

A PYTHIUM WITH STOUT OOGONIAL SPINES AND COILED ANTHERIDIAL BRANCHES

CHARLES DRECHSLER¹

Among the oomycetes that have been isolated from discolored or softened tissues of phanerogamic plants the 2 species I described in 1930 under the binomials *Pythium mastophorum* and *P. polymastum* stand out, together with the flax root-rot fungus referred by Buisman (1927) to *P. megalacanthum* de Bary (1881a and b), as members of an unusually distinctive group (Drechsler, 1939b). When grown on maize meal agar of customary firmness the 3 species produce abundant large oogonia beset with numerous protuberances of conical or somewhat mammiform shape. Since these protuberances are usually of greater basal width and commonly show a thicker wall than the corresponding oogonial modifications in such more familiar congeners as my *P. periplocum*, *P. acanthicum* and *P. oligandrum* (Drechsler 1930, 1939a, 1946) they appear characteristically sturdier. With this difference in appearance are associated differences in mycelial habit and biological relationship; the stoutly spinose group lacking the decidedly strong tendency toward delicate hyphal ramification usual among the familiar echinulate forms, besides being devoid of all capacity for parasitizing other species of *Pythium*. Accordingly it may be presumed that within the genus the stoutly spinose forms have no especially close kinship to the members of the delicate echinulate series. They would seem likewise to be somewhat remote from the digitated species *P. irregulare* Buisman (1927), *P. mamillatum* Meurs (1929), and *P. spinosum* Sawada (1927), all apparently closely related to the very familiar *P. debaryanum* Hesse (1874), wherein the oogonium is beset with protuberances of generally cylindrical shape, bluntly rounded at the tip. As the few members of the stoutly spinose group are obtained from affected plant tissue much less frequently than representatives of either the more delicately echinulate or the digitated series, they have not become known to many plant pathologists. An additional member of extraordinary distinctiveness that came to light among some cultures isolated from discolored roots of sheep sorrel (*Rumex acetosella* L.) collected near Beltsville, Maryland, on April 28, 1949, may perhaps offer readier ex-

¹ Pathologist, Division of Fruit and Vegetable Crops and Diseases, Bureau of Plant Industry, Soils, and Agricultural Engineering, Agricultural Research Administration, United States Department of Agriculture; Plant Industry Station, Beltsville, Maryland.

perience with the group since the host plant concerned here is very widely distributed and rather easily removed from the ground.

The fungus in question grows more rapidly on maize meal agar than *Pythium mastophorum* or *P. polymastum*. Its newly developed mycelium often shows little of the haphazard intermingling of hyphae usual in cultures of the 2 related species, but instead will frequently display a more nearly orderly arrangement like that of *P. irregulare*, *P. mamillatum*, and *P. anandrum* (Drechsler 1930, 1939a), the stout axial hyphae pursuing straightforward radial courses and giving off at intervals narrower, handsomely ramified branches of restricted length. After a few days, however, the original orderliness of the mycelium may become diminished from random development of some additional hyphae. The main hyphae (fig. 1, A-G: a; fig. 2, A-C: a) commonly measure from 3 to 8 μ in width; so that the fungus needs to be reckoned, along with the common damping-off species, among the coarser members of the genus. On the lower side of Petri plate cultures the mycelium often produces moderate numbers of appressoria in contact with the glass floor. These appressoria appear as swollen hyphal terminations (fig. 3, A-P) variously curved and often more than 100 μ in length. Many appressoria grow out distally to form a filamentous hypha (fig. 3, D) whereon a second appressorium may be produced. At the proximal end the appressorium is often found set off by a crosswall, or frequently, again, is delimited by a retaining wall separated by a narrow empty space from a retaining wall that bounds the supporting branch. It remains uncertain to what extent delimitation from the supporting branch may be construed as normal development, or as an abnormality resulting from functional frustration and internal degeneration of the appressorium.

Since liberal production of appressoria often indicates a capacity to invade plant tissue, the fungus was tried out by transferring portions of young mycelium from a pure culture into shallow incisions in cucumber (*Cucumis sativus* L.) fruits. When the inoculated fruits were kept at 28° C. they underwent a rapidly progressive softening of their tissues, with the result that after 2 or 3 days they began to release much water turbid with bacteria. At 17° C. decay was slower and less seriously influenced by secondary organisms. The progress of the invading fungus was noticeable externally in the advance of a water-soaked zone about 20 mm. wide. Behind this zone aerial mycelium grew out, at first appearing as a light fleecy layer (fig. 4, A-C), but later in some instances forming a cottony web that covered the cucumber virtually from end to end (fig. 4, D). On microscopical examination newly invaded tissues were found abundantly permeated with mycelial hyphae of the fungus, all of them filled throughout with living protoplasm of faultless texture. When portions of tissue were kept moist

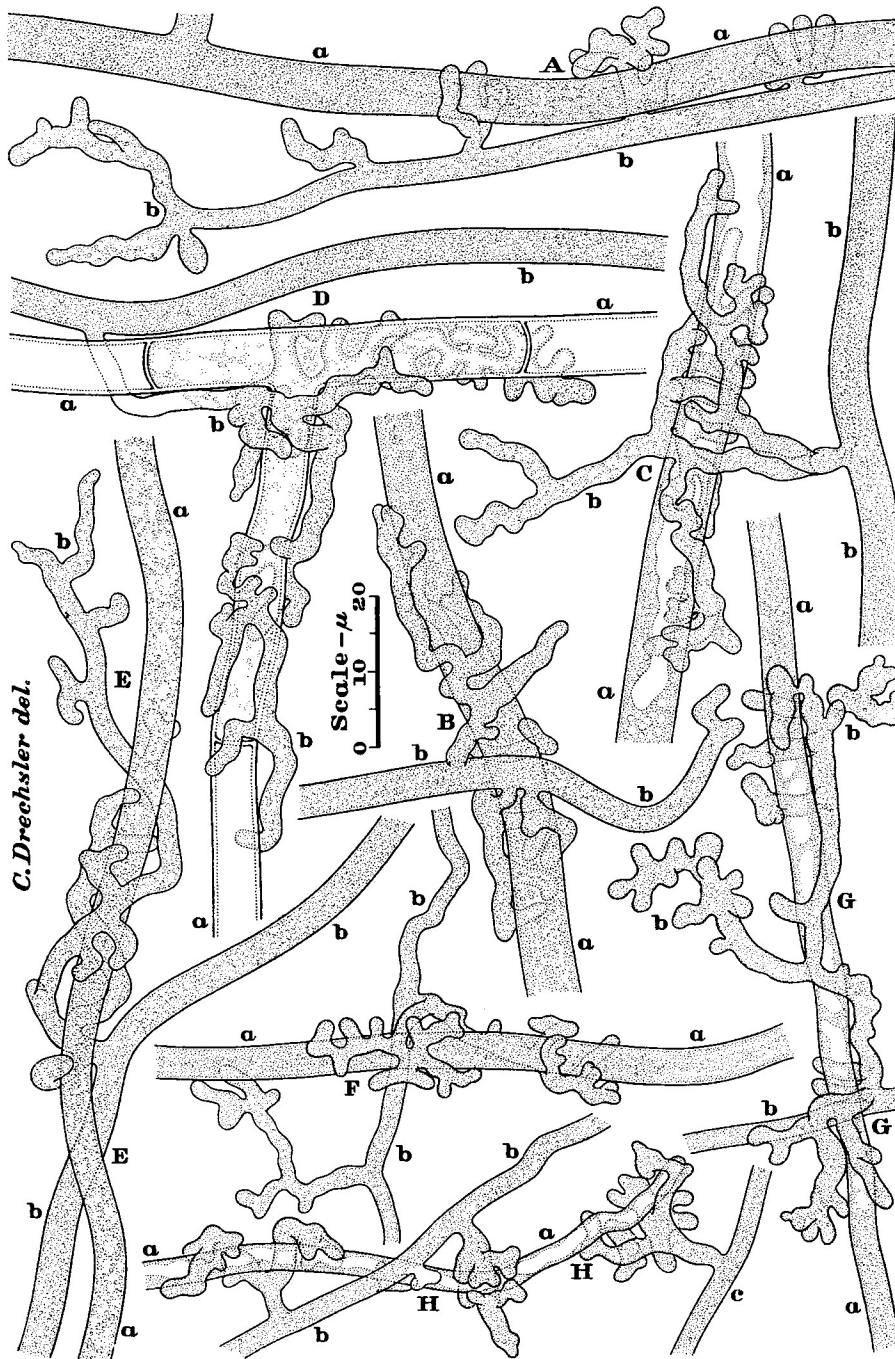


FIG. 1. A-D. Hyphae of *Pythium helicandrum*, a, attacked by ramifications extended from neighboring filaments of *P. oligandrum*, b. E-H. Hyphae of *P. helicandrum*, a, attacked by ramifications extended from neighboring filaments of *P. acanthicum*, b. All parts drawn to a uniform magnification with the aid of a camera lucida; $\times 1000$ throughout.

for a few days the hyphae became progressively emptied as their contents were utilized in the production of numerous oospores.

Although sexual reproduction thus is abundantly displayed in host tissues it can be more conveniently studied in Petri plate cultures prepared with maize meal agar preferably containing a noticeable quantity of finely divided maize meal in suspension. After the fungus has been growing in such cultures for about 2 days, units of sexual apparatus begin to appear in the older portions of the mycelium. They always have their origin in positions where 2 hyphae having no visible mycelial connection come close together (fig. 5, A-N: a, b; fig. 6, A-J: a, b; fig. 7, A-I: a, b), whether at wide or at narrow angles. Judging from appearances, development is initiated where local contact or proximity of 2 hyphae comes about through chance, rather than through special directional growth. In the region of contact or closest proximity each of the 2 hyphae (fig. 5, A-C: a, b) usually puts forth a lateral branch. The 2 branches, which thus from the beginning are in contact with each other, elongate jointly. As they elongate the branch destined to supply the antheridium twines spirally about the branch destined to supply the oogonium, in most instances describing from $1\frac{1}{2}$ to $4\frac{1}{2}$ turns. The oogonial branch sometimes elongates with only meager curvature (fig. 5, E, F, G, I, J; fig. 6, A) but sometimes, again, it likewise shows considerable coiling (fig. 5, B, C, H). Occasionally, indeed, the two branches are coiled in approximately equal measure, and thereby appear entwined in a beautifully symmetrical manner (fig. 5, N, c, d; e, f). Sometimes one of the 2 mycelial hyphae concerned in the production of a unit of sexual apparatus fails to extend a special branch, and is then itself (fig. 5, D, a) entwined by the coiling branch put forth from the other hypha (fig. 5, D, b). In such instances the enwrapped hypha never undergoes any spiral modification at all. Furthermore, it never supplies the antheridium but invariably supplies the oogonium as a mesially or laterally intercalary globose structure (fig. 6, E, a; F, a; fig. 7, E, a).

During their period of elongation and entwinement the two paired sexual branches usually show only slight dimensional differences. Toward the end of this period the oogonial branch is sometimes found with its narrowed tip tightly enveloped in the distal coil of the antheridial branch (fig. 5, A). Rather often an appearance is then given as if the tip of the oogonial branch might be cemented to the wall of the enveloping coil. In instances where the tip of the oogonial branch is thus tightly hemmed in, the oogonium often develops some little distance below through lateral enlargement; the growing globose part pushing its way out sideways between adjacent turns of the coiled antheridial branch (fig. 5, G). More frequently, however, the female branch is not tightly hemmed in at the tip, and the oogonium most often develops as a globose terminal enlargement that pushes its way out:

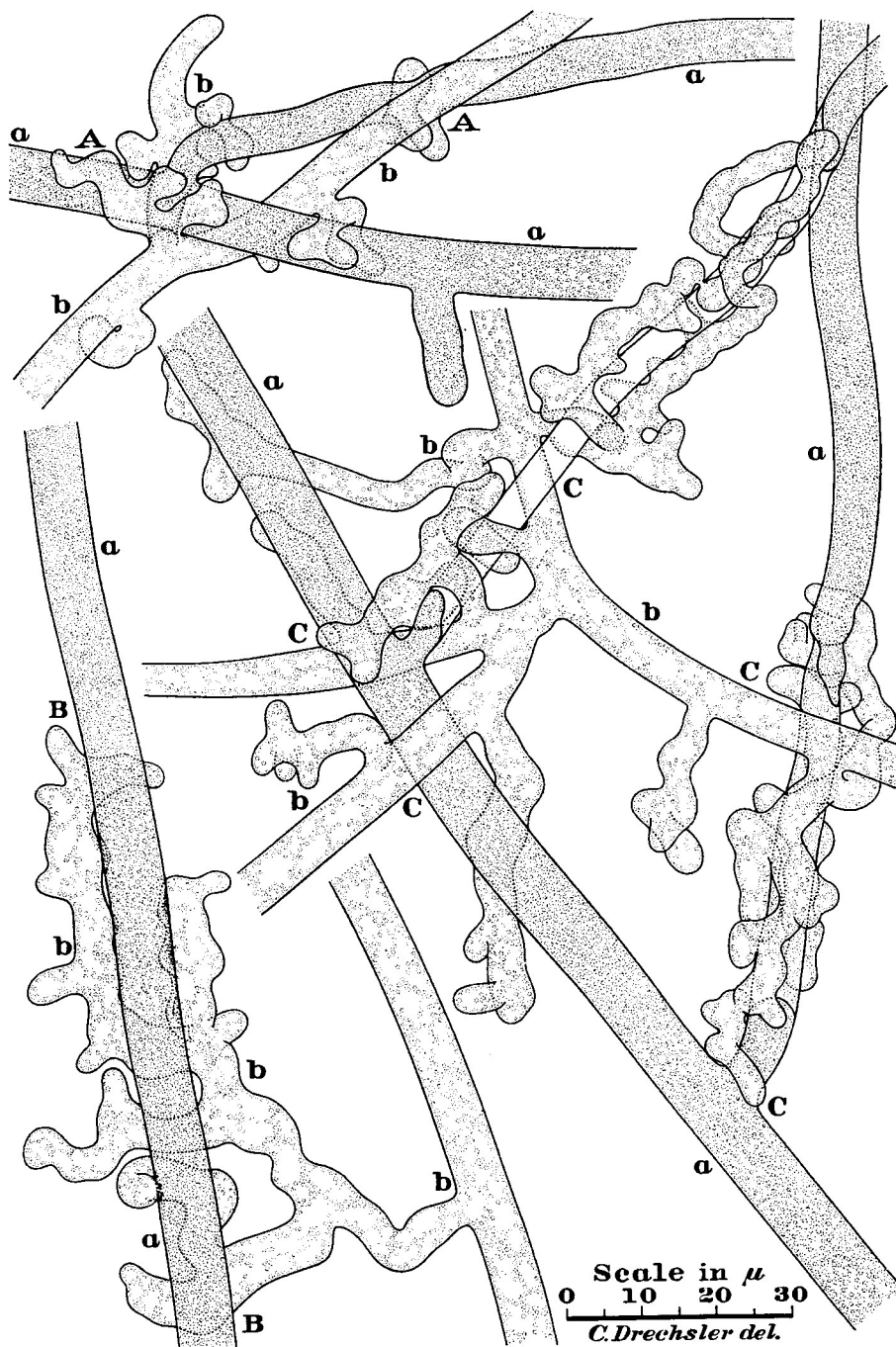


FIG. 2. A. Portion of mycelium of *Pythium helicandrum*, a, in early stage of being enveloped by short ramifications of *Plectospora myriandra*, b. B. Hypha of *Pythium helicandrum*, a, being enveloped by short branches extended from a neighboring filament of *Plectospora myriandra*, b. C. Portion of mycelium of *Pythium helicandrum*, a, showing early injury resulting from envelopment by branches of *Plectospora myriandra*, b. All parts drawn to a uniform magnification with the aid of a camera lucida; $\times 1000$ throughout.

centrally from the distal end of the male coil (fig. 5, E, F, H). The globose enlargement, whether emerging distally or laterally, continues to grow until it reaches a definitive width ranging commonly from 17 to 32 μ . During the later stages of growth it puts forth protuberances in usually somewhat close arrangement. These protuberances at first are dome-shaped and filled with protoplasm (fig. 5, J; fig. 7, A) but soon they become more nearly conical, and after their wall has been thickened they become empty of living contents. At about the same time the globose body is cut off as an oogonium by the laying down of a basal septum in a position approximately flush with the spherical contour (fig. 5, K), or occasionally in a position a few microns below (fig. 7, H).

Concurrently with development of the oogonium the coiled male branch undergoes less conspicuous changes. It appears usually to grow a little in length, and would seem often to increase slightly in width, at least in its distal portion. Now and then its shape is modified in some degree by the production distally of one or more short diverticulations (fig. 5, K; fig. 7, B). Through deposition of a cross-wall, usually 25 to 45 μ below the tip of the branch, a terminal cell is delimited, which, apart from the antheridia that in some species of *Pythium* are formed directly from portions of mycelial hypha, makes up perhaps the most nearly filamentous antheridium known in any member of the genus. In most instances where the female branch elongated centrally through the male coil the antheridium will envelop the distal portion of the stalk and the adjoining basal portion of the oogonium, usually passing around the circumference in a full turn (fig. 5, L, M; fig. 6, C, F, G.; fig. 7, B, C, D, F, G, H, c, d). In other instances the antheridium extends upward over the surface of the oogonium (fig. 5, N; fig. 6, B, I; fig. 7, H) somewhat as in my *P. helicoides* (Drechsler 1939a). Rather frequently, again, the antheridium is found coiled less around the stalk and basal portion of the oogonium than around a stubby projection of the oogonium a little distance from the stalk (fig. 6, J). This curious positional relationship comes about in instances where the female branch expanded laterally to grow through the side of the male coil. The stubby projection here represents, of course, the terminal part of the female branch above the place where enlargement occurred, the same part, therefore that would have composed the distal portion of the stalk had the oogonium been formed terminally after the more usual manner, and that would then similarly have been surrounded by the antheridium. No comparable instances of the oogonium emerging between 2 successive turns of the male coil were noted in any of the units of sexual apparatus that came under observation where the female organ originated directly from an intercalary portion of mycelial hypha. In all such units the male coil was found enveloping only one of the 2 hyphal arms supporting the oogonium, and consequently showed no disturbances of

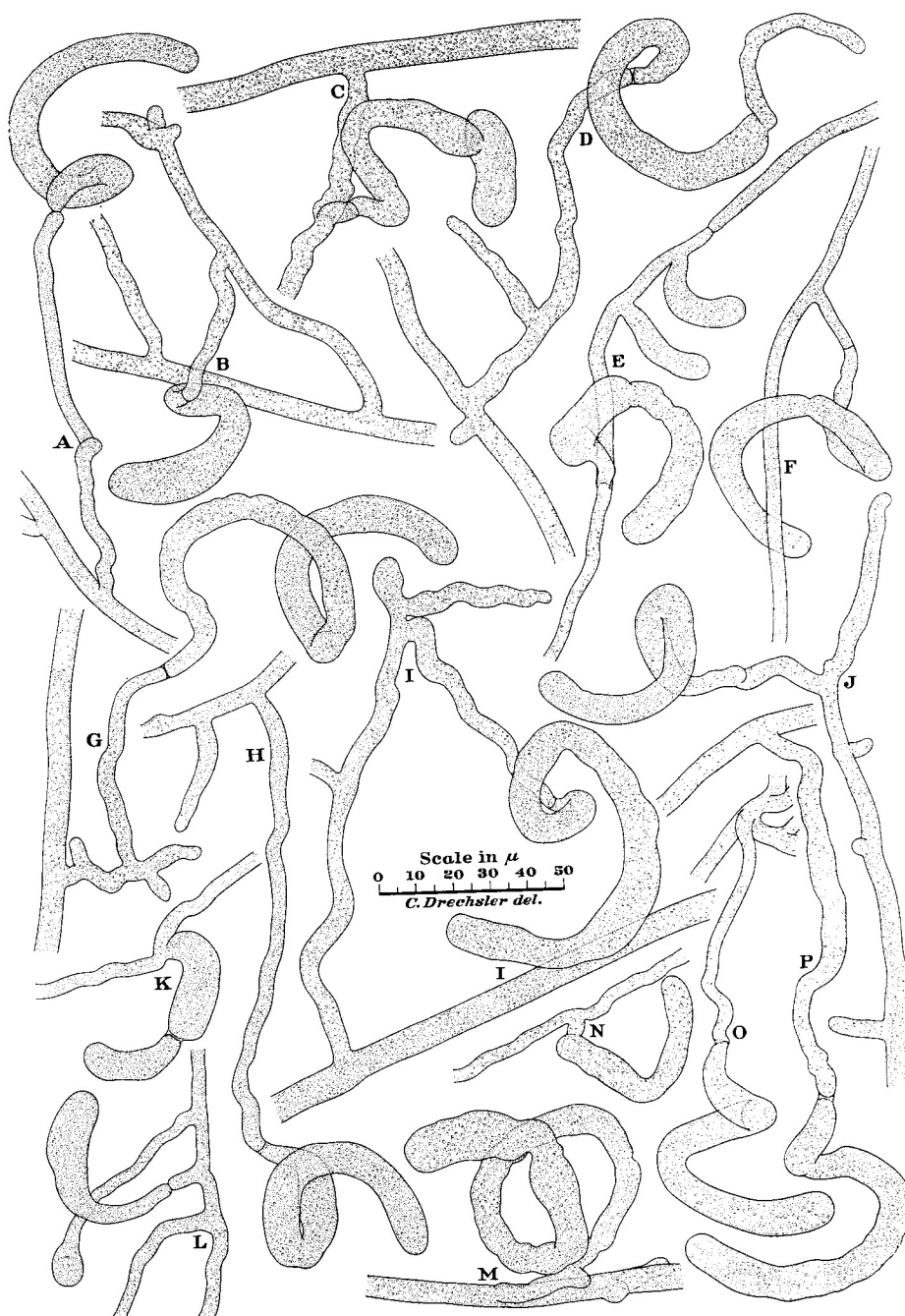


FIG. 3. Portions of hyphae of *Pythium helicandrum*, A-P, bearing appressoria developed in contact with the glass floor of a Petri dish containing a maize meal-agar plate culture of the fungus. All parts drawn to a uniform magnification with the aid of a camera lucida; $\times 500$ throughout.

its geometrical symmetry (fig. 6, E, F; fig. 7, E). In some instances where a relatively narrow supporting hyphal arm had been enveloped by a correspondingly narrow male coil, the terminal antheridium was found to be composed of approximately 2 full helical turns (fig. 7, E).

Owing to serious difficulties of observation that come about from the presence of the crowded oogonial spines, it has not been possible to determine with certainty what kind of passageway serves in fertilization, though now and then a thin-walled fertilization tube seemed to be faintly discernible toward the forward end of the antheridium. In any case, migration of the antheridial contents into the oogonium is followed by the usual sequence of changes entailed in the development of an oospore. The oogonial contents which at the time of fertilization seem to consist mainly of small lumps (fig. 5, K) shrink away from the spiny envelope to form a spherical body. This body reveals a rather coarsely lumpy texture throughout, and soon comes to be surrounded by a thin colorless membrane (fig. 5, L-N; fig. 6, B-E; fig. 7, B-E). Under the colorless membrane a thicker yellowish layer is laid down. A single reserve globule originates in the center, and through gradual enlargement constrains the lumpy material into a parietal layer. Each protoplasmic lump (fig. 6, K, a) becomes divided into a cluster of granules (fig. 6, K, b). The clusters slowly dissolve and merge with one another so that in the mature oospore the parietal layer has a granular texture of rather uniform consistency. Imbedded in the granular layer is a single globose refringent body which presumably represents the resting fusion nucleus (fig. 6, F-J; fig. 7, F-H; I, c, d).

In cultures prepared from maize meal agar containing some finely divided maize meal in suspension the fungus gives rise to sexual apparatus in great abundance and with very little evidence of degeneration. Its morphology as expressed in such cultures may therefore be considered fairly normal for the species. Accordingly maize meal-agar cultures of customary firmness that had been grown at temperatures near 24° C. were used in preparing the relevant illustrations given herein, as well as in making the sets of 100 measurements from which were derived the pertinent metric data given in the diagnosis. The 100 oogonia, taken at random, gave values for diameter, expressed in the nearest integral number of microns, with the following distribution: 17 μ , 2; 18 μ , 1; 19 μ , 1; 20 μ , 1; 22 μ , 3; 23 μ , 3; 24 μ , 8; 25 μ , 10; 26 μ , 28; 27 μ , 24; 28 μ , 7; 29 μ , 10; 31 μ , 1; 32 μ , 1; and the 100 oospores, all of correct internal structure, contained within these oogonia gave values for diameter distributed thus: 14 μ , 1; 15 μ , 1; 16 μ , 1; 17 μ , 2; 19 μ , 1; 20 μ , 6; 21 μ , 14; 22 μ , 24; 23 μ , 23; 24 μ , 18; 25 μ , 6; 26 μ , 2; 27 μ , 1. Oogonia that had developed in very soft agar or in water cultures often bore spines half again as long as those found in firm agar, and, besides, bore them in greater numbers. Under environal conditions widely regarded with favor by students of

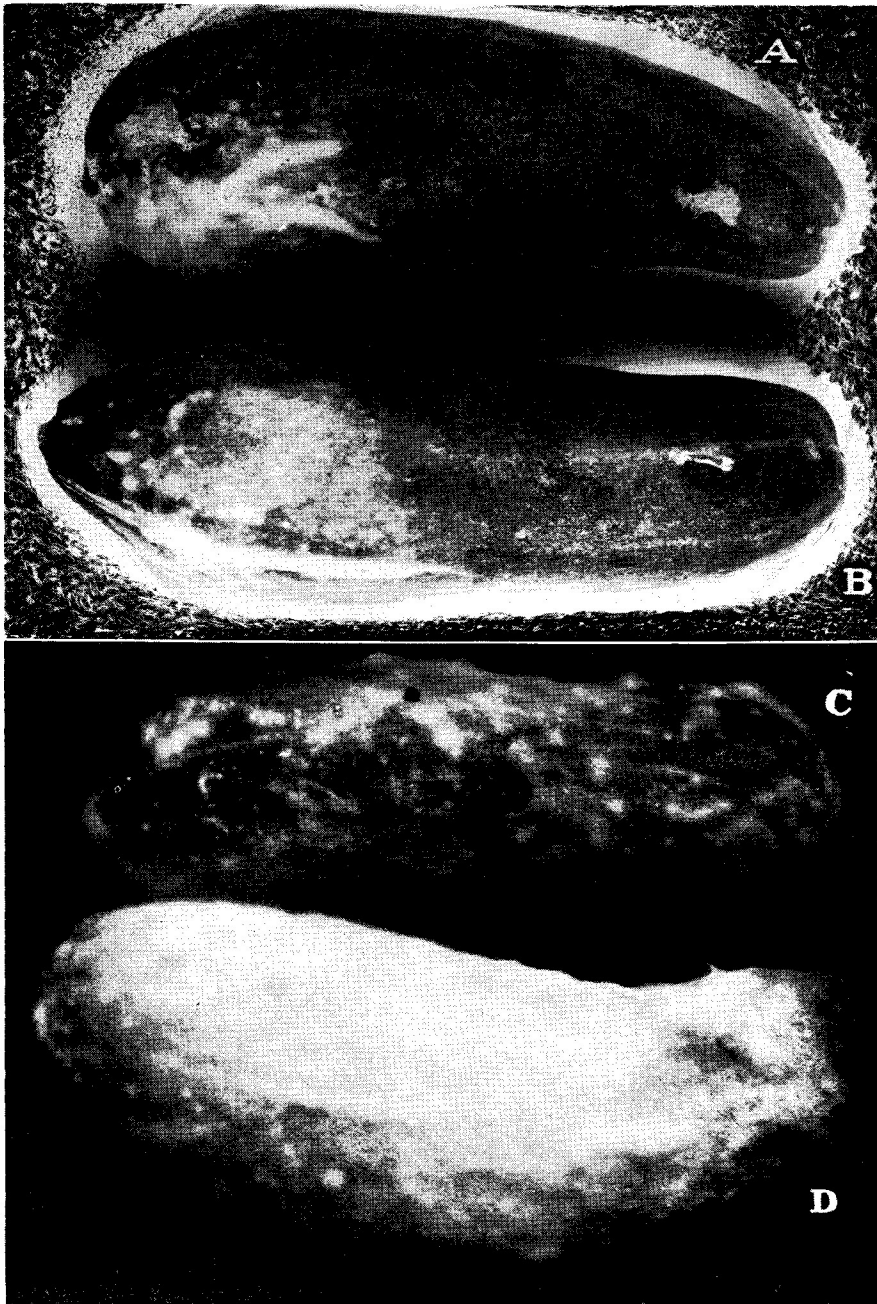


FIG. 4. A, B. Cucumber fruits that after being inoculated with young mycelium of *Pythium helicandrum* were kept for 7 days in a covered dish at 17° C.; in a zone from 2 to 4 mm. wide, immediately surrounding the 2 cucumbers, the background was left unaltered as it appeared in the photograph; beyond this zone ink was applied to obliterate extraneous features. C, D. Cucumber fruits that after being inoculated with young mycelium of *Pythium helicandrum* were kept in a covered dish for 11 days at a temperature of 17° C. Approximately $\times 3/7$.

the aquatic microflora the fungus as a rule has a more formidably bristling appearance than in cultures of the sort commonly employed among plant pathologists.

Newly developed oospores in mature resting condition have shown no capacity for germination when transferred to distilled water. After maize-meal-agar plate cultures had been stored for 9 months at laboratory temperatures ranging from 20° to 35° C. germination ensued on a readily noticeable scale, though even then by far the larger number of oospores, no less than 95 in every 100 individuals, remained inactive. Most of the germinating oospores would put forth a vegetative germ-hypha that soon gave off several main branches, each of which grew to the surface of the water layer and produced there a closely branched floating hyphal system (fig. 8, A). Where many of these branching systems were formed close together they often appeared collectively as a lacy or filigree-like web several square millimeters in extent. Scattered individuals among the germinating 9 month-old oospores (fig. 8, B, a) gave rise to an unbranched germ-hypha (fig. 8, B, b) bearing terminally an elongated ellipsoidal sporangium (fig. 8, B, c; C). Sporangia of such origin were often found emptied of protoplasmic contents and then were provided with a well defined evacuation tube, which at the orifice frequently showed the membrane very slightly reflexed (fig. 8, C). In one observed instance, after the cap of dehiscence on the evacuation tube produced by a sporangium of germinative origin had failed to operate (fig. 8, B, c), a secondary germ hypha (fig. 8, B, d) was put forth a little below the cap and gave rise to a secondary sporangium (fig. 8, B, e) generally resembling its predecessor, but having smaller dimensions in its venter as well as in its evacuation tube. As might be expected, the sparsely scattered oospores that germinated by producing sporangia could provide only a meager display of actively swimming zoospores. These zoospores were of the grooved, laterally biciliate type familiar among species of *Pythium* and related genera. On coming to rest and rounding up they formed cysts approximately 12 μ in diameter (fig. 8, D).

Sporangia of the same citriform type as those resulting from germination of oospores are often obtained in greater abundance by irrigating vigorous mycelium of the fungus. Such irrigation can be accomplished conveniently by cutting sizable slabs from young lima-bean-agar plate cultures and transferring them to a shallow layer of water in a Petri dish. At a temperature of 11° C. a fringe of extramatrical filaments is soon extended from each slab into the surrounding water. After about 24 hours large citriform conidia (fig. 9, A-N) begin to be formed terminally on some of the longer filaments. Development of citriform conidia continues for several days. The distal portion of each supporting filament, which at first is filled with protoplasm (fig. 9, A-D), later is found in an empty condition (fig. 9, E-N). When the my-

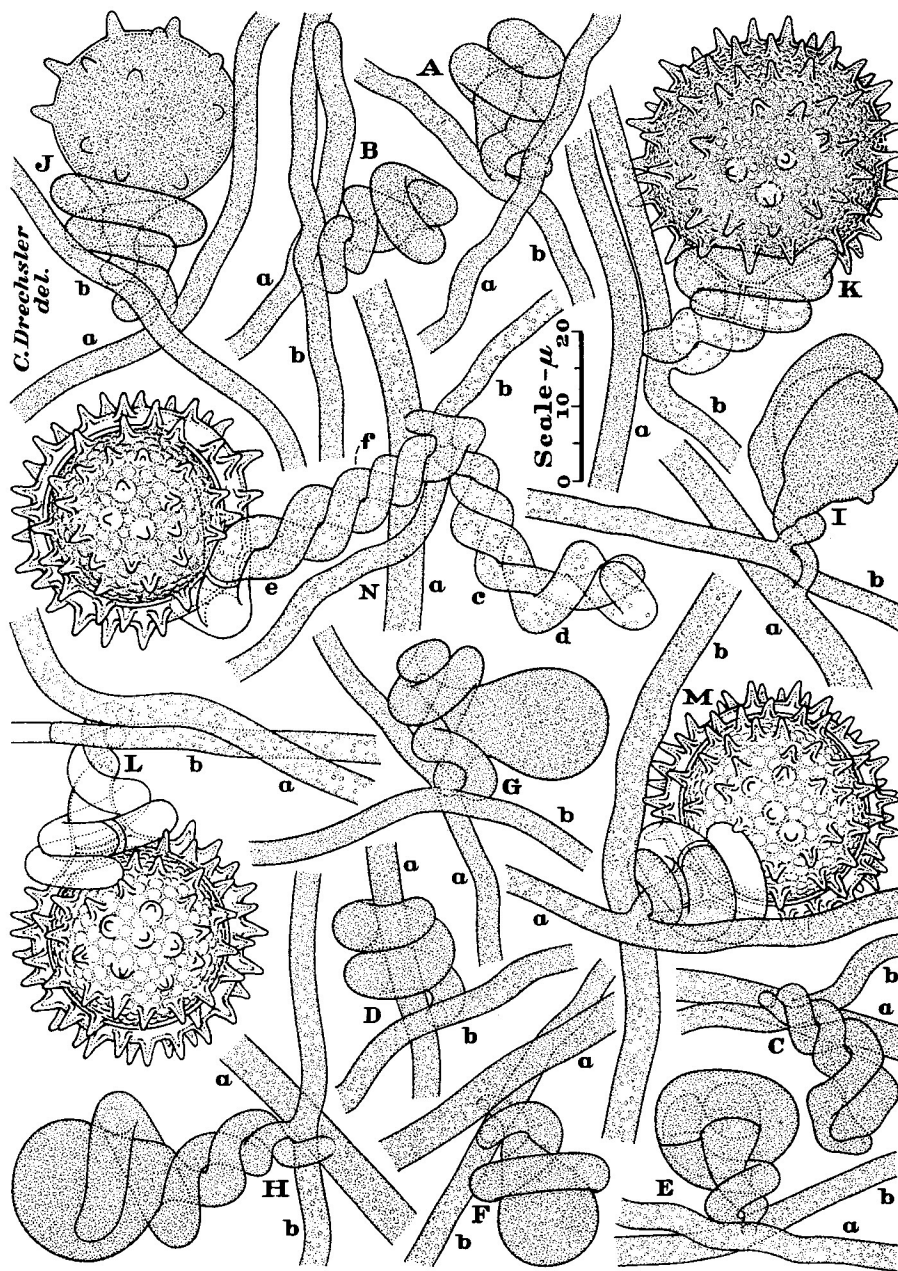


FIG. 5. Sexual reproductive apparatus of *Pythium helicandrum* produced in Petri plate cultures of firm maize meal agar and drawn to a uniform magnification with the aid of a camera lucida; $\times 1000$ throughout. A-M. Single units of sexual apparatus, each originating from 2 neighboring mycelial hyphae, a and b, the former having supplied the female branch (except in D, where an intercalary oogonium should soon be formed) while the latter has supplied the male branch. N. Two neighboring mycelial hyphae, a and b, which together have put forth the paired sexual branches c and d, as well as the paired sexual branches e and f; one of the 2 hyphae, a, having given rise to both female branches, c and e, while its fellow, b, has given off both male branches, d and f.

celium has become partly exhausted, mesially intercalary (fig. 9, O-Q) and laterally intercalary sporangia (fig. 9, R-X), usually of diminishing size, are formed on the shorter extramatrical hyphae as well as on hyphae permeating and overlying the agar slabs. If the water in a preparation is renewed from time to time, production of intercalary sporangia may continue for more than a week; so that in the end large numbers of asexual reproductive bodies are present. Some of the terminal sporangia bear distally a stout prolongation resembling an evacuation tube, though a cap of dehiscence is usually lacking (fig. 9, M, N). Despite their obvious modification for discharge and the faultlessly normal appearance of their protoplasmic contents, the sporangia in my lima-bean-agar preparations have only in very small number given rise to zoospores.

Owing to the meager production of zoospores in all of my irrigated material, the progress of sporangial discharge has so far not come directly under observation. However, since a well developed evacuation tube, surmounted by a conspicuous cap of dehiscence, seems here a regular feature of a correctly maturing sporangium there is ample reason to presume that with respect to manner of discharge and to zoospore development within a vesicle the fungus most probably maintains the parallelism with familiar species of *Pythium* that is manifest in the branching habit and rapid growth rate of its mycelium. As has been mentioned, the massive sturdiness of its oogonial spines bespeaks an intimate kinship with *P. mastophorum*, *P. polymastum*, and *P. megalacanthum sensu* Buisman. Typically citriform sporangia, it is true, have not been found usual in either *P. mastophorum* or *P. polymastum*, but the variously globose sporangia frequent in these two species would seem to correspond fairly well to the intercalary sporangia often formed abundantly by the sheep sorrel fungus. The development of citriform terminal sporangia offers close similarity, among spiny congeners, to *P. anandrum* and to the species described by Shanor (1938) under the binomial *Phytophthora stellata*. With respect to *P. anandrum*, at least, this similarity is sustained by resemblances in mycelial habit. An intimate relationship between the sheep sorrel fungus and *P. anandrum* seems possible, notwithstanding the parthenogenetic development of oospores in the latter, and the thin-walled character of its oogonial spines. The combination of features in the sheep sorrel fungus would appear in some measure to reconcile the wide differences observable between *P. anandrum* and the broadly spinose *mastophorum* series. In addition to resemblances offered by its terminal sporangia, Shanor's fungus shows parallelism with the one from sheep sorrel roots, more especially in the frequent enwrapment of the basal portion of the spiny oogonium by a consistently single antheridium. The antheridium of *P. stellata*, however, is set forth as being of clavate shape, much wider than the supporting stalk. The stalk, too, differs from that of the sheep sorrel fungus

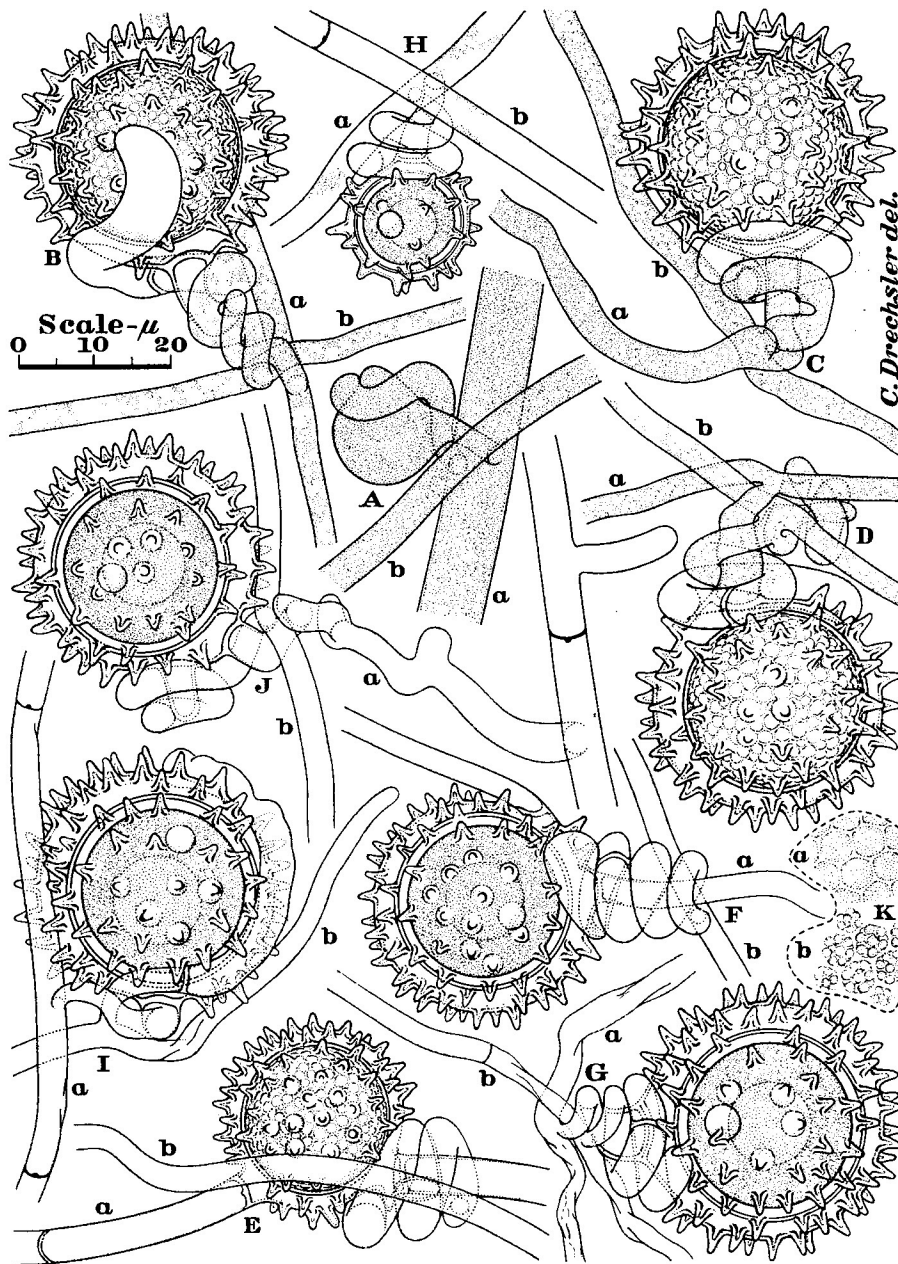


FIG. 6. A-J, Units of sexual reproductive apparatus of *Pythium helicandrum* produced in Petri plate cultures of firm maize meal agar, each unit originating from 2 neighboring hyphae, a and b, whereof the former supplies the female branch or (in E and F) an intercalary oogonium, while the latter supplies the male branch; drawn to a uniform magnification with the aid of a camera lucida; $\times 1000$. K. Structure of oospore protoplast at 2 different stages: a, surface appearance in immature stage, showing arrangement of largish, somewhat angular lumps; b, surface appearance in later stage, showing the lumps becoming resolved into granules of smaller size; approximately $\times 2250$.

in arising most often from the oogonial branch only a short distance below the oogonium, and apparently also in failing to entwine the oogonial stalk to any considerable extent. Judging from measurements given by Shanor, 15.5 to 22.4 μ for oogonial diameter and 13.8 to 17.2 μ for diameter of oospore, *P. stellata* is very appreciably smaller than the sheep sorrel fungus, and, of course, much smaller than *P. mastophorum*, *P. polymastum*, or *P. megalaecanthum sensu* Buisman.

When the sheep sorrel fungus is grown in dual culture with *Pythium ultimum* (Trow 1901) *P. debaryanum*, and other familiar congeneric species it shows no specially antagonistic behavior. Like these familiar species, and also like the 3 intimately related broadly spinose forms of the *mastophorum* series, it is attacked by members of the echinulate series having finely branched mycelium. Thus, when planted in Petri plate cultures in opposition to *P. oligandrum* the growth of its mycelium is halted abruptly at the line of encounter, and its hyphae (fig. 1, A-D: a) are enveloped by delicate ramifications from neighboring *oligandrum* filaments (fig. 1, A-D: b). Many of the enveloped hyphae soon show extensive vacuoles (fig. 1, C) and later are to be found almost wholly empty of living protoplasm (fig. 1, D). Likewise when the fungus is grown in opposition to *P. acanthicum*, advance of its mycelium is arrested along the zone of encounter as its individual hyphae (fig. 1, E-H: a) become enwrapped by branches extended from *acanthicum* filaments (fig. 1, E-H: b), with attendant vacuolization of their contents (fig. 1, G, H). Moreover, like other species of *Pythium*, including the delicately ramifying echinulate species, the fungus suffers injury from antagonism of root-rotting members of the Saprolegniaceae. In dual culture with my *Plectospora myriandra* (Drechsler 1927), for example, its growth is stopped at the zone of encounter; the hyphae along its forefront (fig. 2, A-C: a) promptly being enfolded for variable distances by irregularly ramifying branches of the water mold (fig. 2, A-C: b). The enfolded hyphae are often invaded here and there, but even where invasion does not occur their protoplasmic contents undergo extensive degeneration.

A term having reference to the remarkable spiral arrangement of its antheridium is deemed appropriate as specific epithet for the fungus.

***Pythium helicandrum* sp. nov.** Mycelium hyalinum, ramosum, in hyphis 2-8 μ latis consistens. Zoosporangiis incoloratis, plerumque 25-80 μ longis, 25-55 μ latis, saepissime terminalibus denique vulgo elongato-ellipsoideis vel citriformibus, sed quandoque intercalaribus denique vulgo sphaeroideis vel ellipsoideis, in maturitate tubulo exanitionis 10-60 μ longo 4.5-8 μ crasso praeditis; zoosporis primo reniformibus, a latere biciliatis, mox quietis, tum 12 μ in diametro. Oogoniis incoloratis, valde echinatis, prominentiis conicis subspiniiformibus praeditis, sine aculeis plerumque 17-32 μ (saepe circa 26 μ) latis, interdum in hypha mycelii ordinaria vulgo 3-6 μ crassa intercalaribus sed saepissimi in apice rami praecipui oriundis; ramo praecipuo nunc recto

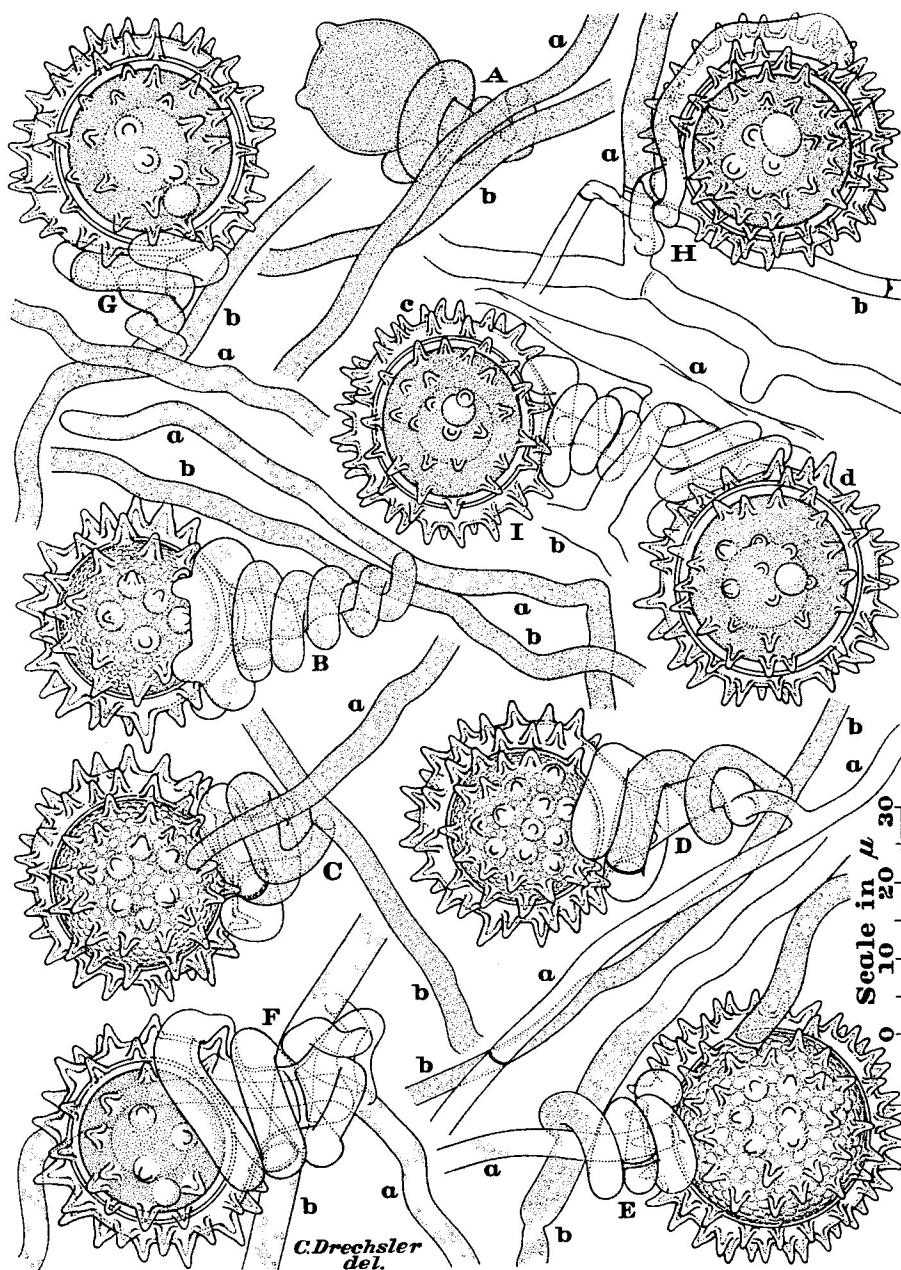


FIG. 7. Units of sexual reproductive apparatus of *Pythium helicandrum*, A-I, produced in Petri plate cultures of firm maize meal agar, each unit originating from 2 neighboring mycelial hyphae, a and b, whereof the former supplies the female branch or (in E) an intercalary oogonium, while the latter supplies the male branch; in one of the units, I, two pairs of sexual branches were given off, and 2 oogonia, c and d, each with an oospore in mature resting condition, were produced. Drawn to a uniform magnification with the aid of a camera lucida; $\times 1000$ throughout.

vel parum curvato, nunc semel vel bis circum ramum marem spiraliter interdum ad modum caulis Phaseoli vulgaris interdum ad modum caulis Humuli lupuli convoluto, 6–45 μ longo, basi saepe tantum 2–3 μ crasso, sursum latescente, apice vulgo 4.5–9 μ lato; aculeis oogonii vulgo 2.4–5.3 μ (saepe circa 3.7 μ) longis et basi 2–4 μ (saepe circa 2.8 μ) latis, sed in aqua vel materia aquatica molli saepe angustioribus et 5–8 μ longis, membrana eorum circa 1 μ crassa. Antheridiis semper singulatim ortis, semper in apice rami maris oriundis, plerumque vermiformibus sed interdum paucis tuberculis praeditis, 25–45 μ longis, 4–7 μ latis, quadoque oogonium terminale oblique vel in longitudinem complectentibus, quadoque circum hypham mycelii oogonium intercalare juxta semel vel bis spiraliter se convolventibus, saepissime basim oogonii terminalis semel cochleatim circumdantibus; ramo mari semper ex alia hypha mycelii atque oogonio vel ramo oogoniophoro oriundo, sine antheridio plerumque 10–50 μ longo, basi 2–4 μ crasso, saepe sursum latescente, apice 3–5.5 μ crasso, interdum parum sinuoso, saepius hypham oogoniophoram vel ramum oogoniophorum semel vel bis vel ter spiraliter interdum ad modum caulis Phaseoli vulgaris interdum ad modum caulis Humuli lupuli circumplicante. Oosporis sphaeralibus, laevibus, vulgo 15–27 μ (saepe circa 22.3 μ) in diametro, membrana flavida 1.2–2 μ (saepe circa 1.6 μ) crassa tectis, unam pilulam oleosam 7–14 μ (saepe circa 11.2 μ) crassam et unum corpuseculum nitidum globosum 3.2–5 μ (saepe circa 4.1 μ) crassum continentibus.

Habitat in radicibus Rumicis acetosellae putrescentibus prope Beltsville, Maryland.

Intramitral mycelium on transparent agar media usually of somewhat radiating appearance, capable of approximately 27 mm. radial extension in 24 hours at 24° C., composed of hyphae mostly 2 to 8 μ wide, the more delicate ramifications usually developed only in moderate quantity, the hyphae in contact with solid objects often forming curved appressoria 25 to 125 μ long and 6 to 11 μ in greatest width; aerial mycelium formed sparingly or in moderate quantity.

Sporangia colorless, under aquatic conditions often produced terminally on long, simple or sparingly branched extramitral hyphae and then mostly elongated ellipsoidal or lemon-shaped, but frequently, too, especially in aging material, formed in mesially or laterally intercalary positions, and then mostly prolate ellipsoidal or subspherical or oblate ellipsoidal; measuring 25 to 80 μ in length and 25 to 55 μ in greatest width; at maturity furnished usually at the distal end with an evacuation tube 10 to 60 μ long and 4.5 to 8 μ wide. Zoospores kidney-shaped, laterally biciliate, after a period of motility coming to rest and rounding up into cysts about 12 μ in diameter.

Oogonia colorless, sometimes formed in intercalary positions in mycelial filaments mostly 3 to 6 μ wide, but much more often formed terminally on special branches, yet in either case boldly spiny and commonly measuring 17 to 32 μ (average 26 μ) in diameter exclusive of the spiny protuberances; these protuberances 2.4 to 5.3 μ (average 3.7 μ) long and 2 to 4 μ (average 2.8 μ) wide at the base, though in water or soft watery ambient often somewhat more slender and from 5 to 8 μ long, wherever well developed having a wall about 1 μ thick; the special female branch below the oogonium (*i.e.*, the oogonial stalk) usually 6 to 45 μ long, proximally often 2 to 3 μ wide, distally 4.5 to 9 μ wide, sometimes straight or only slightly curved, but more often

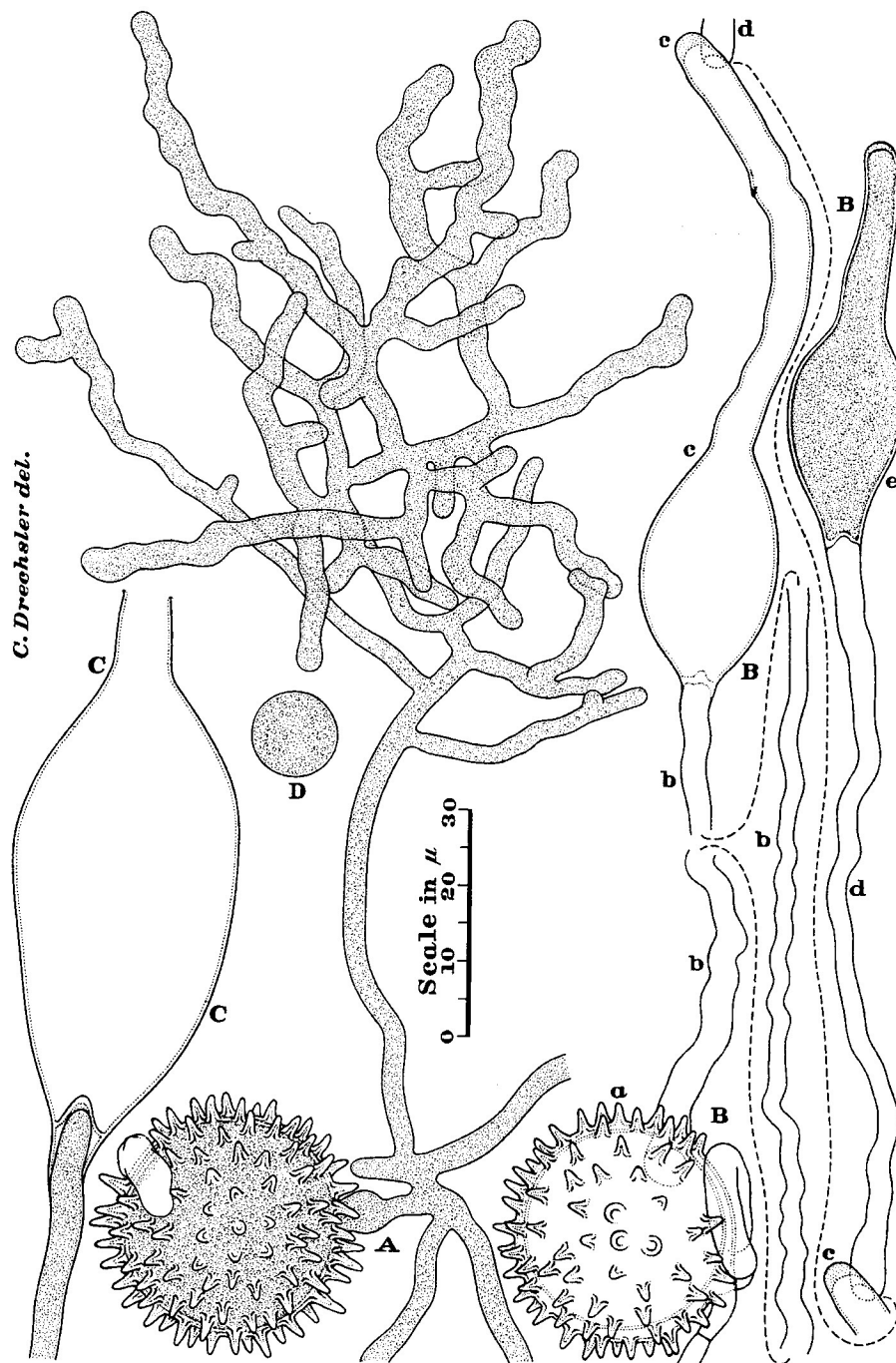


FIG. 8. Germination of oospores of *Pythium helicandrum* taken from a maize meal-agar plate culture. A. Oospore giving rise to several intricately branched hyphal systems on the surface of a shallow layer of water; only one of the hyphal systems is shown. B. Oospore, a, with a germ hypha, b, whereon is borne a sporangium, c, furnished distally with an evacuation tube surmounted by a cap of dehiscence; when the cap failed to open the evacuation tube grew out into a hypha, d, whereon is borne a secondary sporangium, e, provided with a distal evacuation tube and cap of dehiscence. C. Empty envelope of a germ sporangium that discharged its contents in normal manner. D. Encysted zoospore. All parts drawn with the aid of a camera lucida; $\times 1000$ throughout.

entwining the male branch in 1 to 2 spiral turns of right-handed or left-handed rotation.

Antheridia always single, always produced terminally on a special male branch; commonly elongated cylindrical or worm-shaped, though sometimes bearing a few lateral dome-shaped protuberances which usually are directed toward the distal side of the oogonium; mostly measuring 25 to 45 μ in length and 4 to 7 μ in width; sometimes extending lengthwise or obliquely over the oogonium, at other times enveloping a hyphal portion adjacent to an intercalary oogonium in 1 to 2 helical turns, but most often wound spirally about the base of a terminal oogonium in a single turn. The male branch regularly coming from a position close either to the origin of a female branch or to the prospective place of origin of an intercalary oogonium, though in either case arising from a hypha having no close mycelial connection with the one bearing the female branch or the intercalary oogonium; the portion of the male branch below the antheridium (*i.e.*, the antheridial stalk) commonly 10 to 50 μ long, 2 to 4 μ wide proximally, 3 to 5.5 μ wide distally, sometimes wound spirally once or twice about a portion of hypha adjacent to an intercalary oogonium, but more often entwining the stalk of a terminal oogonium in 1 to 3 or even 3½ helical turns of right-handed or left-handed rotation.

Oospores spherical, smooth, mostly 15 to 27 μ (average 22.3 μ) in diameter, enveloped by a wall 1.2 to 2 μ (average 1.6 μ) thick that consists of a thin colorless outer layer and a thicker yellowish inner layer, at maturity containing a parietal granular layer which surrounds a central reserve globule 7 to 14 μ (average 11.2 μ) in diameter and has imbedded in it a single globose refringent body 3.2 to 5 μ (average 4.1 μ) in diameter.

Occurring in darkened decaying roots of *Rumex acetosella* near Beltsville, Maryland.

PLANT INDUSTRY STATION,

BELTSVILLE, MARYLAND

Literature Cited

- Bary, A. de. 1881a. Untersuchungen über die Peronosporaceen und Saprolegniaceen und die Grundlagen eines natürlichen Systems der Pilze. Abhandl. Senckenb. Naturf. Gesell. **12**: 225-370.
- . 1881b. Zur Kenntnis der Peronosporaceen. Bot. Ztg. **39**: 521-625.
- Buisman, C. J. 1927. Root rots caused by Phycomycetes. Meded. Phytopath. Lab. "Willie Commelin Scholten" Baarn **11**: 1-51.
- Drechsler, C. 1927. Two water molds causing tomato rootlet injury. Jour. Agr. Res. **34**: 287-296.
- . 1930. Some new species of *Pythium*. Jour. Wash. Acad. **20**: 398-418.
- . 1939a. Several species of *Pythium* causing blossom-end rot of watermelons. Phytopathology **29**: 391-422.
- . 1939b. Three species of *Pythium* with large oogonial protuberances. Phytopathology **29**: 1005-1031.
- . 1946. Several species of *Pythium* peculiar in their sexual development. Phytopathology **36**: 781-864.
- Hesse, R. 1874. *Pythium de Baryanum* ein endophytischer Schmarotzer in den Geweben der Keimlinge der Leindotter, der Rüben, des Spargels und einiger anderer landwirthschaftlichen Kulturpflanzen. Halle.

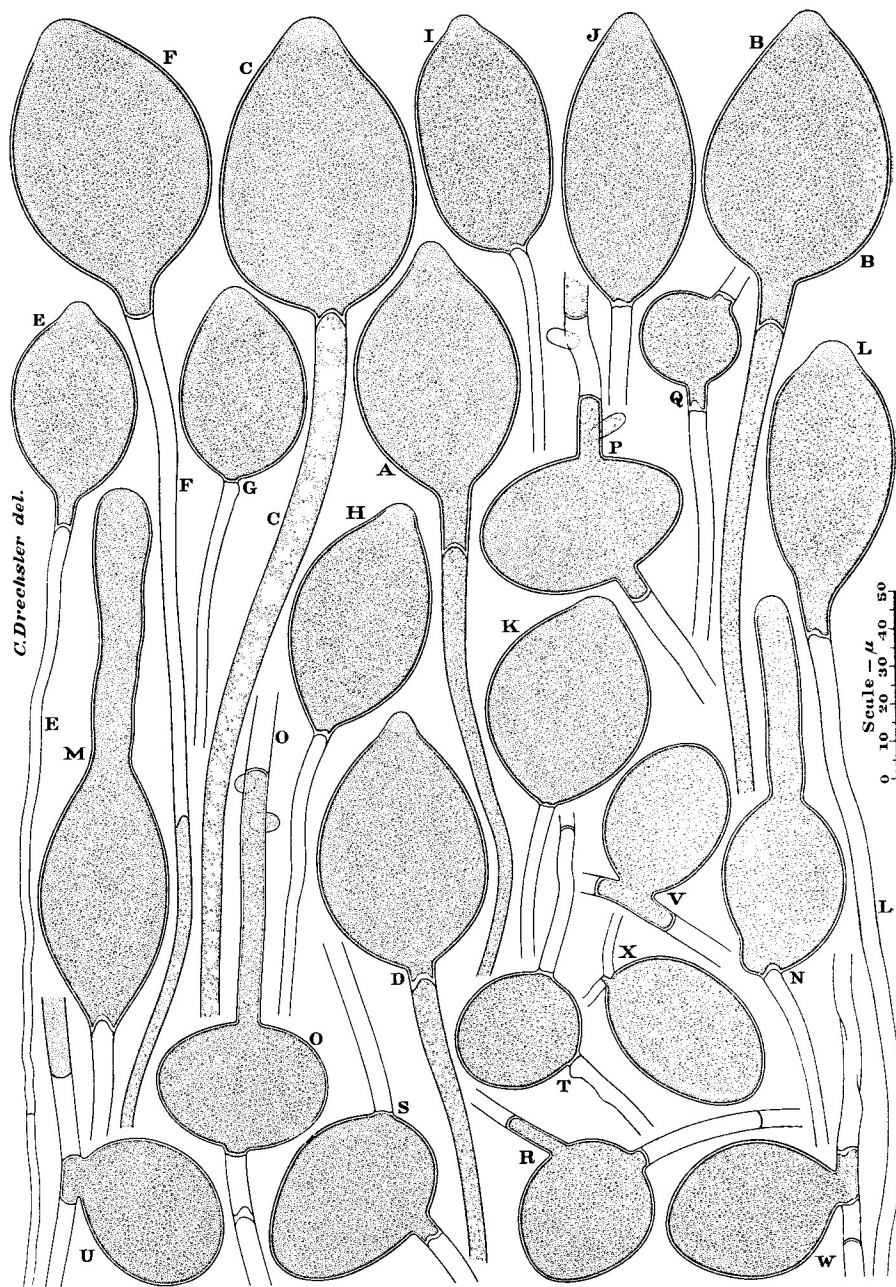


FIG. 9. Sporangia of *Pythium helicandrum* produced at 11° C. on sparingly irrigated slabs excised from a lima-bean-agar plate culture. A-N. Terminal sporangia formed early on long extramatrical hyphae. O-Q. Mesially intercalary sporangia produced later. R-X. Laterally intercalary sporangia also of later origin. All parts drawn to a uniform magnification with the aid of a camera lucida; $\times 500$ throughout.

- Meurs, A.** 1929. Ein neuer Wurzelbranderreger der Zucker-und Futterrüben. *Phytopath. Zeitschr.* 1: 111-116.
- Sawada, K.** 1927. Descriptive catalogue of the Formosan fungi, Part III. Dept. Agr. Gov. Res. Inst. Formosa, Japan, Rept. 27.
- Shanor, L.** 1938. Observations on the development of a new species of *Phytophthora*. *Jour. Elisha Mitchell Sci. Soc.* 54: 154-162.
- Trow, A. H.** 1901. Observations on the biology and cytology of *Pythium ultimum*, n. sp. *Ann. Bot.* 15: 269-312.