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NEW ZOOPAGACEAE CAPTURING AND CONSUMING SOIL AMOEBAE

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(WITH 4 FIGURES)

Four fungi that subsist by the capture of *Amoebae,* evidently to the exclusion of other nourishment, are described herein as new members of the Zoopagaceae. Though production of zygospores has been observed in only one of the species, the morphology of their vegetative and asexual reproductive parts establishes all four alike as undoubted members of the family, and, in addition, permits each to be distinguished from the several previously described forms congeneric with it.

ZOOPAGE MITOSPORA

A predacious species remarkable among conidial Phycomycetes for the length of its usually catenulate spores, was observed in two old maizemeal agar plate cultures started originally from pieces of tomato (*Lycopersicon esculentum* Mill.) roots found affected with cortical decay due to invasion by *Pythium ultimum* Trow. Two weeks after the plantings were made some pinches of leaf mold collected in deciduous woods on a mountain side near Cumberland, Md., in July 1935, had been added to one of the aging cultures; while the other had received similar additions of leaf mold gathered also in July 1935, in deciduous woods near Madison, Wis. In both cultures the fungus was present only in small quantity, being limited in each instance to a circular area of substratum about 15 mm. wide, adjacent to a deposit of the forest refuse. Its restricted extension and meager development within the areas occupied would seem to have been due to scarcity of the single species of *Amoeba* on which it subsisted. Captured specimens of the rhizopod in question showed a range in linear measurements from a minimum width of approximately 20 μ to a maximum length of about 70 μ, rounded individuals showing a variation in diameter between 25 μ

and 65 μ. Structures that appeared to be digestive vacuoles surrounding numbers of bacteria were often visible in the sarcode, as were also bodies of protozoan cysts, and, in a few instances (FIG. 1, *B*), thalli of some undetermined species of *Endocochlus* or *Cochlonema*. Though the protoplasm with its finely, dispersedly granular texture appeared fairly transparent, a nucleus could not be distinguished at all clearly in any of the captives, so that their identity remains, for the time being, uncertain.

In its predacious development the fungus shows most resemblance to *Stylopage areae* Drechsl. The relatively large lump of yellow adhesive material by means of which the animal is held fixed to the rangy mycelial filament, is traversed by a lateral outgrowth that penetrates the pellicle and then bifurcates several times at short intervals to give rise often to about a dozen basal branches (FIG. 1, *A, B*). These branches, for the most part distinctly narrower than the mycelial hypha from which they arise, traverse the protoplasm of the rhizopod in different directions until halted by the enveloping pellicle, sometimes giving off one or more ramifications in their courses. A rangy bushlike haustorial system is thus brought into being, which accomplishes the gradual exhaustion of the animal's substance (FIG. 1, *C; D; E, a*).

Asexual reproduction is most readily detected by examining the fungus under a dry objective without using a cover-glass, as the undisturbed conidial chains are easy to recognize by their erect posture. Even under low magnification the conidia arrest attention because of the considerable length frequently attained by them. Foreknowledge of their dimensions is desirable before a cover-glass is put on material selected for study, since under high magnification the conidia might otherwise be mistaken for segments of mycelial hyphae. In newly developed aerial elements the portions destined to become individual spores (FIG. 1, *F, b, c; G, h, i*) are set off from one another and from the supporting sterigmata (FIG. 1, *F, a; G, d*) by rather pronounced constrictions; wherefore the conidial extremities resulting from separation at the isthmi are characterized by marked tapering (FIG. 1, *E, c; G, f; H, a, b, c, d*), as are also the sterigmata, simple (FIG. 1, *E, b*) or branched (FIG. 1, *G, a–d*), that are easily recognized even after disarticulation has occurred. Similar tapering in a lateral arm borne on a conidium

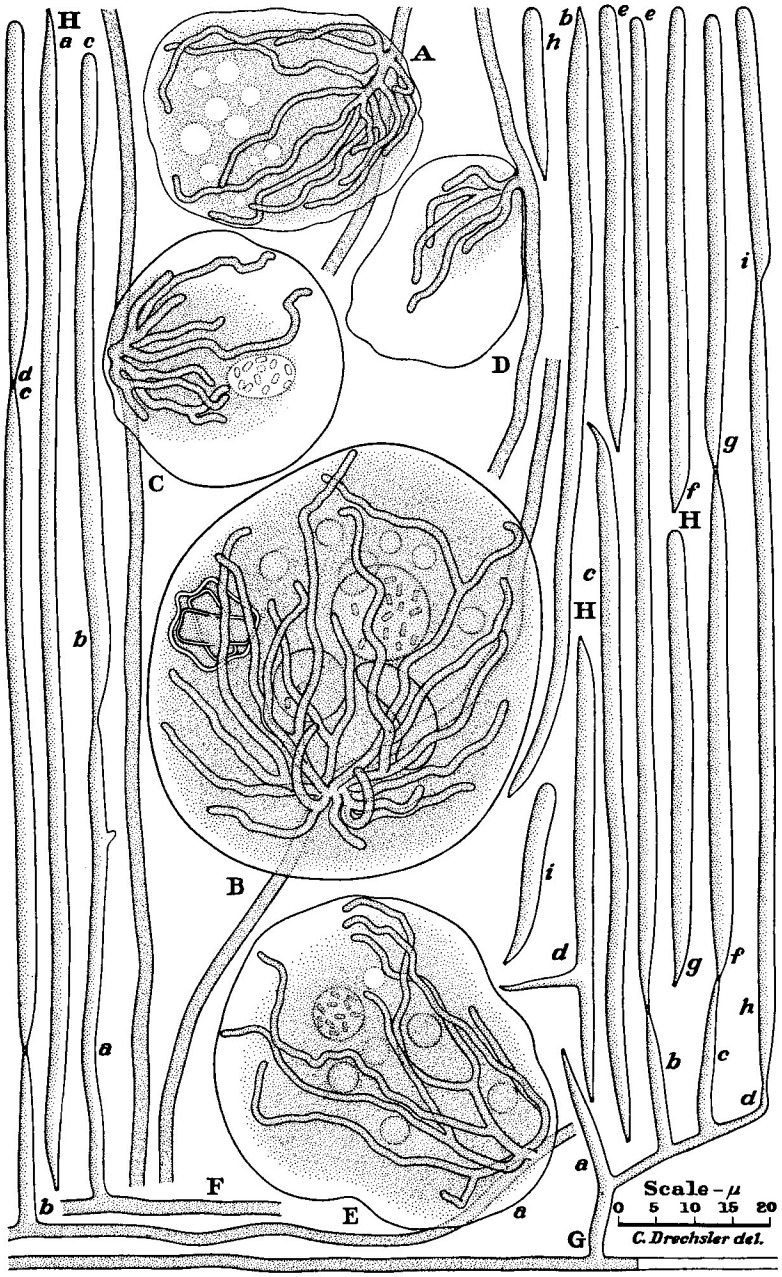

FIG. 1. *Zoopage mitospora.*

now and then (FIG. 1, *H, d*), gives evidence that the spore chains, though usually short, are at least occasionally branched. The distal end of each terminal conidium is distinguished by a bluntly rounded contour (FIG. 1, *E, d; G, g*) as in related catenulate forms. Owing to the small number of spores in a chain, and the replacement, occasionally, of a chain by a single long spore (FIG. 1, *G, e*), terminal conidia with rounded distal and tapering proximal ends (FIG. 1, *H, c, f, g, h, i*) are relatively much more abundant in the present fungus than in any congeneric species that has hitherto become known.

The shape of its conidium suggests for the fungus a specific name compounded from two words meaning " thread " and " seed " respectively.

Zoopage mitospora sp. nov.

Sparsa; hyphis hyalinis, pauciramosis, plus minusve recte positis, 1.5–2.5 μ crassis; haustoriis arbusculiformibus, 5–20 ramulis eorum divaricatis, irregulariter flexuosis, .7–1.4 μ crassis, usque 65 μ longis. Conidia levia, filiformia, interdum bifurcata, 22–156 μ longa, 1.6–3 μ crassa; in catenulas 2–5-sporas plus minusve erectas simplices vel pauciramosas digesta, vel interdum singulatim orta; deorsum semper attenuata, sursum magna ex parte attenuata, sed quandoque ultima in catenula vel singularia apice abrupte rotundata. Sterigmata similiter attenuata, saepe circa 20 μ longa, basi circa 2 μ crassa, simplicia vel paulo ramosa.

Amoebas usque 65 μ latas capiens et consumens habitat in humo silvarum, prope Madison, Wisconsin, et Cumberland, Maryland.

Sparse; vegetative hyphae hyaline, sparingly branched, usually following rather straightforward courses, 1.5 to 2.5 μ wide; haustoria bushlike, with close basal ramification and composed of 5 to 20 branches, mostly somewhat irregular in course, .7 to 1.4 μ wide and up to 65 μ long. Conidia smooth, filiform, sometimes bifurcate, 22 to 156 μ (average 83 μ) long and 1.6 to 3 μ (average 2.3 μ) wide; arising in more or less erect, simple or sparingly branched chains of 2 to 5 each, or sometimes borne singly; always tapering markedly toward the proximal end, and usually toward the distal end, but whenever solitary or borne terminally in a chain, having apex broadly rounded. Sterigmata similarly tapering, simple or occasionally branched, measuring usually about 20 μ in length and about 2 μ in basal diameter.

Occurring in leaf mold, subsisting on a species of *Amoeba* sometimes as much as 65 μ in diameter when rounded up, near Madison, Wis., and Cumberland, Md.

ZOOPAGE THAMNOSPIRA

A species of *Zoopage* remarkable for its extraordinary haustorial development, was observed in two maizemeal agar plate cultures 30 days after they had been started with pieces of decaying tissue from the roots and basal portion of the stem of a tomato plant found wilting in the greenhouse early in December 1935. The fungus subsisted apparently altogether on a species of *Amoeba* whose larger individuals measured approximately 40 μ in diameter when drawn into a more or less rounded shape. Each animal clearly revealed imbedded in its finely granular endoplasm a prolate ellipsoidal nucleus mostly 9 to 12 μ long and 6.5 to 8 μ wide, within which a dozen sphaeroidal bodies about 1.5 μ in diameter could be discerned, mostly in peripheral positions (FIG. 2, *A; B, a; C, a; F; G*). The smaller number and larger size of these nuclear inclusions, which probably represent chromatin bodies, offer some tangible basis for distinguishing the *Amoeba* here concerned from the one serving as prey for *Stylopage rhabdospora* Drechsl. (**6**), as well as from the apparently closely similar species habitually captured by *S. cephalote*.

Capture of the animals is accomplished, as in other members of the Zoopagaceae, by adhesion to a mycelial filament; the small lump of sticky substance effective in arresting each specimen remaining visible after perforation of the delicate pellicle as a yellow ring. Following penetration the invading hyphal branch grows some distance into the sarcode, usually widening markedly in its course, before branching dichotomously (FIG. 2, *A*). When the resulting thickish elements have attained a length usually of 10 to 30 μ, they may branch dichotomously (FIG. 2, *B, a, b; C, c, d*), whereupon renewed elongation and a third bifurcation may ensue in turn; so that in large animals a dichotomous system with 8 terminal elements is often present (FIG. 2, *C, b; D*). Spacial limitations, combined perhaps with continuing movements of the captive, become operative in constraining the rangy branches to grow in handsome curves rather than in straight lines.

The rather massive haustorium thus produced, through conforming to a design common to the homologous structures in various predacious members of the Zoopagaceae, is decidedly suggestive,

in its proportions and graceful coiling, of the vegetative thallus in the endoparasites referable to *Endocochlus* and *Cochlonema*. Apparently the endozoic development here is of an unusual and curious intermediate type, which finds, nevertheless, sufficient explanation in the instances of essentially parasitic infection observed in some number, where an adhering conidium thrusts a germ tube through an *Amoeba* (FIG. 2, *F, G*) to give rise inside to a coiled dichotomous branching system corresponding in the main to a *Cochlonema* thallus. In any case the endozoic apparatus gradually exhausts the protoplasmic materials of the animal (FIG. 2, *C, c–e*), and during the more advanced stages of such depletion becomes itself evacuated of protoplasm, often with the insertion of septa to mark the progress of withdrawal (FIG. 2, *B, b; C, f; E*).

Asexual reproduction takes place through the conversion of aerial filaments showing regularly spaced constrictions (FIG. 2, *H*) into chains of spores wherein verrucose fusoid conidia alternate with short and narrow empty connections (FIG. 2, *I*). As in other catenulate forms, the basal portions of the sporogenous hyphae are often little differentiated from the mycelial hyphae, neither exceeding the latter in width, nor being sculptured in any noticeable degree. These portions of sporogenous hyphae yield smooth, virtually filamentous spores markedly longer and narrower than the well differentiated conidia (FIG. 2, *L–O*) typical of the species, and somewhat longer and narrower than the numerous intergrading structures (FIG. 2, *J, K*) that are sparingly yet recognizably sculptured.

A term compounded from words meaning "bush" and "coil" respectively, and intended to be descriptive of the haustorium, is proposed as specific name for the fungus.

Zoopage thamnospira sp. nov.

Mycelium sparsum, pauciramosum; hyphis hyalinis, .8–1.6 μ crassis; haustoriis propter repetita incrementa 10–30 μ longa plerumque bis vel ter repetite dichotomis, ramis 2–3 μ crassis saepe in spiram laxum pulchre convolutis, itaque hyphae alitae specierum endoparasiticarum Zoopagacearum paulo similibus. Conidia typice minute sed distincte verrucosa, fusoidea, utrimque obtusa, 8–25 μ longa, 1.5–2.6 μ crassa, in catenulas saepe 10–15-sporas plus minusve erectas digesta. Zygosporae ignotae.

Amoebas magnam partem 20–40 μ longas capiens et consumens vel rarius easdem parasitice enecans, habitat in radicibus putrescentibus *Lycopersici esculenti* in viridario prope Beltsville, Maryland.

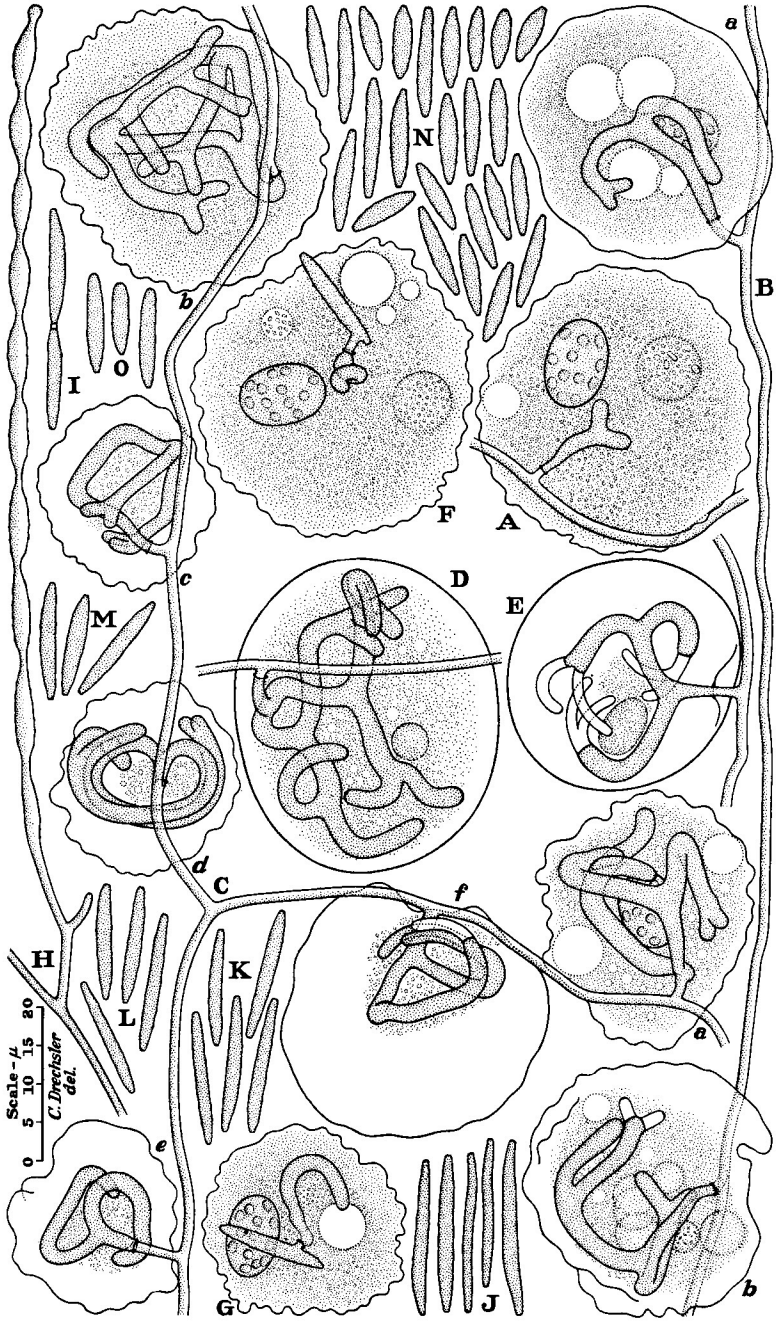

FIG. 2. *Zoopage thamnospira.*

Mycelium sparse, sparingly branched; hyphae hyaline, .8 to 1.6 μ wide; haustoria following repeated elongation by increments 10 to 30 μ in length, mostly bifurcating successively 2 or 3 times, the branches 2 to 3 μ wide, often handsomely convolved in loose spiral coils and thus resembling somewhat the vegetative hyphae in endoparasitic species of the Zoöpagaceae. Conidia sometimes filamentous, smooth, up to 40 μ in length and as little as 1 μ in width; but more frequently, and more typically, spindle-shaped, rounded at both ends, minutely yet distinctly verrucose, 8 to 25 μ (average 14 μ) long and 1.5 to 2.6 μ (average 2.1 μ) wide, and borne in more or less erect chains of 10 to 15 each. Zygospores unknown.

Capturing and consuming, or more rarely parasitically destroying a species of *Amoeba* mostly 20 to 40 μ in diameter; occurring in decaying roots of *Lycopersicon esculentum* in a greenhouse near Beltsville, Md.

STYLOPAGE CEPHALOTE

Early in May 1936, after indoor temperatures generally too high to permit good development of most members of the Zoopagaceae had been prevailing for some time, a handsome species of *Stylopage* made its appearance in an old maizemeal agar plate culture to which had been added earlier a few pinches of leaves partly decomposed in contact with the ground. Two months later the fungus again showed its ability to thrive at summer temperatures by developing spontaneously in an agar plate culture made in the isolation of *Pythium Butleri* Subr. from diseased portions of experimental spinach plants that were wilting and dying at Arlington, Va., evidently as the result of extensive decay in crown and taproot. In both cultures the fungus subsisted on an *Amoeba* rather closely similar to the species previously (6) found preyed upon by *S. rhabdospora* and then referred tentatively to *A. similis* Greeff. The dimensional relationships of the nuclei in the two species gave perhaps the clearest indication of difference in specific identity. Whereas the animals captured by *S. rhabdospora,* measuring mostly 30 to 40 μ in diameter, had an ellipsoidal nucleus 9 to 10 μ long and 7 to 8 μ wide, those captured by the fungus under consideration were each provided with a nucleus of similar prolate shape, 10 to 14.5 μ long and 7.5 to 8.5 μ wide. This large nucleus revealed close under its membrane approximately 30 darkish

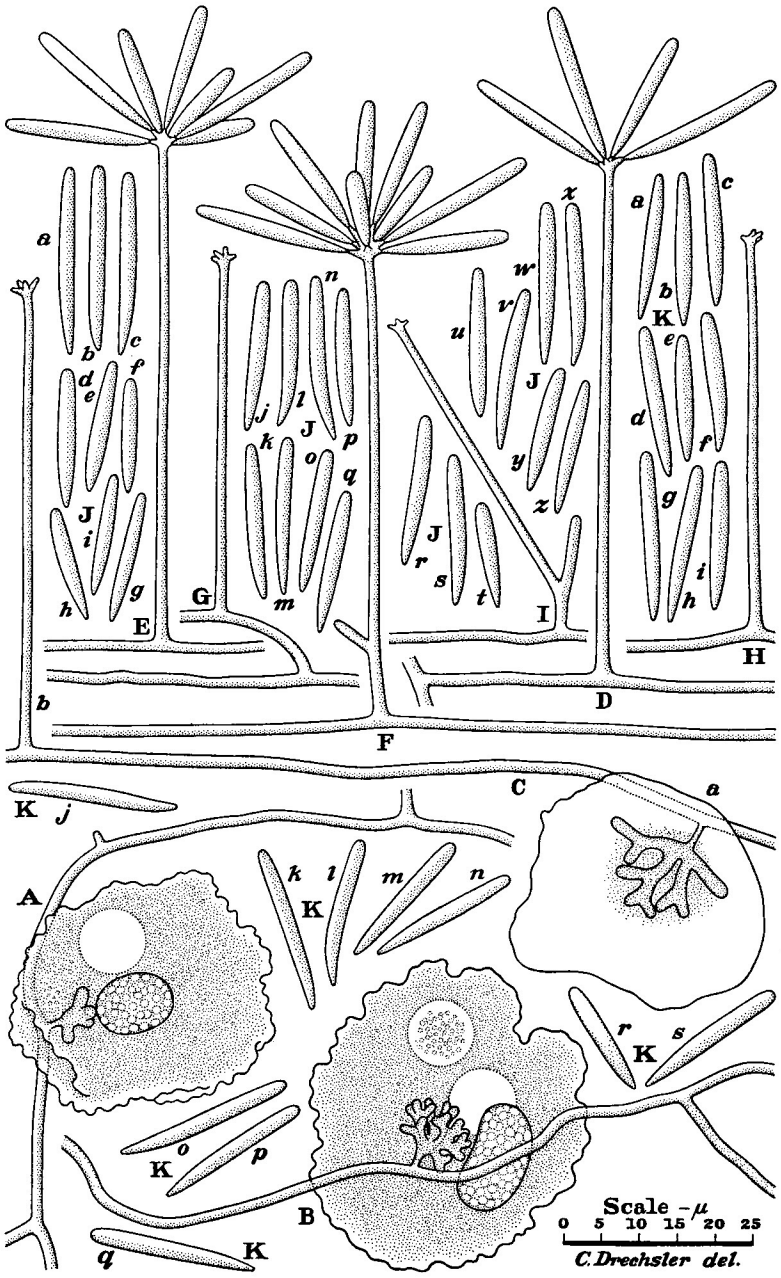

FIG. 3. *Stylopage cephalote.*

sphaeroidal bodies measuring about 1 to 1.2 μ in diameter, and distributed more or less evenly in a peripheral layer, wherein they maintained a continuous circulatory movement that was reminiscent somewhat of the movement of chloroplasts in epidermal cells of *Elodea* leaves, familiar from classroom demonstrations of cyclosis.

The mycelium of the fungus, like that of most predacious forms, is sparse. Yet branching would seem to occur here at closer intervals than in *Stylopage rhabdospora,* and the individual hyphae, while of the same width as the filaments of that species, often take courses with capricious curves and turns. Capture of a susceptible *Amoeba* by adhesion to a mycelial filament is promptly followed by perforation of the delicate pellicle and development of a haustorium (FIG. 3, *A;* 4, *A*), which through variation in the number and closeness of its bifurcations, may show in its definitive condition either an open (FIG. 3, *C, a;* 4, *B*) or a more compact (FIG. 3, *B*) arrangement of parts. After gradual appropriation both of the animal's finely granular cytoplasm and of its impressive nucleus, only the empty pellicle remains behind, to collapse and finally to disappear.

Asexual reproduction takes place somewhat more sparingly than might be expected from the number of animals consumed. The erect conidiophores (FIG. 3, *C, a; D–J*) that arise here and there from superficial hyphae, are of about the same stature as the more nearly medium-sized fertile hyphae of *Stylopage rhabdospora.* On them are borne in bristling capitate arrangement from 4 to 9 conidia decidedly smaller than the homologous structures of *S. rhabdospora,* but closely similar to those of *S. haploe* Drechsl. in shape and size (FIG. 3, *J, a–z; K, a–s*). The resulting aerial apparatus (FIG. 3, *D, E, F*) is of handsome appearance, modestly imitating, as it does, the beautiful habit of various nematode-capturing Hyphomycetes, as, for example, *Dactylaria candida* (Nees) Sacc.; the imitation furnishing another striking instance of convergence brought about evidently by a predacious mode of life.

Sexual apparatus is produced in moderate quantity, often through fusion of a mycelial branch with the germ tube of a fallen conidium (FIG. 4, *C, a–e*), so that confusion with homologous ap-

paratus of other members of the Zoopagaceae present in the same tract of substratum, is conveniently obviated. In such zygophoric germination of conidia, as in dimensions of conjugating elements, of zygosporangium and zygospore (FIG. 4, *C*, *f–h*), close similarity to *Stylopage rhabdospora* is again apparent.

Although the original definition of *Stylopage* does not make provision for a distinctly capitate arrangement of the conidia, the fungus is referred to that genus because of its obviously close relationship to *S. haploe* and *S. rhabdospora*. No emendation of the generic diagnosis is proposed at present, in view of the possibility that discovery of other capitate species may sooner or later make advisable the erection of a separate genus related to *Stylopage* in the same way as *Dactylaria* is related to *Dactylella* among the predacious Hyphomycetes. In the meantime a specific epithet meaning "headed" may aptly direct attention to the most striking characteristic of the fungus.

Stylopage cephalote sp. nov.

Sparsa; hyphis sterilibus incoloratis, 1.2–1.8 μ crassis, haustoria pedicellata evolventibus; pedicello saepius .6–.7 μ crasso, 2–4 μ longo, ramulis usque quater dichotomis, divaricatis, 1–2 μ crassis, usque 10 μ longis; hyphis fertilibus incoloratis, saepius 45–75 μ altis, basi 1.2–2 μ crassis, sursum paulatim attenuatis, apice 1.1–1.3 μ crassis, ibi 4–9 conidia in capitulum pulchrum radians digesta ferentibus. Conidia elongato-cylindracea, sursum abrupte rotundata, deorsum plerumque attenuata, basi acutiuscula, 14–25 μ longa, 1.8–2.5 μ lata. Zygosporangia primo levia, sphaeroidea, 8–10 μ diam., in maturitate membrana circa zygosporam collabente; zygospora flavida, sphaeroidea, 7–9 μ diam., membrana .7–1.8 μ crassa, 10–20 verrucis ornata.

Amoebas plerumque 25–35 μ latas capiens et consumens, habitat in radicibus putrescentibus *Spinaceae oleraceae* et in foliis semisepultis putrescentibus, in Arlington, Virginia, et prope Beltsville, Maryland.

Sparse; vegetative hyphae colorless, 1.2 to 1.8 μ wide, producing haustoria composed individually of a stalk mostly .6 to .7 μ wide and 2 to 4 μ long, together with branches bifurcating successively 2 to 4 times, and measuring 1 to 2 μ in width by 10 μ in length; fertile hyphae colorless, mostly 45 to 75 μ high, 1.2 to 2 μ wide at the base, gradually tapering to a width of 1.1 to 1.3 μ at the apex, where on short tapering projections 4 to 9 conidia are borne in bristling capitate arrangement. Conidium cylindrical, abruptly rounded at the apex, mostly tapering markedly toward the somewhat acute base, 14 to 25 μ (average 20 μ) long and 1.8 to 2.5 μ (average 2.2 μ) wide. Zygosporangium at first smooth, spherical,

8 to 10 μ in diameter, its wall at maturity collapsing about the zygospore; zygospore yellowish, subspherical, 7 to 9 μ in diameter, with a wall .7 to 1.8 μ thick, ornamented with 10 to 20 wartlike protuberances of which 6 to 8 are visible in the sigillate profile.

Occurring in decaying roots of *Spinacea oleracea* L., and in partly buried decaying leaves, capturing and consuming a species of *Amoeba* mostly from 25 to 35 μ in diameter, in Arlington, Va., and near Beltsville, Md.

ACAULOPAGE ACANTHOSPORA

In an old maizemeal agar plate culture to which some greenhouse refuse undergoing moist decomposition had previously been added, conidia of small dimensions but striking appearance were observed scattered sparsely over the surface of the substratum close to the deposits of decaying material. As an obvious similarity in general habit to *Acaulopage tetraceros* Drechsl. (3) was strongly suggestive of membership in the Zoopagaceae, a closer examination was made, with the result that the underlying mycelium was, indeed, found to be of the sparse, non-septate predacious type usual in this family. Though the rather delicate hyphae were in part superficial, in the main they followed their somewhat irregular courses under the surface of the agar. *Amoebae* in varying stages of depletion were found attached here and there both to the superficial and to the submerged filamentous elements (FIG. 4, *D–I; J, a*). Some of the captured animals gave no indication of their identity, except such as might be conveyed in moderate or small dimensions, a frequently elongate shape, and a relatively small nucleus, showing a darkish central globose body within a narrow lighter peripheral layer (FIG. 4, *D; F; G, a; I*). In addition to these features, other adhering specimens exhibited unmistakably a tuftlike group of minute digitations (FIG. 4, *H*), or a less crowded array of deltoid protuberances manifestly representing a cluster of digitations partly relaxed and in process of obliteration. The captured rhizopods were therefore readily referred to *Amoeba limax* Duj., of which species, in truth, numerous living individuals could still be seen moving on or through the substratum.

Since in locomotion *Amoeba limax* always carries its tuft of digitation in the rear, it might be expected that captured specimens

would nearly always be attached by a portion of pellicle diametrically opposite to it in position. Such, however, is not the case, for rather frequently the adhesion takes place in close proximity to the posterior tuft (FIG. 4, *E; G, b; H*), indicating that capture does not always result at once whenever contact occurs, but is influenced a good deal by the caprice of circumstance. In any case, following capture, the lateral branch thrust through the pellicle of the animal ramifies almost immediately upon reaching the interior to give rise to a few flexuous elements of approximately the same width as the mycelial hyphae. These haustorial elements gradually bring about the assimilation of the animal's substance, and during the later stages of depletion are themselves progressively evacuated of protoplasm (FIG. 4, *G, b; H; I*), much like the homologous structures in other members of the family.

The conidia of the fungus are formed singly flush on the surface of the substratum, in large part at least, on the up-curved tips of somewhat short, superficial or nearly superficial hyphal branches (FIG. 4, *J, b; K; L*). In the beginning they develop as smooth globose terminal bodies (FIG. 4, *J, b; K*); but on approaching definitive size, each proliferates from its distal hemisphere usually a dozen or more tapering digitiform protuberances (FIG. 4, *L*). These protuberances are some time later evacuated by the retreat of their protoplasmic contents, and thus converted into empty appendages (FIG. 4, *M–W*). In some conidia an empty basal stipe is present as a prolongation of the noticeable pedicellus (FIG. 4, *M, O, S, U*), duplicating the condition usual in *Acaulopage ceratospora* Drechsl. (3) and *A. tetraceros;* though, perhaps more frequently, no empty basal appendage is visible here (FIG. 4, *N, P, Q, R, T*) whether because of abortive development, or early collapse, or damage suffered during disarticulation. More constant characters decisively distinguishing the species from *A. tetraceros,* are, of course, represented in the distribution of the more numerous and smaller appendages generally over the distal hemisphere of the conidium instead of in an apical zone, and in the smaller volume and globose rather than inverted lageniform shape of the living cell.

It is intended to bring into relief the characteristic bristling appearance of the conidium in a name composed from words meaning "spine" and "seed" respectively.

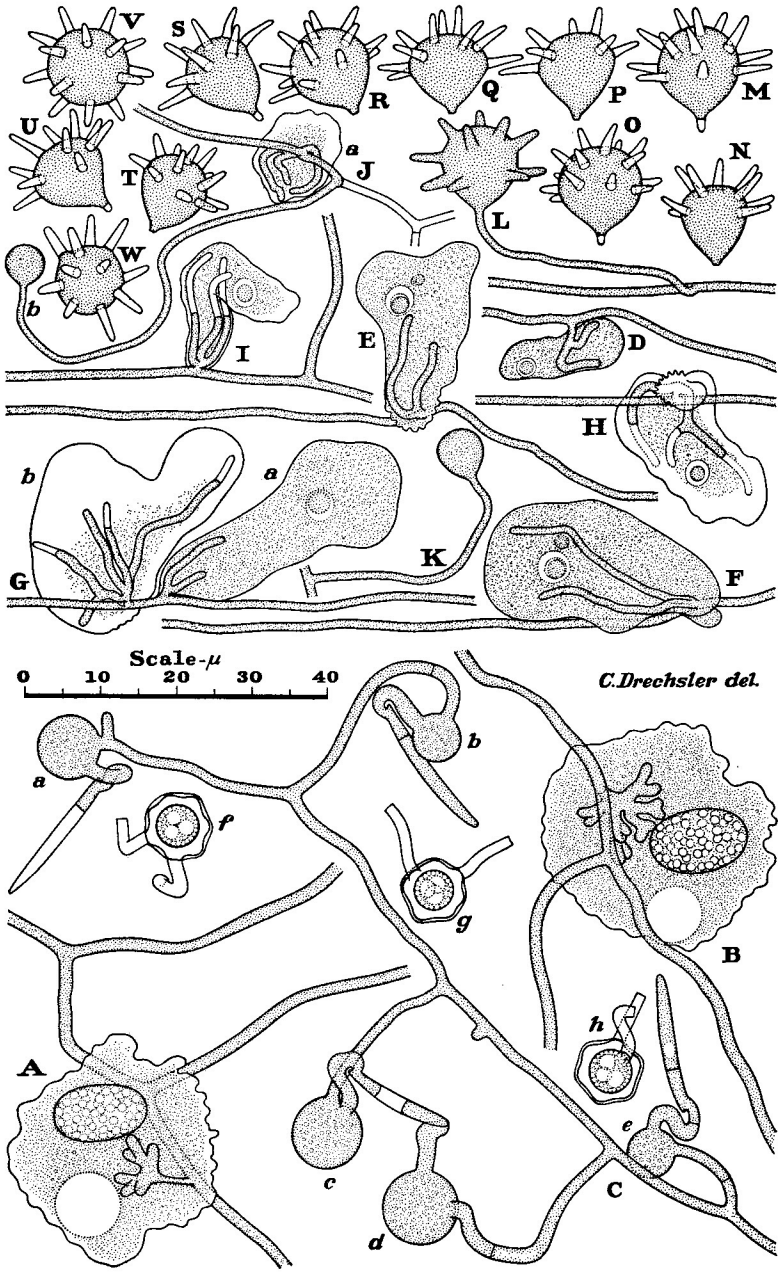

FIG. 4. *A–C, Stylopage cephalote; D–W, Acaulopage acanthospora.*

Acaulopage acanthospora sp. nov.

Sparsa; hyphis incoloratis, .7–1.4 μ crassis; haustoriis praecipue basi dichotomis, ex 2–4 ramulis flexuosis, 5–30 μ longis, 1–1.3 μ crassis compositis. Conidia hyalina, minute pedicellata; cellula viventi protoplasmatis repleta, globosa, interdum paulo applanata tum plus minusve turbinea, saepius 10–12 μ longa, 9–10.5 μ lata, in dimidio supero 7–18 appendicibus vacuis divergentibus digitiformibus, 3–6 μ longis, basi 1–2 μ crassis, sursum attenuatis, apice rotundatis praedita.

Amoebam limacem capiens et consumens, habitat in materiis plantarum putrescentibus, prope Beltsville, Maryland.

Sparse; hyphae colorless, .7 to 1.4 μ wide, producing haustoria mostly basally dichotomous and composed of 2 to 4 flexuous branches 5 to 30 μ long and 1 to 1.3 μ wide. Conidia hyaline, noticeably pedicellate; the single living cell of each, mostly globose but occasionally flattened into somewhat turbinate shape, in any case measuring 10 to 12 μ in length by 9 to 10.5 μ in transverse diameter, and bearing distributed over its distal hemisphere 7 to 18 empty divaricate slightly tapering digitate appendages measuring 3 to 6 μ in length and 1 to 2 μ in basal diameter.

Occurring in decaying plant remains, capturing and consuming *Amoeba limax,* near Beltsville, Md.

DEFINITION OF THE FAMILY

With the four fungi presented herein thirty species have been described in the Zoopagaceae. When the family was first proposed (2) a definition was intentionally postponed in the hope that discovery of additional members might reveal more adequately the scope of morphological diversity within the group, and at the same time supply clearer indications of the relationships to some of the older established taxonomic subdivisions in the Phycomycetes. The species found since then have, indeed, brought to light unexpected departures in vegetative and reproductive development, such as are embodied, for example, in the long filamentous conidium of *Zoopage nitospora,* in the curiously appendaged asexual spore of *Acaulopage acanthospora,* in the circinate thallus of *Cochlonema cylindricum* Dreschsl. (7), and in the dentate zygosporangium of *Z. odontosperma* Drechsl. (7). Somewhat surprisingly, too, the two tendencies in design of endozoic parts represented in the short thick spirally coiled vegetative hypha characteristic of most endoparasitic species, on the one hand, and in the divaricately branched

haustorium usual in predacious forms on the other (3), are largely reconciled when the moderately thickened and extensively coiled thallus of *C. megaspirema* Drechsl. (7) is considered in conjunction with the typically dichotomous, spirally disposed, swollen haustorium of *Z. thamnospira.*

Yet concerning the relationship of the Zoopagaceae to older groups within the Zygomycetes little additional information has been gained. Though asexual reproductive apparatus in all species of *Cochlonema* and *Zoopage* was carefully examined, nothing has been observed that could be held to argue in favor of endogenous development of the conidia in catenulate members of the family, or otherwise to sustain any supposition of homology between the conidial chains in these members and the rows of spores in the Piptocephalidaceae. Again, the rather initimately suggestive resemblance of *Stylopage hadra* Drechsl. to the insectivorous Entomophthoraceae (2, 4) has been found merely repeated without amplification in *S. leiohypha* Drechsl. (5).

While the Zoopagaceae show general similarity to the Entomophthoraceae in subsisting on living animals, and in reproducing asexually by conidia and sexually by zygospores, the differences between the two families are, nevertheless, very obvious. Of the thirty forms destructive to rhizopods and nematodes, not any shoot away their conidia or show the least adaptation for the violent discharge of spores that provides an outstanding characteristic of the older group. In visible habit, especially under natural conditions but to a marked degree even on transparent artificial culture media, the Zoopagaceae simulate the more delicate of the saprophytic molds; their conidial apparatus appearing sparsely distributed on the surface of the substratum in a manner certainly not at all reminiscent of the insectivorous Entomophthoraceae, nor, for that matter, of *Conidiobolus* or *Basidiobolus,* despite the effuse vegetative development usual in these two genera. Such scattered distribution is naturally to be expected in terricolous fungi living by the capture of microscopic animals that roam about in the decaying materials underneath; being, indeed, shared also by the predacious Hyphomycetes belonging mostly to the genera *Trichothecium, Arthrobotrys, Dactylella* and *Dactylaria,* when these develop under natural conditions. Much the same scattering of

conidial apparatus with concealment of biogenous relationship, prevails likewise among the endoparasitic and ectoparasitic members of the Zoopagaceae. As an infected host animal usually succumbs well under the surface of the substratum, the origin of the plural conidiiferous filaments is under natural conditions completely hidden from view; so that when these filaments emerge into the air at well separated points to extend themselves recumbently considerable distances in various directions and often to mingle with similar filaments from other sources, their common origin in a parasitized individual organism could hardly be suspected. Through the rangy disposition of sporiferous hyphae, the conidia formed from them are from the outset spread over a comparatively large area, and are thus given a better chance for encountering susceptible animals than would be provided by a closer arrangement. The relatively extensive development of the sparse mycelium in predacious members of the family, and the spindling aerial development in parasitic members, seem therefore to operate toward an end that is accomplished spectacularly in the Entomophthoraceae by the forcible discharge of conidia, and that perhaps is somehow promoted in the Harpellaceae by the helicoid spore appendages first described by Léger and Gauthier (9), and more recently figured for one species by Gauthier (8).

The rangy mycelial habit of the predacious forms offers a marked contrast to the compact vegetative habit shown by species of *Actinomyces* especially in liquid or agar or gelatin culture media. Yet the contrast may be less significant than conspicuous, possibly resulting from the exigencies of a predacious mode of obtaining nourishment as contrasted with a saprophytic or a parasitic mode. Certainly the thallus in the parasitic genera *Endocochlus* and *Cochlonema,* which during most of its growing period is everywhere immersed in food material, is not lacking in compactness. If pronounced thickening and spiral convolvement make this thallus look much different from the mycelium of *Actinomyces,* or of other groups of fungi, these modifications evidently are representative not so much of a fundamental morphological tendency in the family as of physical adaptation to life in a rather small animal with indeterminate rolling locomotion.

The production in *Cochlonema cylindricum* of relatively small

rod-like smooth conidia through segmentation of decidedly little differentiated aerial filaments, shows much similarity to spore formation in those species of *Actinomyces* that likewise have very simple conidial apparatus. Divergent tendencies in differentiation obscure this similarity in the more distinctive forms: verrucose sculpturing, unknown in *Actinomyces,* adding character to the conidia of many catenulate members of the Zoopagaceae; while elaborate coiling of aerial sporiferous branches, altogether alien to the Zoopagaceae, beautifies the conidial apparatus in numerous species of *Actinomyces.*

As the phycomycete with *Pythium*-like chlamydospores that in an earlier summary was figured synoptically (**1**: *p. 269, fig. 15; p. 270, lines 7–19*) among other fungi also predacious on nematodes, has not yet been definitely referred to the family under discussion, it is conveniently omitted from consideration in the diagnosis here submitted.

Zoopagaceae fam. nov.

Fungi plerumque minuti, terrestres, animalcula (Rhizopoda et Nematoda) enecantes. Mycelium specierum animalia capientium hyalinum, continuum, late effusum, irregulariter ramosum, haustorium ramosum in captum insinuans, hoc carnem illius exhauriens; hyphae alitae specierum intra animalia crescentium autem plerumque breves, crassae, simplices vel bifurcatae vel repetite dichotomae, saepius semel vel pluries spiraliter convolutae. Conidia hyalina, levia vel verrucosa, saepe filiformia vel fusoidea rarius globosa, interdum appendiculas vacuas praecipue sursum ferentia; nunc singulatim hinc illinc ex hyphis repentibus mycelii vel hyphis fertilibus arachnoideis recumbentibus assurgentia, nunc ex apice hypharum fertilium erectarum oriunda singularia vel in capitula laxa aggregata, nunc in catenulas plus minusve elongatas digesta; illa unius speciei cognitae ad animalia haerentia, haustorium intus evolventia, tum ipsa magnopere tumescentia. Zygosporangia saepissime in materia circum animalia vel sub animalibus raro intra animalia, ex copulatione hypharum similium orta, membrana modo zygosporam laxe circumdans, modo verisimiliter cum hac concreta.

Mostly minute terricolous fungi subsisting by the destruction of small animals (rhizopods and nematodes). Vegetative thallus in predacious species consisting of a hyaline, continuous, extensive, irregularly and rather sparsely ramifying mycelium, which gives rise to variously branched haustoria within the captured animals and by means of these haustoria appropriates the fleshy contents; in endoparasitic species consisting of a hypha, short,

thick, simple or bifurcate or repeatedly dichotomous, and, when well developed, wound spirally in a coil of one or more turns; in ectoparasitic species consisting of a swollen conidium adhering externally to the animal, together with the branching haustorium inside produced directly by germination of the conidium. Conidia aerial, hyaline, smooth or somewhat verrucose, mostly filiform or spindle-shaped though occasionally globose, sometimes bearing empty appendages in mainly distal positions; now arising laterally and singly at intervals from prostrate mycelial hyphae or from recumbent arachnoid sporiferous filaments; now budded off terminally one by one, or more nearly simultaneously and in loose heads, on approximately erect conidiophores; now produced in chains of variable lengths. Zygosporangium resulting from the conjugation of two similar hyphae, produced rarely within the animals attacked but much more frequently in the solid substratum surrounding or underlying them; its membrane at maturity in some species well separated from and loosely collapsed about the zygospore, in other species rather indistinguishably fused with the zygospore wall.

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EXPLANATION OF FIGURES

FIG. 1. *Zoopage mitospora;* drawn with the aid of a camera lucida at a uniform magnification; × 1000 throughout. *A,* Portion of hypha with a well developed haustorium in a relatively small captured *Amoeba. B,* Portion of hypha with an extensive haustorial system in a large captured *Amoeba;* within the animal are visible, in addition, an encysted organism, several digestive vacuoles, and a young thallus of an endoparasitic member of the Zoopagaceae. *C,* Portion of hypha with a small captured *Amoeba,* mostly depleted of protoplasm. *D,* Portion of hypha with a small captured *Amoeba,* whose contents have been almost wholly appropriated by means of the correspondingly small haustorium. *E,* Portion of hypha on which are borne a moderately extensive haustorium in the medium-size *Amoeba, a,* and at some distance a sterigma, *b,* with two catenated conidia, *c* and *d. F,* Portion of a superficial hypha with an erect sporogenous branch, wherein a basal portion, *a,* and two spore initials, *b* and *c,* are distinguishable. *G,* Portion of hypha with a branching sterigma: one spur, *a,* being denuded; a second, *b,* bearing a single long conidium, *e*; a third, *c,* bearing two catenated conidia, *f* and *g*; and a fourth, *d,* being continuous with the sporogenous filament consisting of the spore initials, *h* and *i. H,* Conidia, *a–i,* showing variations in size and shape.

FIG. 2. *Zoopage thamnospira;* drawn with the aid of a camera lucida at a uniform magnification; × 1000 throughout. *A,* Portion of hypha with a young haustorium in a captured *Amoeba,* within which is shown, besides, a small contractile vacuole, a spherical digestive vacuole and an ellipsoidal nucleus. *B,* Portion of hypha with a partly developed haustorium in a captured *Amoeba, a,* and a partly evacuated haustorium in the largely depleted *Amoeba, b. C,* Branched portion of mycelium on which are being held six captured *Amoebae* with protoplasmic contents in different stages of depletion, and occupied by haustoria variously developed. *D,* Portion of hypha that has given rise within a captured *Amoeba* to a well developed haustorium, which shows spiral curvature of the regularly dichotomous branches. *E,* Portion of hypha that has produced within a captured *Amoeba* a well developed haustorium with rather regularly dichotomous, handsomely curved branches; the distal branches having become evacuated with the approaching exhaustion of the captive's protoplasmic materials. *F,* A large *Amoeba* being invaded by a germ tube from an adhering conidium; a contractile vacuole, two digestive vacuoles, and the nucleus are visible within the animal. *G,* A smaller *Amoeba* similarly being invaded by the germ tube of an adhering conidium. *H,* Portion of a superficial hypha with an aerial conidiiferous filament. *I,* Two adjacent conidia in a mature chain, showing the empty connection between them. *J–O,* Conidia, showing variations in shape and size.

FIG. 3. *Stylopage cephalote;* drawn with the aid of a camera lucida at a uniform magnification; × 1000 throughout. *A,* Portion of hypha showing

a haustorium partly developed, within a captured *Amoeba;* in the animal is seen besides, a spherical contractile vacuole and an ellipsoidal nucleus. *B,* Portion of hypha with a well branched haustorium visible in a captured *Amoeba. C,* Portion of hypha on which have been produced a well developed haustorium within the almost wholly depleted *Amoeba, a,* and, some distance away, a conodiophore, *b,* now denuded of its spores. *D, E, F,* Conidiophores bearing four, seven and nine conidia respectively. *G, H, I,* Denuded conidiophores. *J, a–z; K, a–s,* Conidia, showing variations in size and shape.

FIG. 4. Drawn with the aid of a camera lucida at a uniform magnification; × 1000 throughout.

A–C, Stylopage cephalote: A, B, Portions of mycelium, each with a partly developed haustorium inside of a captured *Amoeba;* within each invaded animal are shown also a spherical contractile vacuole and an ellipsoidal nucleus. *C,* Sexual apparatus: *a–e,* five young zygosporangia, each resulting from the union of a mycelial hypha or hyphal branch with a germ tube from a conidium; *f–h,* mature zygosporangia, the relaxed membrane of each zygosporangium loosely surrounding the mature zygospore.

D–W, Acaulopage acanthospora: D, E, F, Portions of hypha, each of which has given rise to a bifurcate haustorium within a captured specimen of *Amoeba limax. G,* Portion of hypha that has given rise to a partly developed haustorium in a newly captured specimen of *A. limax, a;* and, close by, to a fully developed haustorium, which, on the nearly complete appropriation of the protoplasmic materials in the captured specimen of *A. limax, b,* has become partly evacuated. *H, I,* Portions of hypha, showing a more advanced stage in the withdrawal of contents from the haustorial branches in the largely depleted captured specimens of *A. limax. J,* Portion of a superficial hypha showing a captured specimen of *A. limax, a,* and a young growing conidium, *b. K,* Portion of hypha with a young conidium at a slightly later stage of development. *L,* Portion of mycelium with a fully grown but still immature conidium. *M–U,* Mature conidia in lateral view, showing variations in size, in shape, and in number and arrangement of the empty spiny appendages. *V, W,* Conidia in upper (*i.e.* distal polar) aspect.