Reprinted from MYCOLOGIA, Vol. XXXI, No. 2, 128-153, March-April, 1939
Printed in U. S. A.

A FEW NEW ZOÖPAGACEAE DESTRUCTIVE TO LARGE SOIL RHIZOPODS

A FEW NEW ZOÖPAGACEAE DESTRUCTIVE TO LARGE SOIL RHIZOPODS

CHARLES DRECHSLER

(WITH 7 FIGURES)

Additional fungi referable to the Zoöpagaceae having been brought to light through inspection of old Petri plate cultures started from various decaying vegetable materials, three of the larger forms among them will be newly described herein. Like most members of the family previously made known, each of the three forms were found subsisting exclusively on a particular species of rhizopod; all other microscopic animals infesting the agar substrata consistently remaining unharmed. The enormous destruction suffered by the protozoan concerned in each instance—destruction amounting often to extermination of all active individuals present—suggests that the feeding operations of the Zoöpagaceae may have an important relation to the pronounced fluctuations in populations of soil protozoa disclosed when determinations of their numbers are made from day to day (1).

COCHLONEMA MEGALOSOMUM

The most impressive of the three fungi was found killing off a large *Amoeba* in aging *Pythium* cultures to which had been added some pinches of decaying plant materials collected in open woods with a luxuriant undergrowth of coarse herbaceous weeds, near Beltsville, Md., early in October 1937. As even the smaller infected rhizopods measured about 75 μ in diameter when drawn into an approximately rounded shape (FIG. 1, *A*, *B*), while the larger specimens of similar conformation often attained a width of 125 μ (FIG. 1, *D*), the animals were of dimensions making them visible to the naked eye as minute specks peppered over the surface of the substratum. A thick pellicle surrounded the massive sarcode, whose pseudopodial protuberances it confined usually in broadly lobate contours. One (FIG. 1, *B*, *z*: FIG. 2, *A*, *z*; *B*, *z*),

two (FIG. 2, *C, y, z*) or three (FIG. 1, *D, x, y, z*) digestive vacuoles were often present, and contained always accumulations of somewhat large bacteria. The single large prolate ellipsoidal nucleus, measuring mostly 18 to 24 μ in length and 13 to 19 μ in width, revealed in healthy condition an outer hyaline layer surrounding a perceptibly darker central portion (FIG. 1, *A, n; B, n; C, n; D, n:* FIG. 2, *A, n; B, n; C, n*). Because of a close similarity in nuclear structure thus evident, there can be little doubt that the *Amoeba* concerned here is specifically identical with the one encountered earlier as the prey of a hyphomycete I then described as *Dactylella tylopaga* (4). This identity encourages the application again of the binomial *Amoeba verrucosa* Ehrenb., whereby, besides, the rhizopod is distinguished advantageously from the several animals that in accordance with a deplorably indiscriminate usage sanctioned in protozoological writings I have elsewhere discussed as *A. terricola* Greeff. With respect to outward shape and nuclear structure no less than with respect to shape and appearance of contractile and digestive vacuoles, the rhizopod conforms well to at least one of the specimens figured by Leidy as *A. verrucosa* (8: *pl. 3, fig. 36*), though differing certainly from some other specimens depicted as likewise illustrative of that species (8: *pl. 3, fig. 34, 38*).

Infection of the *Amoeba* is accomplished through germination of an adhering conidium. After the germ-tube has penetrated the pellicle and grown a short distance, usually not much in excess of 5 μ, into the granular sarcode, it gives rise to a terminal expansion (FIG. 1, *A, a*) into which are soon received the entire conidial contents. The globose body thus formed then becomes separated from the germ-tube, and begins autonomous growth within the animal's protoplasmic interior. At the beginning the young thallus (FIG. 1, *A, b:* FIG. 2, *A, a*) shows little to distinguish it from the thalli of other members of the Zoöpagaceae endoparasitic in Amoebae. A more pronounced distal widening than is known in any related form hitherto described becomes evident as the body elongates into the latter half of its first spiral turn (FIG. 1, *A, c:* FIG. 2, *B, a–e*). A maximum width is usually attained when the hypha has made one and one-half turns, a first bifurcation then intervening to reduce the width perceptibly in the two resulting

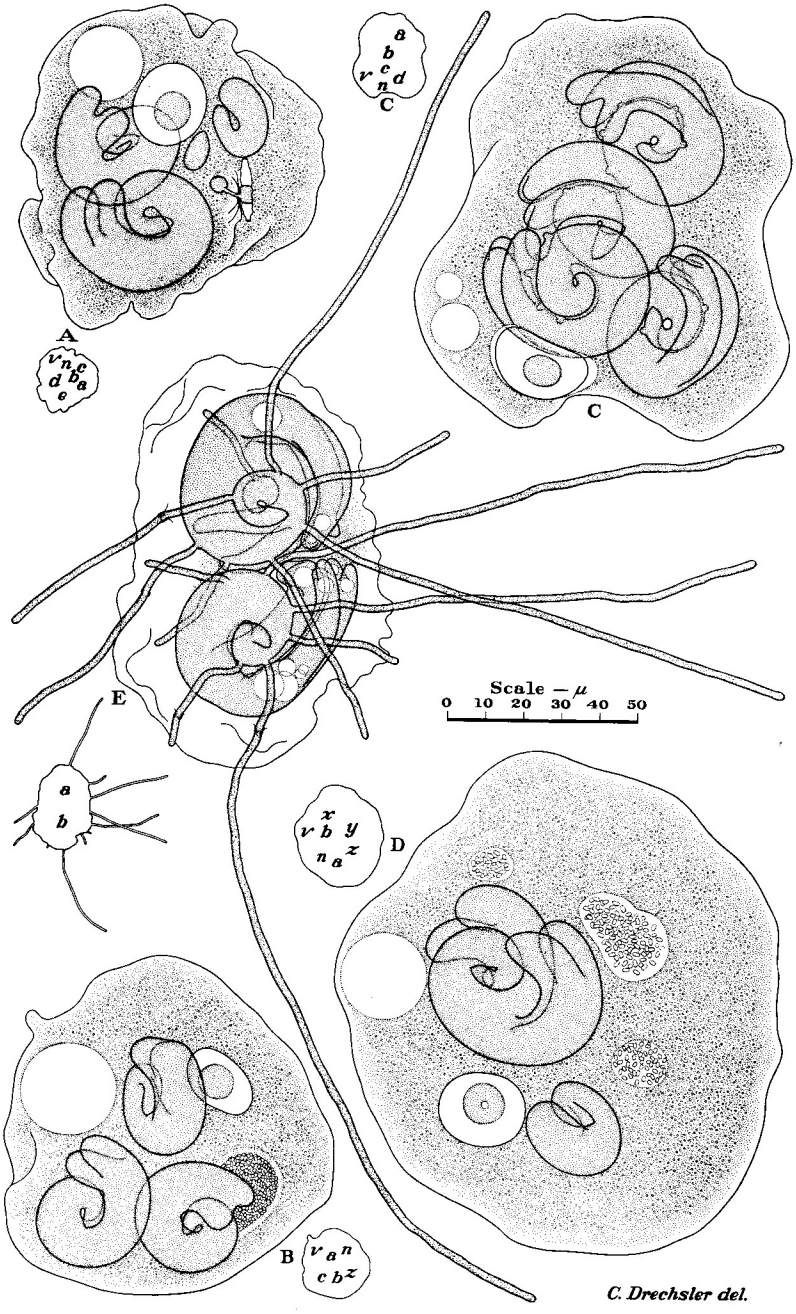

FIG. 1. *Cochlonema megalosomum.*

elements. In instances where a single thallus develops in a large animal, it may describe nearly three successive turns and bifurcate successively four times before the materials of the host are finally exhausted (FIG. 2, *E:* FIG. 3, *A*). Such well developed thalli, more than any other structure now known in the family, reveal the magnificence of form and dimensions that has long made the Zygomycetes a favorite group among mycological virtuosi. Bifurcation here often presents a peculiarity in that it frequently takes place in the plane of the first coil, rather than in a plane perpendicular thereto; so that the daughter elements, instead of being equidistant from and symmetrically placed relative to the axis of the first coil, are represented by an inner branch and an outer one. As a result of this peculiarity in branching, the well-developed thallus of the present species is usually disposed in a markedly flattened spiral rather than in a globose clew as are generally the thalli of *Endocochlus gigas* Drechsl. (5) and *Cochlonema megaspirema* Drechsl. (6).

The parasite regularly gives rise to profuse conidial apparatus. At a stage when the host animal, if weakened through expropriation in large part of its protoplasmic contents, yet remains capable of movement and continues to operate its contractile vacuole in an apparently normal manner, wart-like protuberances appear on the older or proximal portion of the thallus. Whenever the spiral vegetative body is of relatively small volume, as often when it shares the nourishment in an animal with a number of other similar bodies, these protuberances are restricted closely to the outer profile of the first coil, along which they are usually spaced at approximately equal intervals (FIG. 1, *C, a–d*). Apparently these protuberances undergo little change until the *Amoeba* has been quite disabled from advanced depletion of its substance, when they grow out into filaments (FIG. 2, *D, d, e*) thrusting their way through the pellicle (FIG. 1, *E*) and extending themselves more or less erectly into the air to heights often in excess of 0.5 mm. The aerial hyphae thus formed soon become converted into chains of conidia (FIG. 2, *E*); wherefore the fungus manifestly is to be referred to the genus *Cochlonema.*

Like the homologous filaments of many allied catenulate forms, the continuous aerial hyphae show in their proximal portion little

external modification of any kind, but in their median and distal portions reveal pronouncedly warty sculpturing and regularly spaced constrictions (FIG. 3, *C*). Consequently, the basal members of a conidial chain are mostly cylindrical structures with very short connections, only slightly constricted (FIG. 2, *F*: FIG. 3, *B*, *a–c*; *E*, *r*), whereas the spores in median and distal positions are shorter, fusiform, pronouncedly warty bodies, tapering toward both bluntly rounded ends (FIG. 2, *G*, *a–z*; *H*, *a–t*: FIG. 3, *E*, *a–q*, *s–z*), where they are joined to their neighbors by narrow isthmi (FIG. 3, *D*). For the most part the connecting isthmi would seem not wholly empty, since the convex end walls of neighboring conidia often come into contact centrally with one another. In a general way, despite some differences in dimensions and shape, the conidia of the fungus recall those of the congeneric *Cochlonema megaspirema*.

Though large thalli, like the smaller ones, emit conidiiferous hyphae only from their proximal portions, they utilize for such emission a broader expanse of the surface available in these portions (FIG. 2, *E*: FIG. 3, *A*). Regardless of the size of the thallus, the progressive evacuation of protoplasmic contents accompanying production of fertile hyphae was never seen to be associated with the laying down of successive cross-walls so familiar in allied forms. The number and quantity of sporiferous filaments arising from an infected animal depends naturally altogether on the animal's size rather than on the number of thalli participating in its expropriation. Well developed specimens of the susceptible *Amoeba* often yield more than a dozen fertile hyphae (FIG. 3, *A*) that collectively may become visible to the naked eye as a minute whitish speck, and that under a microscope of low magnification appear loosely intertangled in an erect and often impressively luxuriant tuft. Disintegration of the aerial chains leaves hundreds of conidia strewn about on the substratum, each ready to adhere to any susceptible *Amoeba* that may by chance pass over it.

Among several hundred infected animals only three were observed to be instrumental in the development by the parasite of a sexual stage. Judging from this meager material, the fungus would seem to be strictly heterothallic. Thus in each of the seven pairs of sexual hyphae whose conjugation resulted in the seven

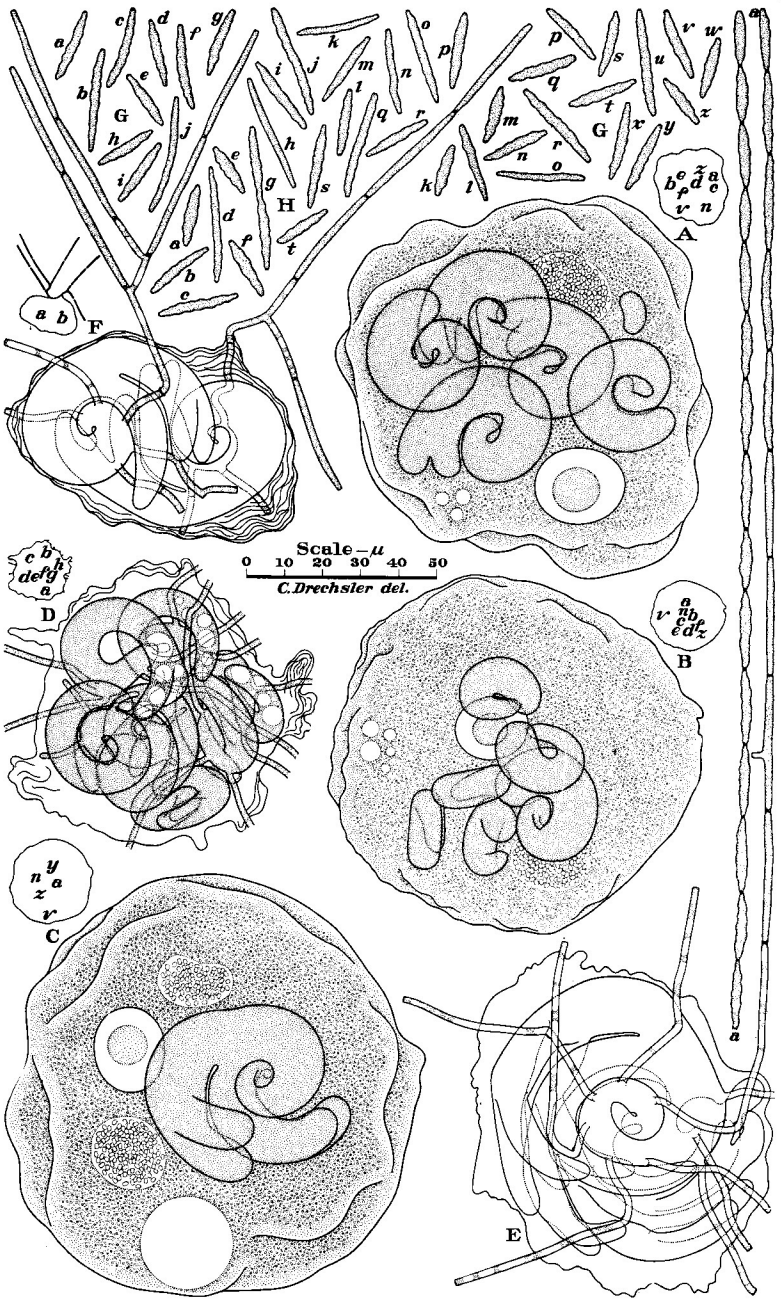

FIG. 2. *Cochlonema megalosomum.*

zygosporangia shown in figure 3, *F*, one hypha has its origin either in thallus *a* or thallus *b*, while the other has its origin either in thallus *c* or thallus *d*. Marked distal inflation of the sexual filaments provides a conspicuous feature in the morphology of the species. The zygosporangia, borne close to the union of the sexual hyphae, are to be reckoned among the largest known in the family. Their stubby protuberances invite comparison more especially with the homologous protuberances of *Cochlonema odontosperma* Drechsl. (6), though lacking any cuspidal modification. In two of the thalli that had participated in sexual reproduction, a few heavy crosswalls were observed (FIG. 3, *F, a, d*), these presumably having been inserted as retaining septa at the time the vegetative elements were being evacuated.

A word meaning "large-bodied" is deemed appropriate as a specific name for the fungus.

Cochlonema megalosomum sp. nov.

Hyphae alitae 4–20 μ crassae, semel vel quater repetite dichotomae, semel vel ter spiraliter convolutae, saepe praecipue ubicumque solitariae in animalibus magnis crescentes in spiram mirificam se circumvolventes. Conidia hyalina, 8–38 μ longa, 1.6–3.6 μ crassa, in catenulas 15–35-sporas, plus minusve erectas, 300–700 μ longas digesta, prope basin catenulae fere longiuscula, angusta, levia, cylindrata vel filiformia, in medio et prope apicem catenulae fere latiora, breviora, crasse verrucosa, fusiformia, utrimque abrupte rotundata. Hyphae zygosporiferae 25–75 μ longae, basi circa 1.5 μ crassae, sursum latescentes, apice 6–12 μ crassae, binae ex duabus hyphis alitis enatae. Zygosporangia sphaeroidea, saepe 13–16 μ crassa, 25–45 verrucis circa 1 μ altis basi circa .8 μ latis ornata; zygosporis maturis ignotis.

Amoebam verrucosam (sensu strictiore) enecans habitat in materiis plantarum putrescentibus prope Beltsville, Maryland.

Vegetative hyphae 4 to 20 μ wide, simple or repeatedly dichotomous up to 4 times, and wound spirally into a somewhat flattened coil of 1 to 3 successive turns. Conidia hyaline, 8 to 38 μ (average 20.5 μ) long, 1.6 to 3.6 μ (average 2.6 μ) wide, formed in numbers from 15 to 35 in more or less erect chains often 300 to 700 μ long—those in the proximal portion of a chain usually long, narrow, smooth, cylindrical to filiform—those in the middle and distal portions of a chain shorter, wider, rather coarsely warty, fusiform, abruptly rounded at the ends. Zygophoric hyphae 25 to 75 μ long, approximately 1.5 μ wide at the base, widening to a diameter of 6 to 12 μ at the apex, those of each conjugating pair arising from separate vegetative hyphae, each becoming divided by a

FIG. 3. *Cochlonema megalosomum.*

septum placed 20 to 30 μ below its apex; zygosporangium formed close to the union of the sexual hyphae, subspherical, sessile, usually 13 to 16 μ in diameter, ornamented with 25 to 45 thimble-like protuberances about 1 μ in height and 0.8 μ in basal width; mature zygospores unknown.

Destructive to *Amoeba verrucosa* (*sensu strictiore*) it occurs in decaying herbaceous plant materials in open woods near Beltsville, Md.

In some of the cultures in which *Cochlonema megalosomum* was found multiplying, it encountered competition from two other fungi. One of these fungi, unquestionably a member of the Zoöpagaceae, captured numerous specimens of *Amoeba verrucosa* by adhesion to sparse continuous mycelial filaments mostly about 2 μ wide, and intruded into each captive an extensively branched, bushy haustorium most similar to the haustorium of *Zoöpage mitospora* Drechsl. (7). In many instances the fungus captured animals already infected by *C. megalosomum;* both of the organisms unconcernedly preceeding with their normal development side by side, and in apparently congenial relationship dividing the protoplasmic materials of the rhizopods between them.

The other of the two fungi competing with *Cochlonema megalosomum* has likewise become known only by its vegetative stage, which is, however, of truly remarkable character, consisting of narrow filamentous hyphae that singly pursue conspicuously straightforward courses on the surface of the substratum for distances varying mostly between 0.5 mm. and 5 mm. before bifurcating abruptly and symmetrically at angles of approximately 120 degrees. Each of the resulting elements repeats the prolonged straightforward course and geometrical bifurcation of its parent, with the result that an exceedingly sparse arachnoid mycelial network is soon extended far over the substratum. Any specimen of *Amoeba verrucosa* captured on a filament of the predacious zoöpagaceous form in close proximity to one of the conspicuously straightforward hyphae, is promptly invaded by a branch from that hypha, and depleted of its protoplasmic material by a copious, somewhat inflated, apparently septate, ramifying haustorial system arising from the branch. Such haustorial elements as may have been intruded into the animal by the zoöpagaceous form are caused to

degenerate completely, the newcomer thus excluding the true captor from further utilization of its prey. Now and then, also, a specimen of *A. verrucosa* disabled by *C. megalosomum* was found invaded by a branch from the arachnoid fungus, but as disablement of an animal by the endoparasite usually does not occur until the fleshy contents have been largely depleted, the intruder here developed only meager haustorial apparatus which exerted no noticeable ill effects on the massive spiral thalli nearby.

COCHLONEMA BACTROSPORUM

Among the larger testaceous rhizopods that multiply in old agar plate cultures following the addition of decaying herbaceous vegetable detritus, is a member of the genus *Heleopera* Leidy agreeing well with the description of *H. sylvatica* Penard (**9**: p. 389–390), and accordingly referred to that species. After a few weeks of development under favorable conditions, the animal often attains populations in excess of 100 individuals. In a number of cases such flourishing colonies of the rhizopod then suffered a rapid reduction of living specimens that apparently always ended in complete extermination.

That the agent responsible for the devastation might most probably be a parasite belonging to the Zoöpagaceae was immediately suggested by the presence of more or less erect, isolated tufts, each composed of 2 to 10 tall aerial filaments arising from the substratum in immediate proximity to one of the animals (FIG. 4, *A*). On closer examination the aerial filaments were indeed revealed as consisting either of chains of rod-like conidia (FIG. 4, *B, a, c, d, e:* FIG. 5, *A, a–c*) or of continuous hyphae manifestly representing younger stages in the development of such chains (FIG. 4, *B, b*). While the individual conidia rather strongly resembled those of *Cochlonema cylindricum* Drechsl. (**6**) in shape, they offered easily recognizable differences not only in their greater dimensions, but also in the persistance of a somewhat papillate protrusion at each of their ends. These curious polar modifications have their origin in the partial delimitation of the conidia from one another through localized evacuation of protoplasm in such a manner as to leave an empty groove surrounding a narrow axial isthmus; separation of

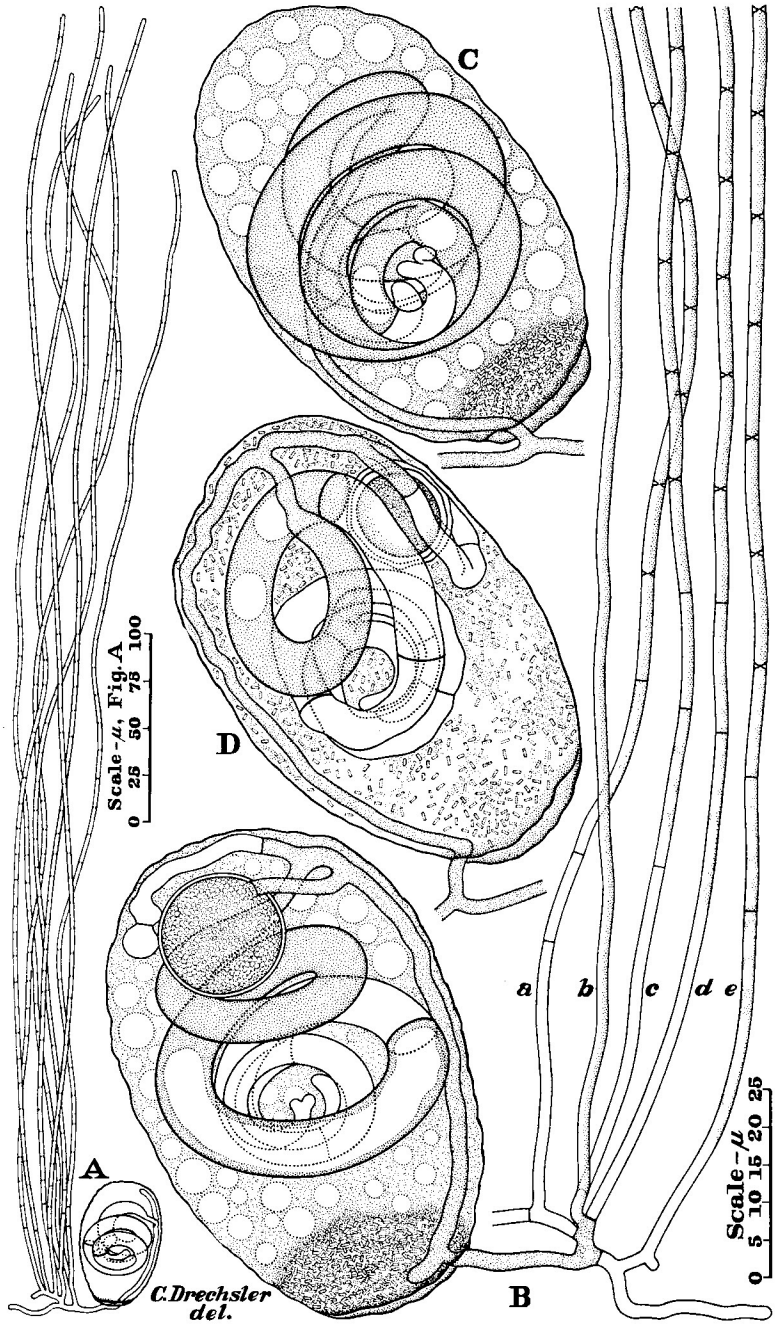

FIG. 4. *Cochlonema bactrosporum.*

adjacent spores being then completed by the insertion of a cross-wall at the middle of the isthmus. It appears possible that conidial development may follow an essentially similar course in *C. cylindricum,* even if the spores of that form show little distinctive outward modification.

As was expected from the character of the conidial apparatus that they represented, the tufts of aerial filaments were in each instance found to have a close hyphal connection with a spiral thallus inside the specimen of *Heleopera sylvatica* nearby (FIG. 4, *A, B:* FIG. 5, *A*). A few thalli that could be followed satisfactorily under the difficult optical conditions brought about by the murky, vacuolate consistency of the surrounding protoplasm, showed very handsome helicoid arrangement: the vegetative hypha in its first turn, usually nearest the fundus of the host, widening gradually to a maximum diameter maintained throughout the grandiose second turn, then gradually diminishing in width in the narrowing distal turns closest to the mouth of the animal (FIG. 4, *B, C*). Branching was observed only in the distal portion of the thallus, a first bifurcation often occurring at the beginning of the fourth turn, and a second, where present, at the beginning of the fifth turn. The meager and inconspicuous branching is hardly sufficient to counteract the deceptive impression that the vegetative body usually conveys of having grown opposite to its actual direction of growth. After the initiation of reproductive development, the thallus is progressively evacuated of protoplasm from the distal toward the proximal portion, and retaining septa are laid down in positions successively closer to the proximal end (FIG. 4, *A–D*). The single reproductive filament arising from the proximal end of the thallus often needs to thrust its way almost the entire length of the animal before it can emerge from the oral opening. Once outside of its host, the reproductive filament sends a few short branches into the substratum, and then gives rise successively to the aerial hyphae that, except for a sterile basal part, become converted, likewise successively, to chains of cylindrical conidia.

Aside from its copious display of conidial apparatus, the fungus also reproduces sexually. Approximately a third of the animals seen destroyed were partly utilized in the development of zygospores. The sexual spores of the parasite, unlike any of the

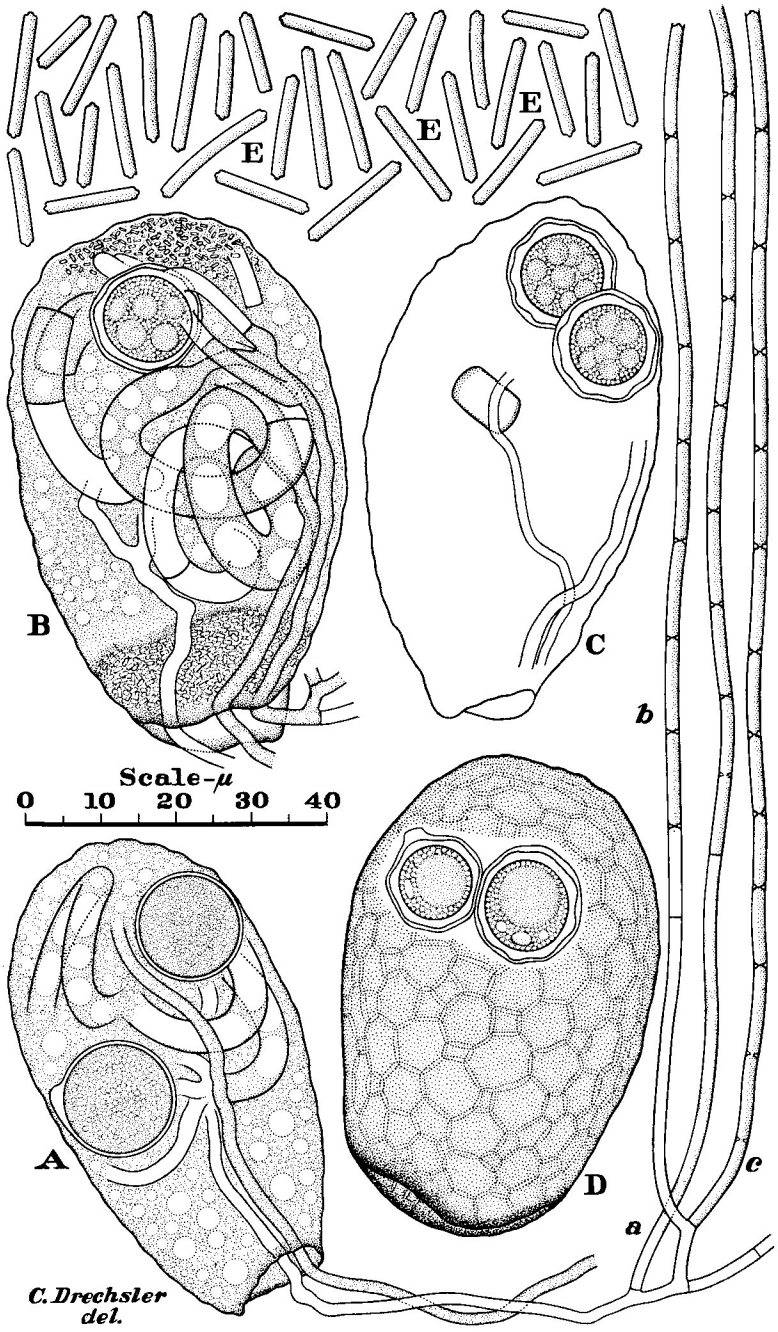

FIG. 5. *Cochlonema bactrosporum.*

homologous bodies hitherto made known in related species, usually are formed within the host—more often indeed, in positions near the fundus than near the mouth, and only rarely in the substratum a short distance from the mouth. As frequently an animal in which a zygospore was visible contained only a single thallus, it would seem that the fungus is definitely homothallic (FIG. 4, *B, D*). Apparently the zygosporangium is formed at the union of two rather short sexual elements, which in some cases (FIG. 4, *B*) arise separately from the reproductive filament short distances from its origin, and in other cases arise through bifurcation of a single branch similarly given off by the reproductive filament close to its attachment (FIG. 4, *D*). On attaining its definitive size the zygosporangium consists of a smoothly spherical cell, densely filled with coarsely granular contents (FIG. 4, *B:* FIG. 5, *A*). The coarsely granular protoplasmic structure is retained during the earlier stages in the development of the zygospore proper, when there is deposited within the zygosporangial wall a thicker wall having perceptible sigillate thickenings. These thickenings become slightly more pronounced as maturation proceeds with accompanying formation and enlargement of reserve vacuoles, often from 5 to 10 in number (FIG. 5, *B, C*). These vacuoles later coalesce, so that in its fully mature condition the zygospore of the fungus under consideration, like that of other members of the Zoöpagaceae, shows an internal organization more familiar in oöspores: a large central reserve globule being surrounded by a parietal protoplasmic layer of coarsely granular texture, in which is imbedded on one side an oblate ellipsoidal refringent body (FIG. 5, *D*).

As in all instances where an animal clearly was parasitized by a single thallus, only a single reproductive filament could be seen emerging from the oral opening and no more than one zygospore could be discerned developing inside. It is believed that plural production of these structures from individual thalli, if occurring at all, is at least infrequent. The presence of two or three reproductive filaments (FIG. 5, *A, B, C*), or of two zygosporangia (FIG. 5, *A, C, D*) would therefore, in the main, seem to imply the presence of a corresponding number of thalli. Plural infection would appear to be concerned also in cases where spiral hyphal coils, only

partly visible, are found in markedly confused arrangement (FIG. 5, *A, B*).

A term made up from words meaning "staff" and "seed," respectively, and intended to be descriptive of the cylindrical conidium, is deemed appropriate as a specific name for the fungus.

Cochlonema bactrosporum sp. nov.

Hyphae alitae 2–8 μ latae, primo latescentes deinde minuentes, ter vel quater in spiram primo latescentem deinde minuentem cocleatim convolutae, saepius semel vel bis sursum dichotomae, unusquisque ex basi hypham filiformem 1.5–2.5 crassam evolvens quae non solum in aera extra testam animalis invasi 2–10 hyphas erectas 300–750 μ altas deinceps profert sed subinde etiam binos ramos zygosporiferos intra testam emittit; hyphis aeriis se vertentibus in conidia catenulata, hyalina, levia, cylindrata, 9–19 μ longa, 1.6–1.9 μ crassa, utrimque ad instar verruculae rotundata; ramis zygosporiferis 10–45 μ longis, circa 2 μ crassis; zygosporangiis sphaeroideis 13–17 μ crassis, membrana postea circum zygosporam collapsa; zygosporis paulo flavidis, plerumque 11–15 μ crassis, maturitate ab membrana 0.5–1.8 μ crassa in extremitate ad instar sigillorum undulata circumseptis.

Heleoperam sylvaticam enecans habitat in reliquiis plantarum putrescentibus prope Beltsville, Maryland.

Vegetative hypha disposed in a more or less extended helicoid spiral of 3 or 4 successive turns; attaining a width of 5 to 8 μ in the second and widest turn that often measures 35 to 40 μ across; in the successively smaller third and fourth turns often narrowing to a diameter of 2 or 3 μ; sometimes branching dichotomously once or twice in its distal portion; putting forth from its base a filament 1.5 to 2.5 μ wide that not only produces successively 2 to 10 erect aerial hyphae 300 to 750 μ high outside the testa of the host animal, but in addition sometimes gives rise, most often inside the testa, to paired zygophoric branches: each of the aerial hyphae becoming converted into a chain of hyaline conidia 9 to 19 μ (average 14.3 μ) long, 1.6 to 1.9 μ wide, smooth, cylindrical, with a small wart-like protuberance at both ends; the zygophoric hyphae, 10 to 45 μ long and about 2 μ wide, after conjugation bearing a subspherical zygosporangium 13 to 17 μ in diameter and surrounded by a wall originally smooth but later collapsing rather closely about the yellowish zygospore, which measures usually 11 to 15 μ in diameter and at maturity is surrounded by a wall 0.5 to 1.8 μ thick with sigillate undulating outer contour.

Destroying *Heleopera sylvatica* it occurs in decaying plant remains on moist ground near Beltsville, Md.

ACAULOPAGE MARANTICA

One of the old maize-meal agar plate cultures, in which *Cochlonema megalosomum* made its appearance, showed also the development of another relatively coarse though morphologically less remarkable member of the Zoöpagaceae. This second fungus subsisted exclusively on a large *Amoeba* that often attained a length of 150 μ when drawn into its usual slightly elongated form (FIG. 6, *A, B, C*). The animal was further distinguished by a thickish pellicle cast in boldly undulating contours over broad pseudopodial protrusions, as well as by a single large prolate ellipsoidal nucleus often 30 to 35 μ long and 15 to 20 μ wide, the generally homogeneous consistency of which was interrupted close under the delimiting membrane by a parietal layer of noticeably darker material, appearing in profile as disjunctive rods arranged end to end. From these morphological features the identity of the rhizopod with the one previously found serving *Endocochlus gigas* as prey and *C. megaspirema* as host was sufficiently evident; wherefore it will be referred to as *Amoeba terricola* Greeff (*sensu strictiore*).

Nourished on an abundant supply of living shelled rhizopods, including mainly *Trinema enchelys* Ehrenb. (FIG. 6, *B*) and a small species of *Euglypha* (FIG. 6, *A–C*), the large *Amoeba* had multiplied until more than 100 individuals were present. The animals, which because of their size were clearly visible to the naked eye, first invited attention through an abnormally dense concentration of some dozens of specimens in a small area adjacent to a pinch of decaying herbaceous material planted there some weeks earlier—the crowded tract presenting a rather densely stippled macroscopic appearance. Examination under the microscope revealed a relationship wholly analogous to that described earlier (2) as existent between the large but decidedly different *Amoeba* then provisionally designated as *A. terricola* III, on the one hand, and the predacious *Zoöpage planera* Drechsl. on the other. At the margin of the crowded area specimens of *A. terricola* (*sensu strictiore*) were seen adhering to hyphae of an aseptate, irregularly disposed mycelium, some of the hyphae, indeed, being enveloped here and there in pseudopodial folds (FIG. 1, *A*). The small number of stalked, dichotomously branched haustoria thrust into the individ-

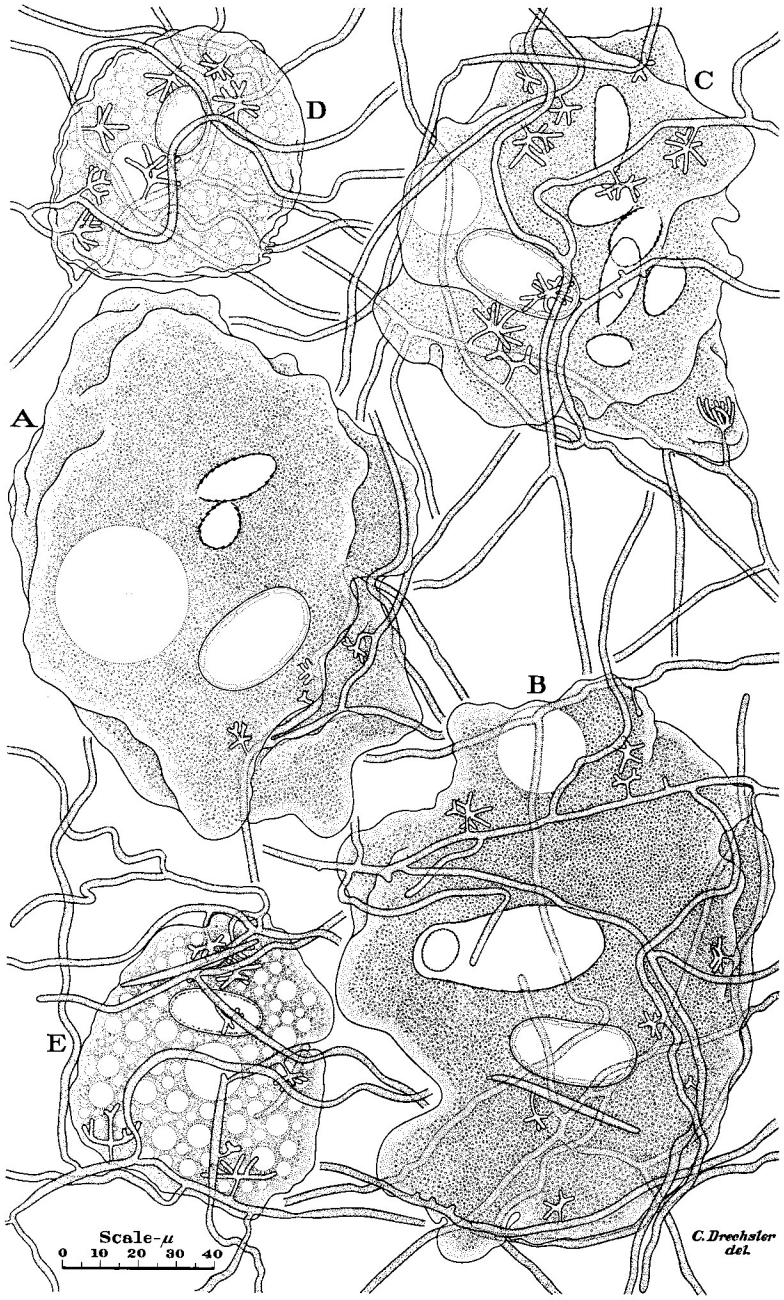

FIG. 6. *Aculopage marantica.*

ual animal, together with the apparently undiminished density of the granular protoplasm, the unceasing extension and retraction of pseudopodia in attempted locomotion, the normal discharge of the contractile vacuole and the healthy appearance of the large nucleus, gave evidence that expropriation of the rhizopod was still in an early stage. By far the larger number of closely congregated animals showed much more extensive enwrapment by the mycelium (FIG. 6, *B, C*). A conspicuously irregular disposition of the enveloping branched filaments, and their presence not only on the under side of each captive but on its upper exposed side as well were to be explained undoubtedly by the persistent wallowing movements through which the animal, instead of freeing itself, merely succeeded in enmeshing itself more securely. Intrusion of additional haustoria consequent to more extensive mycelial engagement hastened the depletion of the captive's fleshy contents: the diminishing cytoplasm becoming pronouncedly vacuolate (FIG. 6, *D*); the large nucleus betraying internal degeneration in a gradual obliteration of its interrupted darker layer (FIG. 6, *E*). Eventually nothing remained visible but the empty collapsed pellicle, within which the haustoria had disappeared from view when their protoplasmic contents had been withdrawn into the parent mycelial filaments.

The fungus reproduced asexually by giving rise to an abundance of elongated fusiform conidia, appendaged at both ends. Development of the individual conidium was found to begin with the production from a superficial hypha of an erect continuous outgrowth narrowing for a short distance above its base, then rather markedly widening upward for a somewhat greater distance, and then again gradually narrowing throughout the distal two-thirds of its length (FIG. 7, *A; B, c*). From the slender apical portion embracing about a third of the length of the outgrowth the contents were then retracted, and a confining septum was deposited to delimit the filled from the empty part. In the meantime a cross-wall had been inserted in the narrow isthmus a short distance above the base of the outgrowth, a small segment immediately above the cross-wall being thereupon emptied of protoplasm, and another confining septum deposited (FIG. 7, *B, a, b, d–g*). Through disarticulation at the lowest septum, the conidium with its short empty

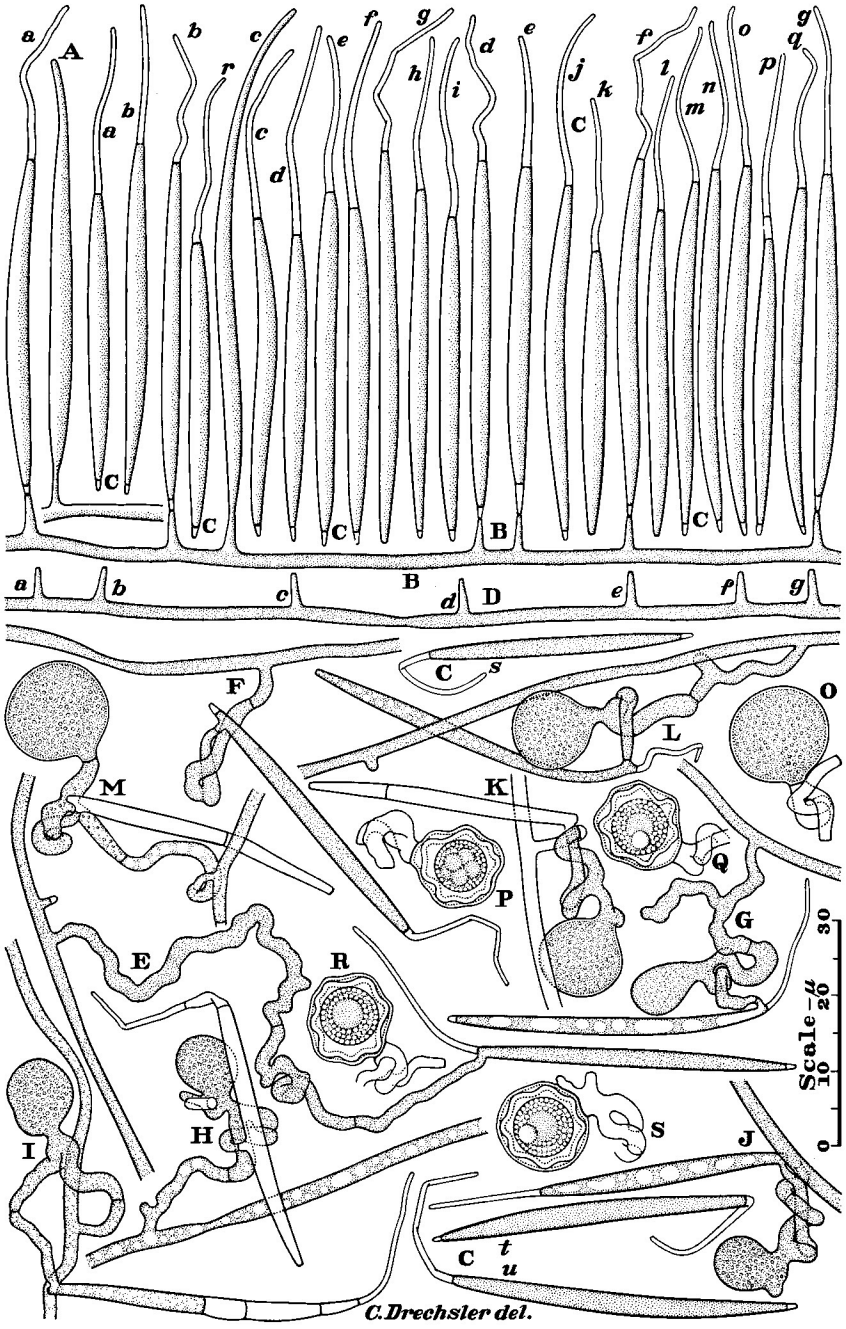

FIG. 7. *Acaulopage marantica.*

basal stipe, its spindle-shaped living cell, and its more or less collapsed, narrow, empty distal appendage (FIG. 7, *C, a–f, h–j, m–u*) became separated from the short erect sterigma. Except for its considerably greater dimensions, and for the presence of its empty basal stipe, which, for that matter, was occasionally absent (FIG. 7, *C, g, k, l*), the conidium strongly resembles that of the obviously congeneric *Acaulopage rhicnospora* Drechsl. (3), though the close bristling arrangement of the erect spores on the prostrate filaments would seem more especially suggestive of *A. cercospora* Drechsl. (5).

Sexual reproduction of the fungus took place abundantly in the culture, and as in many related forms appeared to be further encouraged when portions of occupied substratum were removed to glass slides for microscopic examination. Of each pair of zygophoric branches, one always came from a mycelial filament, while the other consisted of a germ-tube from a conidium. Instances of conjugation between two branches arising from mycelial hyphae, or of conjugation between two germ-tubes were never seen among the hundreds of units of sexual apparatus that came under observation. Contact of the zygophoric branches was found associated usually with only slight twisting, and was regularly accompanied by the deposition of cross-walls partitioning off the paired gametangia (FIG. 7, *E, F*). The subspherical zygosporangium was developed generally on a rather short stalk arising at a variable but usually inconsiderable distance from the union of the sexual hyphae (FIG. 7, *E–M*). Delimitation of the organ by a basal septum (FIG. 7, *M, O*), and conversion of the contents into a zygospore with a sculptured wall of undulating profile well separated from the sporangial envelope except at the projecting crests, followed a sequence familiar in most other members of the family (FIG. 7, *P–S*). In its mature condition the zygospore showed a relationship of parts hitherto found only in species of *Endocochlus* —the inner surface of the thick undulate wall appearing distinctly separated from the subspherical protoplast (FIG. 7, *P–S*). The protoplast, as in related forms, revealed, on full maturation, a single central reserve globule surrounded by a parietal layer of uniform granules; and imbedded in the granular layer was usually discernible a globular refringent body (FIG. 7, *Q–S*).

Though the fungus was active in a culture that permitted abundant development also of *Cochlonema megalosomum,* it was never observed to capture specimens of *Amoeba verrucosa,* nor, on the other hand, was *C. megalosomum* observed to parasitize *A. terricola* (*sensu strictiore*). Like the endoparasite, however, and, indeed, to a greater extent and more frequently, it suffered from interference by the sparsely arachnoid, geometrically disposed mycelial form of intrusive propensities. The arachnoid form by itself was evidently no more able to attack *A. terricola* than *A. verrucosa,* but when once a specimen of the former was captured, it extended within the captive its characteristically swollen, branching haustorial system, the presence of which promptly caused degeneration in the haustoria of the predacious species under consideration, just as it brought about degeneration in the haustoria of the unindentified predacious form often destructive to *A. verrucosa.*

A term meaning " withered " and believed to be aptly descriptive of the conidia of the fungus, with their frequently collapsed distal appendages, is offered as an appropriate specific name.

Acaulopage marantica sp. nov.

Mycelium ramosum, effusum; hyphis hyalinis, saepe irregulariter flexuosis, 1–2.8 μ crassis, ad animalcula inhaerentibus, vulgo ea extense circumplicantibus, pelliculam eorum perforantibus, haustoria intus evolventibus quae carnem exhauriunt; haustoriis pedicellatis, pedicello saepius 2.5–6 μ longo, 0.6–1 μ crasso, apice abrupte latescente, semel vel ter repetite bifurco, ita 2–8 ramulos divaricatos, 1–10 μ longos, 0.8–1.6 μ crassos ferente. Conidia hyalina, ex sterigmatis erectis, vulgo 3–5 μ altis, basi 1–1.5 μ crassis, sursum attenuatis, apice 0.5–0.8 μ crassis, inter se saepius 5–35 μ distantibus oriunda, vulgo ex partibus tribus composita: parte supera vacua, 15–30 μ longa, basi 0.8–1.3 μ crassa, sursum leniter attenuata, saepius plus minusve marcida vel collapsa; parte media protoplasmatis repleta, elongato-fusoidea, 33–52 μ longa, 2.4–3.1 μ crassa; parte infera vacua, 0.8–4 μ longa, sursum 0.6–1.2 μ crassa. Hyphae zygosporiferae 10–75 μ longae, 1–3 μ crassae, saepe plus minusve irregulariter flexuosae, 10–15 μ ab junctione septo divisae, interdum aliquantulum inter se circumplicantes, una ex hypha mycelii, altera ex conidio germinanti oriunda. Zygosporangia primo levia, sphaeroidea, vulgo 12–14 μ crassa, maturitate membrana circa zygosporam laxe collapsa; zygospora flavida, globosa, circa 9–12 μ crassa, maturitate membrana late verrucosa vel sinuosa, cellulam viventem sphaeralem 6.5–8 μ latam laxe circumdante.

Amoebam terricolam (sensu strictiore) capiens consumensque habitat in materiis plantarum putrescentibus prope Beltsville, Maryland.

Mycelium branched, spreading; vegetative hyphae colorless, often irregularly flexuous, 1 to 2.8 μ (mostly about 2 μ wide), ad-

hering to and often becoming extensively wrapped about minute animals, penetrating the pellicle of each captive and intruding haustoria to appropriate the fleshy contents; haustoria pedicellate, the pedicel often 2.5 to 6 μ long, 0.6 to 1 μ wide, abruptly widening and bifurcating one to three times at wide angles to terminate in 2 to 8 branches 1 to 10 μ long and 0.8 to 1.6 μ wide. Sterigmata arising abruptly from superficial hyphae at intervals of 5 to 35 μ, erect, 3 to 5 μ high, 1 to 1.5 μ wide at the base, tapering upward to a width of 0.5 to 0.8 μ at the tip whereon is borne erectly a single conidium. Conidia hyaline, each usually composed of three parts: the distal part empty, 15 to 30 μ (average 21.6 μ) long, 0.8 to 1.3 μ (average 1.1 μ) wide at the base, tapering upward slightly, often more or less collapsed; the middle part filled with protoplasm, elongate spindle-shaped, 33 to 52 μ (average 42.9 μ) long, 2.4 to 3.1 μ (average 2.7 μ) wide; the lowest part obconical, empty, 0.8 to 4 μ (average 1.5 μ) long, 0.6 to 1.2 μ wide at its distal attachment. Zygophoric hyphae 10 to 75 μ long, 1 to 3 μ (mostly about 2 μ) wide, often more or less irregularly flexuous, the two of a pair sometimes slightly intertwined, one commonly arising as a branch from a mycelial filament, the other commonly consisting of a germ-tube from a conidium, each with a distal portion, or gametangium, 10 to 15 μ long, set off by a septum. Zygosporangium at first smoothly subspherical and commonly 12 to 14 μ in diameter, at maturity collapsing loosely about the zygospore; the latter yellowish, 9 to 12 μ in diameter, its wall, at maturity broadly verrucose and pronouncedly sinuous in contour, loosely surrounding a subspherical living cell usually 6.5 to 8 μ in diameter.

Capturing and consuming *Amoeba terricola* (*sensu strictiore*) it occurs in decaying plant remains near Beltsville, Md.

DIVISION OF FRUIT AND VEGETABLE CROPS AND DISEASES,
BUREAU OF PLANT INDUSTRY,
U. S. HORTICULTURAL STATION,
BELTSVILLE, MARYLAND

LITERATURE CITED

1. **Cutler, D. W. & Crump, L. M.** Problems in soil microbiology. (Rothamsted Monographs on Agricultural Science.) 1935.
2. **Drechsler, C.** Some conidial Phycomycetes destructive to terricolous Amoebae. Mycologia 27: 6–40. 1935.
3. ——. Some non-catenulate conidial Phycomycetes preying on terricolous Amoebae. Mycologia 27: 176–205. 1935.
4. ——. A new mucedinaceous fungus capturing and consuming *Amoeba verrucosa*. Mycologia 27: 216–223. 1935.

5. ——. New conidial Phycomycetes destructive to terricolous Amoebae. Mycologia **28**: 363–389. 1936.
6. ——. New Zoöpagaceae destructive to soil rhizopods. Mycologia **29**: 229–249. 1937.
7. ——. New Zoöpagaceae capturing and consuming soil Amoebae. Mycologia **30**: 137–157. 1938.
8. **Leidy, J.** Freshwater rhizopods of North America. (Rept. U. S. Geol. Surv., vol. 12.) 1879.
9. **Penard, E.** Faune rhizopodique du bassin du Léman. 1902.

EXPLANATION OF FIGURES

FIG. 1. *Cochlonema megalosomum;* drawn with the aid of a camera lucida to a uniform magnification; × 500 throughout. *A,* specimen of *Amoeba verrucosa* in a condition of active motion, showing besides its nucleus, *n,* and its contractile vacuole, *v,* five thalli of the fungus, *a–e: a* representing a very early stage, protoplasmic materials still being received from the externally adhering conidium; *b,* a stage soon after separation from the parent conidium; *c,* a thallus of one turn with marked distal widening; *d* and *e,* older and more massive thalli, each of which has undergone a single bifurcation. *B,* specimen of *A. verrucosa* in active state, containing three bifurcating thalli of the fungus, *a–c,* besides its own nucleus, *n,* its contractile vacuole, *v,* and a digestive vacuole, *z,* inclosing many ingested bacteria. *C,* specimen of *A. verrucosa* containing besides its nucleus, *n,* and its contractile vacuole, *v,* four thalli of the fungus, *a–d,* of which two, *b* and *d,* are twice dichotomous throughout, the others, *a* and *c,* showing a second dichotomy in only one of the two elements resulting from the first bifurcation; in each of the thalli hyphae are just beginning to grow out from the outer contour of the older or proximal portion. *D,* a large specimen of *A. verrucosa* in active state, showing a rather young thallus, *a,* and an older, larger, successively twice bifurcate thallus, *b,* of approximately two successive turns, besides revealing its own nucleus, *n,* its contractile vacuole, *v,* and three digestive vacuoles, *x–z,* surrounding groups of ingested bacteria. *E,* pellicle of *A. verrucosa,* the contents of which have been depleted by two thalli, *a* and *b,* that have put forth, respectively, eight and six sporiferous hyphae of variable lengths.

FIG. 2. *Cochlonema megalosomum;* drawn with the aid of a camera lucida to a uniform magnification; × 500 throughout. *A,* specimen of *Amoeba verrucosa* in active condition, infected with a very young thallus, *a,* and five much larger thalli, *b–f; n,* nucleus of host animal; *v,* contractile vacuole in incipient stage of expansion; *z,* digestive vacuole containing numerous ingested bacteria. *B,* specimen of *A. verrucosa* in state of active locomotion, containing six thalli, *a–f; n,* nucleus of host animal; *v,* contractile vacuole in incipient stage of expansion; *z,* digestive vacuole containing numerous ingested bacteria. *C,* specimen of *A. verrucosa* in a state of active locomotion, though burdened with the large thallus *a; n,* nucleus of host animal; *v,* contractile vacuole; *y* and *z,* digestive vacuoles containing numerous ingested bacteria. *D,* shrunken pellicle of *A. verrucosa,* the protoplasmic contents of which have been consumed by the eight thalli, *a–h;* from

seven of the thalli, *b–h,* sporiferous hyphae have begun to grow out. *E,* wrinkled pellicle of *A. verrucosa* surrounding an empty envelope of a large spiral thallus whose protoplasmic contents have been used up in the production of eight conidiiferous filaments; of these filaments seven are represented, from lack of space, only by their sterile basal parts, the other one being shown in two sections connecting at the common point *a. F,* wrinkled pellicle of *A. verrucosa* surrounding two largish empty envelopes of thalli that have been exhausted of contents in the production of conidiiferous hyphae, whereof, from lack of space, only proximal portions are shown. *G, a–z; H, a–t,* conidia showing variations in dimensions, shape and sculpturing.

FIG. 3. *Cochlonema megalosomum;* drawn with the aid of a camera lucida to a uniform magnification; × 1000 throughout. *A,* collapsed pellicle of *Amoeba verrucosa,* the fleshy contents of which have been consumed in the growth of an unusually large thallus, now represented only by an empty aseptate envelope, owing to the depletion of its protoplasm in the production of eighteen conidiiferous hyphae; from lack of space only the proximal portions of the fertile hyphae are shown. *B,* a conidiiferous filament branching within the host pellicle, and showing long, smooth conidia in the proximal portions of spore chains. *C,* distal portion of growing aseptate conidial filament, showing regularly spaced constrictions and coarsely warty sculpturing. *D,* distal portion of mature conidial chain, showing narrow contact of adjacent conidia at the axis of each isthmus. *E,* conidia, showing variations in dimensions, shape and sculpturing. *F,* collapsed pellicle of *A. verrucosa* within which are found four empty thalli of the parasite, *a–d;* from these thalli have been produced zygophoric hyphae that have united in pairs by their greatly widened apices to give rise to the handsomely mammillated zygosporangia *e–k;* as the two zygosporangia *e* and *k* have each resulted from union of paired hyphae arising from thalli *a* and *c,* the two zygosporangia *f* and *i* each from union of paired hyphae arising from thalli *b* and *d,* and the three zygosporangia *g, h* and *j* each from union of paired hyphae arising from thalli *a* and *d,* presumably the thalli *a* and *b* are of one sexual constitution, and the thalli *c* and *d* of the opposite sexual constitution.

FIG. 4. *Cochlonema bactrosporum;* drawn with the aid of a camera lucida to a uniform magnification. *A,* depleted specimen of *Heleopera sylvatica* containing the empty envelope of a single thallus that has used up its contents in the production of a tuft of seven conidial chains; × 250. *B,* specimen of *H. sylvatica* containing a thallus that has given rise inside of the testa to a young but fully grown zygosporangium, and outside of the testa to a tuft of five erect asexual reproductive filaments, *a–e,* of which, for lack of space, only the proximal portions are shown—while the continuous filament *b* is in a young growing condition, the others, *a, c, d* and *e,* consist largely of conidial chains; × 1000. *C,* specimen of *H. sylvatica* containing a well developed thallus of the parasite, from whose younger branched extremity protoplasm is being withdrawn for the extension of conidial filaments outside of the testa; × 1000. *D,* specimen of *H. sylvatica* containing a thallus from which the protoplasmic contents have mostly been withdrawn

to provide for the formation within the animal's testa of a zygospore, and of conidiiferous filaments outside of the testa; × 1000.

FIG. 5. *Cochlonema bactrosporum;* drawn with the aid of a camera lucida to a uniform magnification; × 1000 throughout. *A,* specimen of *Heleopera sylvatica* within which are indistinctly visible several curving portions of hyphae belonging probably to two separate thalli; two zygosporangia of definitive size, but still immature, are more clearly visible inside, as are also two hyphae growing out of the animal's mouth, one of which has given rise to three conidial chains, *a–c,* whereof, from lack of space, only basal portions are shown. *B,* specimen of *H. sylvatica* containing presumably three thalli of the parasite, each extending a separate filament through the oral opening to produce conidial chains externally; one having, in addition, produced a zygosporangium with nearly mature zygospore, inside of the testa. *C,* depleted specimen of *H. sylvatica* within which a small segment of thallus, two outgrowing filaments, and two zygosporangia with nearly mature zygospores are visible. *D,* depleted specimen of *H. sylvatica,* showing inside of the testa with its characteristic arrangement of plates, two fully mature zygospores, each surrounded by its sporangial membrane. *E,* conidia, showing variations in dimensions and shape.

FIG. 6. *Acaulopage marantica;* drawn to a uniform magnification with the aid of a camera lucida; × 500 throughout. *A,* specimen of *Amoeba terricola* (*sensu strictiore*) in active condition, entangled on one side with adhesive mycelial filaments, from which four haustoria have been thrust through the pellicle into the sarcode; within the animal are shown also the fully expanded contractile vacuole, the large nucleus, and two depleted testae of ingested rhizopods referable apparently to the genus *Euglypha. B,* living specimen of *A. terricola* extensively inwrapped in adhesive mycelial filaments, from which collectively eight haustoria have been thrust into the sarcode exclusive of the haustorium arising from an adhering conidium; within the animal's body are shown also its contractile vacuole, its ellipsoidal nucleus, and the large empty testa of an ingested specimen of *Trinema enchelys. C,* a living specimen of *A. terricola* extensively inwrapped with adhesive mycelial filaments from which collectively ten haustoria have been thrust into the sarcode; within the animal are distinguishable its contractile vacuole, its ellipsoidal nucleus, and six empty testae of ingested rhizopods belonging apparently to a small species of *Euglypha. D,* a rather small specimen of *A. terricola* securely entangled in adhesive mycelial filaments; the abundance of vacuoles distributed through the sarcode indicating a somewhat advanced stage of protoplasmic depletion, accomplished by means of the seven well developed haustoria. *E,* another smallish specimen of *A. terricola* entangled in adhesive mycelial filaments; from these filaments and a germinating conidium have been intruded eight haustoria, which have brought about a well advanced stage of protoplasmic depletion in the animal, as is manifest from the presence of very numerous vacuoles, and from the partial obliteration of the interrupted parietal layer in the nucleus.

FIG. 7. *Acaulopage marantica;* drawn to a uniform magnification with the aid of a camera lucida; × 1000 throughout. *A,* portion of prostrate

hypha on which is borne an erect process later to develop into a conidium. *B*, a prostrate filament with seven conidia, *a–g*, borne erectly on separate erect sterigmata; all of the conidia are mature except one, *c*, which though of approximately definitive size, has not been partitioned off from its sterigma, nor undergone evacuation either in its proximal or in its distal part. *C*, *a–u*, conidia, showing variations in dimensions and shape of living cell, empty basal stipe, and empty distal appendage. *D*, prostrate hypha with seven erect sterigmata, *a–g*, all denuded of their conidia. *E*, *F*, young sexual apparatus; in each unit a zygophoric hypha arising as a branch from a mycelial filament has fused apically with another zygophoric hypha arising as a germ-tube from a fallen conidium. *G–L*, sexual apparatus in somewhat later stages of development, likewise showing origin of each unit through union of one zygophoric hypha, arising as a branch from a mycelial filament, with another consisting of a germ-tube from a conidium. *M*, sexual apparatus at still later stage, showing the fully grown zygosporangium set off from its supporting stalk by a septum. *O*, fully grown zygosporangium set off by a septum from evacuated zygophoric elements. *P*, nearly mature zygospore lying within the somewhat collapsed sporangial membrane, to which is shown attached the empty envelope of the united gametangia. *Q–S*, mature zygospores, each lying within its slightly relaxed sporangial envelope.