 1000 throughout. *A,* Two mycelial hyphae, *a* and *b,* that have put forth the sexual branches *c* and *d,* respectively, which have paired and are conjugating apically; *u,* place of union. *B, C,* Two young units of sexual apparatus; in each a conidium, *a,* and a mycelial hypha, *b,* have produced the sexual branches *c* and *d,* respectively, which through deposition of septa have formed gametangia that are conjugating apically. *D,* Two units of sexual apparatus derived from a conidium, *a,* and two separate mycelial hyphae *b* and *c;* the two sexual branches, *d* and *e,* arising as germ-tubes have been cut off to form gametangia which have conjugated severally with the gametangia formed on the sexual branches *f* and *g,* originating from the hyphae *b* and *c.* *E,* Two sexual units derived from a conidium, *a,* and a mycelial filament, *b;* the germ hyphae *c* and *d* have formed gametangia that have conjugated with others formed on the two sexual branches, *e* and *f,* extended from the filament *b;* a third sexual branch, *g,* given off by the filament *b* has attached itself as a supernumerary element to the conjugating pair *c* and *e.* *F, G,* Two units of sexual apparatus, each deriving from a conidium, *a,* and a mycelial filament, *b;* a gametangium supplied mainly, if not wholly, by the germ-tube *c* having conjugated with a gametangium borne on a sexual branch, *d,* from the mycelial hypha. *H,* Two sexual reproductive units derived from a germinating conidium, *a,* and two mycelial hyphae, *b* and *c;* gametangia supplied by two germ hyphae, *d* and *e,* have conjugated with gametangia borne on the sexual branches *g* and *h,* coming from *b* and *c,* respectively; the conidium has further put forth a third germ-tube, *f.* *I, J,* Two sexual reproductive units, each deriving from a conidium, *a,* and a mycelial hypha, *b;* in each unit a gametangium borne on a germ-hypha, *c,* has conjugated with one supplied by a sexual branch, *d,* coming from mycelial hypha *b.* *K–U,* Random assortment of mature zygospores showing usual variations in size, shape, and internal organization, as well as in disposition of membranous zygosporangial envelope. (*u,* Place of union between paired gametangia.)

FIG. 4. *Acaulopage ischnospora;* drawn at a uniform magnification with the aid of a camera lucida; × 1000 throughout. *A,* Portion of mycelium with two captured amoebae, *a* and *b,* into each of which a haustorium has been intruded; the captive *a* has a nucleus with about twelve flattened peripheral bodies. *B,* Portion of hypha with a captured amoeba having a nucleus of same structure as in *A, a;* a haustorium bearing four assimilative branches has been intruded. *C,* Portion of hypha with two captured amoebae, *a* and *b,* each containing a nucleus with a darkish central body; captive *a* shows an ingested fungus spore on the left side; captive *b* shows two similar ingested spores on the lower side and a smaller spore on the upper right side. *D–F,* Portions of hyphae, each holding captive a specimen of the same *Amoeba* sp. as that shown in *C, a* and *b;* a well developed haustorium is present in each animal. *G,* Detached conidia, *a–e.* *H,* Four conidia, *a–d,* attached to an *Amoeba* of the same species as *A, a;* the ypsiliform haustorium intruded by each conidium illustrates an early stage of development. *I,* Conidium that has captured a small amoeba, *a,* and has intruded a haustorium into it; a

germ-tube, *b,* is being extended from a distal position adjacent to the apical appendage. *J,* Two mycelial hyphae, *a* and *b,* that have supplied sexual branches with conjugating gametangia; a globose zygosporangium is being formed in the gametangium from *a; u,* place of union. *K–X,* Mature zygospores showing usual variations in size, shape, and internal organization, as well as in disposition of the surrounding membranous envelope.

FIG. 5. *Acaulopage ischnospora;* drawn at a uniform magnification with the aid of a camera lucida; × 1000 throughout. *A,* Portion of prostrate hypha with seven sterigmata, each bearing a (*a–g*) conidium that terminates in an empty appendage. *B,* Portion of prostrate hypha with a sterigma from which has been delimited a small, somewhat immature conidium still filled with protoplasm throughout. *C, D,* Portions of prostrate hyphae, each supporting erectly a mature, distally appendaged conidium. *E, F,* Portions of prostrate mycelial hyphae whereon are borne denuded sterigmata in numbers of nine (*a–i*) and seven (*a–g*), respectively. *G,* Somewhat immature detached conidia, *a–c,* filled with protoplasm throughout. *H,* Mature detached conidia, *a–p,* showing usual variations in size and shape, and in length of empty appendages. *I,* Mycelial hypha, *a,* that has produced two sexual branches, one of which has paired with a sexual branch from another mycelial hypha, *b,* while the other has paired with a sexual germ hypha from a detached conidium, *c; u,* place of union. *J–L,* Sexual reproductive units wherein a sexual branch from a mycelial hypha, *a,* has conjugated with a germ hypha coming from a detached conidium, *b.* *M,* Sexual reproductive unit likewise resulting from conjugation of a gametangium contributed by a mycelial hypha, *a,* with a gametangium supplied by a germinating conidium, *b; c, d,* cross-walls proximally delimiting the two gametangia; *e,* gametangium of mycelial origin in which the zygosporangium is developing; *u,* place of union. *N–S,* Mature zygospores showing usual variations in size, shape, and internal organization, as well as in disposition of the surrounding membrane.

FIG. 6. *Acaulopage crobylospora;* drawn at a uniform magnification with the aid of a camera lucida; × 1000 throughout. *A,* Portion of branching mycelium surrounded with untidy deposits of granular protoplasmic detritus, *b;* connected to it is a full-grown conidium, *a,* whose apical processes are still filled with protoplasm. *B,* Portion of mycelium bordered with masses of degenerating protoplasm; connected with it is a full-grown but slightly immature conidium, *a.* *C,* Portion of mycelium bordered with masses of degenerating protoplasm; connected to it is a mature conidium, *a,* with empty apical appendage. *D,* Random assortment of detached conidia, *a–y,* showing usual variations in size and shape of the ovoid living cell as well as in make-up of the apical appendage.

FIG. 7. *Acaulopage crobylospora;* drawn at a uniform magnification with the aid of a camera lucida; × 1000 throughout. *A,* Portion of branching mycelium with a captured specimen of *Leptomyxa* sp. (possibly *L. reticulata*); *a–n,* assimilative branches; *o–q,* narrow spurs perhaps having an adhesive function; *r–w,* nuclei of rhizopod. *B,* Portion of mycelium bordered with masses of degenerating protoplasm; connected to it is a young growing conidium, *a.* *C, D,* Small portions of mycelium, each bordered with several masses of degenerating protoplasm; connected to each portion is a full-grown conidium, *a,* with its apical outgrowths still filled with protoplasm.

E, Portion of mycelium bordered with masses of degenerating protoplasm; connected to it is a mature conidium, *a,* with empty appendage. *F,* Random assortment of detached conidia, *a–v,* showing variations in size and shape of the living ovoid cell, as well as in make-up of the apical appendage; in *a* three of the six branches in the appendage are still filled with protoplasm; in *v* two appendages are present on opposite sides of the flattened apical end.

FIG. 8. Mycelium of a hyphomycete distributed in an untidy expanse of granular detritus left after disintegration of a captured specimen of *Leptomyxa* sp. (possibly *L. reticulata*); two main mycelial filaments, *A* and *B,* are present, together with several irregularly ramifying assimilative branches attached to them.