Two root-rot fungi closely related to Pythium ultimum.

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With Plates XVI—XX.

When Trow (1901) described under the binomial *Pythium ultimum* a fungus he obtained from cress (*Lepidium sativum L.*) at Cardiff, he intended that the specific epithet might connote complete incapacity for the production of swarm spores. According to his account the globose asexual bodies, or conidia, produced terminally or intercalarily by the fungus failed altogether to germinate in distilled water. In nutrient solution they germinated soon, but instead of forming sporangia they developed only vegetatively, each putting forth one or more germ tubes. Trow found also that oospores which after a resting period had assumed the internal organization usual in conidia would similarly not give rise to zoospores. He reported that when such after-ripened oospores were transferred to cabbage water a small proportion of them germinated by extending one or more germ tubes and the remainder in a puzzling way burst under considerable pressure, so that their protoplasmic contents perished within the oogonial envelope.

Some of Trow's negative findings invite speculation, as after-ripened oospores of *Pythium ultimum* are now known to germinate rather readily by developing into sporangia (Drechsler, 1946, 1952), though their germination may take place also through emission of a wholly vegetative hypha or of a hypha on which are borne one or several conidia capable of giving rise to swarmers. Nutrient solutions would now as a matter of course be expected to encourage vegetative growth rather than zoospore formation in any species of *Pythium*. Complete failure to germinate in distilled water, however, would still appear quite unnatural in conidia and after-ripened oospores of *P. ultimum*, or, for that matter, in the corresponding reproductive bodies of any congeneric fungus. The inert behavior recorded by Trow and the violent bursting of spores can only be held thoroughly abnormal for any member of the genus. The abnormalities would ordinarily indicate the presence of a toxic agent, such, for example, as might unknowingly have been introduced in earlier times through use of distilled water from a still fitted with copper tubing.

While Trow's observations on the asexual reproduction of his fungus were carried out on material that somehow must have been abnormal, it yet remains true that the conidia of *Pythium ultimum* commonly fail to produce zoospores under conditions where related species regularly show abundant development of swarmers. This reluctance to produce swarmers from sporangia of mycelial origin appears to be a usual feature of *P. ultimum,* whether the fungus is cultured on artificial media of varied composition or grows spontaneously on tissues of different host plants. The apparent preference of *P. ultimum* for zoospore development from after-ripened oospores would seem advantageous for facilitating infection of roots at varying depths early in the growing season, whereas during the somewhat warmer period late in spring the fungus can spread extensively through the extramatrical mycelial growth it often displays destructively in the seed-bed. Rather similar adaption for asexual reproductive development early in spring is encountered in *Basidiobolus haptosporus* Drechsler (1956), which, unlike other members of its genus, gives rise to conidia in much greater numbers on conidiophores sent up by its after-ripened zygospores than on conidiophores arising from hyphal segments.

As the sporangia produced on germ hyphae extended from many after-ripened oospores of *Pythium ultimum* readily give rise to zoospores, yet outwardly are much like conidia of mycelial origin, the unusual aspects presented by the asexual reproduction of the fungus are somewhat less decisive in defining the species than was earlier believed. Fortunately characters pertaining to the vegetative and asexual reproductive stages have been sufficient to distinguish the fungus (D r e c h s l e r, 1952) from *P. debaryanum* Hesse (1874) and *P. paroecandrum* Drechsler (1940), two species of rather similar morphology and parasitic habit. To bring the group into better perspective consideration is given herein to 2 other closely related fungi that have appeared in cultures prepared from diseased roots gathered in and near the District of Columbia.

1. *Pythium ultimum* var. **sporangiferum** var. nov.

A typo speciei differt praecipue conidiis in sporangia transeuntibus, ac probabiliter differt oosporis maturis plerumque longius dormientibus et oosporis germinantibus vulgo duas tenues membranulas omnino separatas relinquentibus; efferenti tubulo sporangii simplici, recto vel aliquid pravo, plerumque 5—156 μ longo, 3—11 μ lato; zoosporis vulgo 3—35 in vesicula generatis, primo reniformibus et duobus ciliis praeditis, postea quietis, globosis, vulgo 8—11 μ in diametro.

Habitat in radicibus putrescentibus *Chenopodii albi* prope Beltsville, Maryland.

Typus: National Fungus Collection 71632; American Type Culture Collection 13647.

The several cultures on which the description of *Pythium ultimum* var. *sporangiferum* is based were isolated from separate rootlets of lamb's-quarters (*Chenopodium album* L.) all collected on August 18, 1955, near the Plant Industry Station, in a relatively dry area less than 1 square meter in extent. As they originated from similar plant parts found in positions close together the cultures are considered as having come from a single source. No difference could be observed between the several parent cultures isolated from separate roots or between 4 single-zoospore cultures derived from them.

The fungus first arrested attention by its occurrence during the period of high midsummer temperature, when ordinarily in central Maryland *Pythium ultimum* var. *ultimum* is encountered much less frequently than during the cooler spring and autumn months. Its occurrence at high temperature would seem noteworthy also because the black-rot disease of orchids, which Ark and Middleton (1949) found caused by a strain of *P. ultimum* readily producing zoosporangia of mycelial origin, has in California, according to these authors, always been associated with low temperature.

When the fungus from lamb's-quarters is grown on maize-meal agar either in Petri dishes or in slanted test-tubes it presents much the same appearance as *Pythium ultimum* var. *ultimum*. It extends its mycelium somewhat more slowly than several isolations of *P. ultimum* var. *ultimum* with which it has been compared side by side. Thus, in Petri plates of maize-meal agar maintained at 26° C. its mycelium was found advancing 27 mm in 24 hours, while two isolations of *P. ultimum* var. *ultimum*, in which no conidia of mycelial origin develop into sporangia, grew 33 mm and 34 mm, respectively, during the same period. Like *P. ultimum* var. *ultimum* and *P. debaryanum* the fungus soon produces aerial mycelium, especially in slanted tube cultures. It differs conspicuously from *P. paroecandrum*, which grows more slowly and which, as a rule, forms little or no aerial mycelium.

In the fungus from lamb's-quarters asexual reproduction proceeds after the manner long familiar in *Pythium debaryanum*. The globose or elongated-ellipsoidal sporangia (Pl. I, A, B) are filled with densely granular protoplasm through which some indistinct vacuoles are haphazardly distributed. On being shallowly irrigated with distilled water each puts forth an evacuation tube (Pl. I, C, t; D, t) that forms at its tip a hyaline cap of dehiscence. The hyaline cap finally yields and becomes inflated into a vesicle (Pl. I, E, v) as it receives the protoplasm streaming through the tube (Pl. I, E, t). Thereupon the mass of granular material is fashioned into laterally biciliated zoospores (Pl. I, F, v), which become increasingly active until they escape as motile swarmers, leaving behind the empty sporangial envelope and equally empty evacuation tube (Pl. I, F—P: t; Pl. II, A—J: t) with open tip. After swimming about for some time the zoospores come to rest and round up into globose cysts (Pl. II, K—T). Some of the cysts soon germinate by putting forth a germ hypha approximately 2 μ wide (Pl. II, U—W).

The sporangial envelopes of the fungus from lamb's-quarters, like those of *Pythium paroecandrum,* appear slightly thicker than the corresponding envelopes of ***P. debaryanum*** and accordingly seem to retain their shape somewhat better after being emptied of contents. In judiciously irrigated material the evacuation tube varies in length mainly between 10 and 50 μ. Tubes between 50 and 100 μ long (Pl. II, J, t) usually occur in small numbers, while examples exceeding 100 μ (Pl. II, D, t) or 150 μ (Pl. II, I, t) in length are relatively exceptional. Here and there an empty sporangial envelope is found supplied with 2 evacuation tubes (Pl. II, F, t), each of them open at the tip.

In irrigated agar slabs (Pl. III, A—C), as also in Petri plate cultures (Pl. III, D—L), the sexual reproductive apparatus of the fungus from lamb's-quarters agrees well during its formative and mature resting stages with that of *Pythium ultimum* var. *ultimum.* Fertilization is often accomplished by a single antheridium formed by the oogonial hypha in a position immediately adjacent to the oogonium (Pl. III, A—I). Sometimes 2 adjacent antheridia are present (Pl. III, J—L) and a third antheridium (Pl. III, L) may be supplied by a neighboring filament. In diclinous units one or more antheridia may be contributed by a single neighboring hypha, or plural antheridia may be supplied by separate neighboring filaments. The mature oospore has the unitary internal organization which De Bary (1881) found in many oomycetes, its single large reserve globule being surrounded by a parietal layer of densely granular protoplasm in which is embedded a single globose or flattened ellipsoidal refringent body (Pl. III, D—L). After a variable period of after-ripening the oospore shows an internal organization like that of a thin-walled globose conidium (Pl. III, M). When irrigated with distilled water it now germinates readily either by extending a vegetative germ hypha or by discharging its contents through an evacuation tube (Pl. III, N—T: t) into a vesicle to undergo conversion into motile swarm spores. Each swarm spore eventually encysts and then may germinate by extending a germ tube (Pl. III, U, V), or its contents may escape from the cyst membrane (Pl. III, W—Y) to form a secondary zoospore.

After-ripening of oospores usually proceeds more slowly in the fungus from lamb's-quarters than in isolations of *Pythium ultimum* var. *ultimum.* In a comparative test several maize-meal-agar plate cultures of the fungus from lamb's-quarters showed only 2 per cent of the oospores in an after-ripened state 34 days after inoculation, whereas in parallel cultures of *P. ultimum* var. *ultimum* fully 40 per cent were ready for germination. Another set of maize-meal-agar plate cultures showed all oospores of the lamb's-quarters fungus in a resting state 73 days after inoculation. Although the culture from which came the after-ripened specimen figured in Plate III, M, was 114 days old, approximately half of the oospores in it were then still in a dormant state.

When an oospore of the fungus from lamb's-qarters has completed its germination the outer and the inner contour of its wall appear conserved as 2 separate membranes which together make up a double-walled pouch. In instances where the oogonial envelope had vanished before germination began, the 2 membranes and the evacuation tube (Pl. III, N, t), together sometimes with one or more imprisoned zoospores, comprise the entire visible residue of the reproductive unit. Where the oogonial envelope persists it loosely surrounds the 2 membranes and is pierced by the evacuation tube (Pl. III, O—T: t), which is continuous with the inner membrane. The fungus thus is reminiscent of *Pythium butleri* Subramaniam (1919), in which likewise the oospore wall is commonly recognizable after germination as a pouch composed of 2 separate membranes (Drechsler, 1955). In smaller measure the fungus shows parallelism with *P. debaryanum,* for although in that species some few oospores leave behind a double-walled pouch most oospores leave a mantle composed of a single layer in some portions and of two separate membranous layers in others (Drechsler, 1952). The oospore in isolations of *P. ultimum* var. *ultimum* leaves behind a pouch that as a rule consists very largely of a single layer, though in limited regions, and more especially in the region near the base of the evacuation tube, two layers are often discernible (Drechsler, 1952).

As characters pertaining to the after-ripening and germination of oospores have not hitherto received much attention in distinguishing pythiaceous fungi it remains uncertain whether the zoospore-producing parasite reported by Ark and Middleton was strictly identical with the fungus I isolated from lamb's-quarters. There is some reason to believe, nevertheless, that when midsummer isolations generally resembling Trow's species in the make-up of their sexual reproductive units are obtained from various sources and in ample number, more than a few among them will be found combining the characters distinguishing *Pythium ultimum* var. *sporangiferum.*

If Trow's failure to obtain swarmers from after-ripened oospores is to be ascribed to some toxic agent in the distilled water used by him, the possibility must be considered that his failure to obtain zoospores from conidia of mycelial origin was likewise due to toxicity rather than to inherent developmental tendencies. With all zoospore development repressed, material of *Pythium paroecandrum* or of *P. ultimum* var. *sporangiferum* could conceivably have provided the basis for Trow's account. Fortunately, as Trow's fungus developed on damped-off cress his description can with sufficient confidence be held based on the destructive seedling parasite encountered year after year in temperate lands.

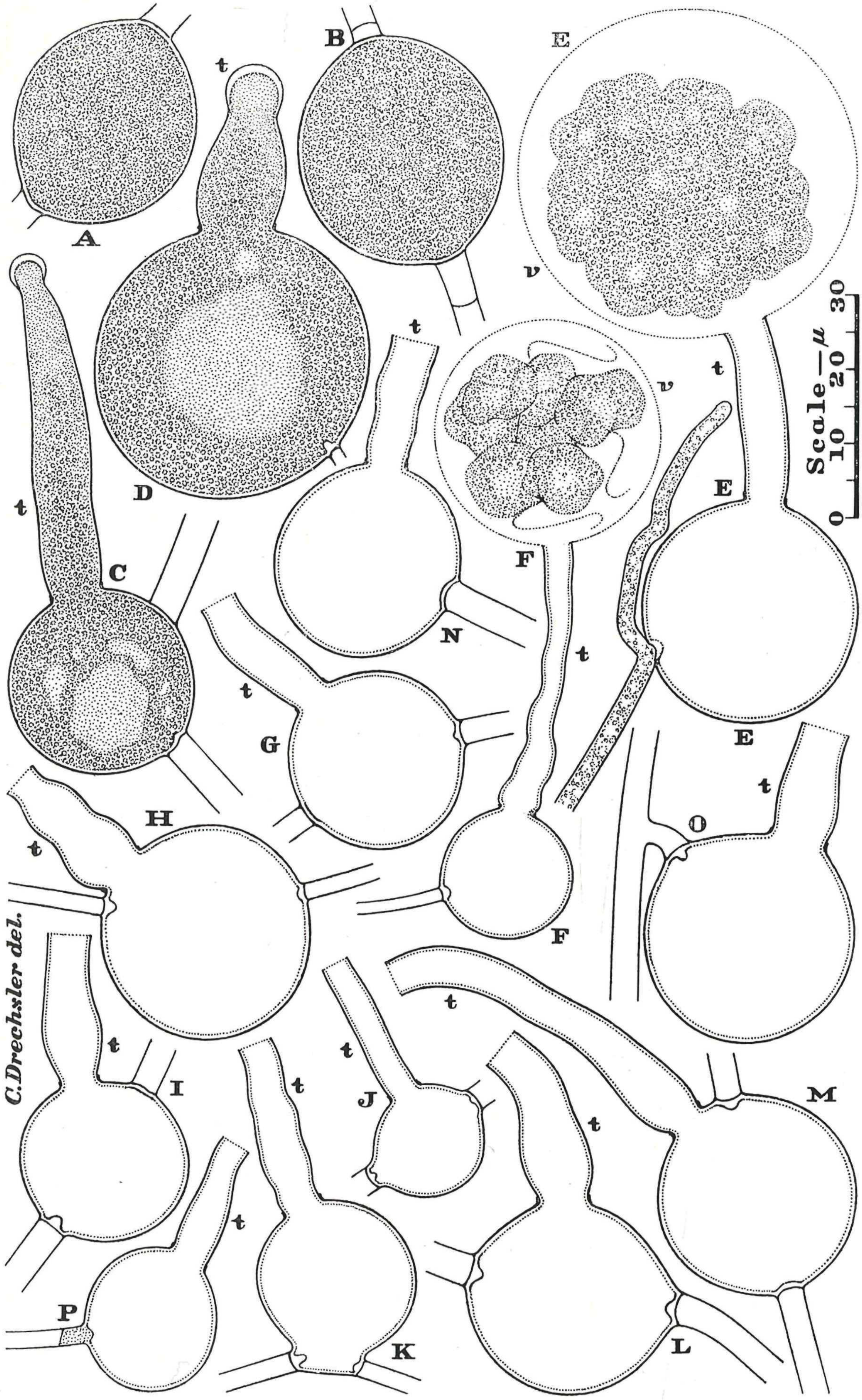
2. *Pythium violae* Chesters and Hickman (1944) was mentioned among some other members of the genus in a brief abstract (Drechsler, 1949) concerning the longevity of oospores in dry agar cultures. The fungus here in question had been isolated from softened cortex of diseased roots and stems of pansies (*Viola tricolor* var. *hortensis* Hort.) taken on May 24, 1938, from a garden in one of the older districts (Georgetown) in Washington, D. C. Its identification with the species that Chesters and Hickman found present as the causal agent of decay in many varieties of *Viola* from widely separated localities in Britain is based on similarity of host relationship and on moderate agreement with respect to morphology. Opportunity for comparing my cultures with relevant British isolations has been lacking.

The Washington pansy fungus agrees with the characterization of *Pythium violae* in that its oogonia and oospores (Pl. IV, A—N; Pl. V, A—I) and, indeed, also its globose conidia (Pl. V, J—L) are generally larger than the corresponding reproductive bodies of *P. ultimum* var. *ultimum*. While in exceptional instances (Pl. IV, I) its oogonia attain a diameter of 38 μ and contain an oospore fully 33 μ in average diameter, its more usual maximum measurements for diameter of oogonium and of oospore would seem, as in *P. violae*, near 34 μ and 28 μ, respectively. Like most other robust species it produces also some sexual reproductive units of relatively small dimensions (Pl. IV, E; Pl. V, B), in which the oogonium may measure less than 15 μ in width and may contain an oospore only 11 to 12 μ in diameter.

The sexual reproductive apparatus of the Washington fungus, like that of *Pythium violae*, appears predominantly of monoclinous origin. The antheridium in many monoclinous units (Pl. IV, A—H: a; Pl. V, A—D: a; H, a, b; I, b) consists of an unmodified cylindrical hyphal segment immediately adjacent to the oogonium, while in others it consists of an adjacent portion of hypha that is either markedly distended (Pl. IV, H, b: J, b) or is furnished with a sizeable lateral protrusion (Pl. IV, I, a, b: J, a; Pl. V, E, a; F, a; I, a). From the words "very occasionally epi- or hypogeal" used by Chesters and Hickmann (1944, p. 56, line 12) — presumably "epi- or hypogynal" was intended — it would appear that antheridia of similar positional relationship are recognized as occurring in ***P. violae.*** A relationship of parts corresponding to that illustrated several times by Chesters and Hickman (1944, Fig. 1, A, B, F, I, K, P) is displayed by the Washington fungus in scattered sexual units wherein the antheridium (Pl. V, G, a) is borne terminally on a short branch arising from the oogonial hypha in proximity to the oogonium. Some oogonia that are fertilized by an adjacent antheridium of monoclinous origin (Pl. IV, K, a; L, a) are further supplied with one or more antheridia (Pl. IV, K, b, c; L, b, c) contributed by neighboring hyphae. Here as also in more purely diclinous reproductive units (Pl. IV, M, N) the antheridia originating from neighboring hyphae are sometimes sessile (Pl. IV, K, b, c; M, a; N, a) and sometimes are terminal on a branch of variable length (Pl. IV, L, b, c).

Owing to the considerable depth of their dense contents the large oogonia of the Washington fungus, much like the large oogonia of some other robust members of the genus, permit little light to pass through them, with the result that under the microscope they present the dark appearance usual in relatively opaque objects. Although Chesters and Hickman describe the contents of the oogonium in ***Pythium violae*** as "dark oily" and "dark almost black", the presence of a dark pigment is probably not to be inferred from these terms. The strong expressions used may in part have been suggested by the pronounced degeneration that usually follows when sexual reproductive units of ***Pythium*** or ***Phytophthora*** species are subjected during their earlier formative stages to prolonged examination in the bright beam supplied by a modern microscope lamp. Exposure for 5 or 10 minutes to microscopical scrutiny at high magnification sometimes appears sufficient to prevent all further normal development in an immature oogonium. While such exposure has no apparent effect on ***Pythium*** oospores in a mature resting state, it often induces immediate germination in after-ripened oospores, though no water has been added to the mounted material, and though the oospores remain imbedded in stale substratum that is constantly losing water by evaporation. In contrast to the destructive effect it exerts on the formative stages of sexual reproduction in the ***Pythiaceae,*** exposure to the bright beam from a microscope condenser does not impede conjugation and normal zygospore formation in species of ***Conidiobolus*** and ***Basidiobolus*** or in members of the ***Zoopagaceae.*** Indeed, some ***Zoopagaceae*** while undergoing microscopical examination have been found initiating normal sexual reproduction abundantly in the illuminated area, though zygospore formation remained wholly absent elsewhere in the mounted material.

The internal changes whereby the lumpy contents of the young oospore (Pl. V, E, G, I) are converted into a parietal granular layer and a central reserve globule (Pl. IV, G, M; Pl. V, A—D, H) usually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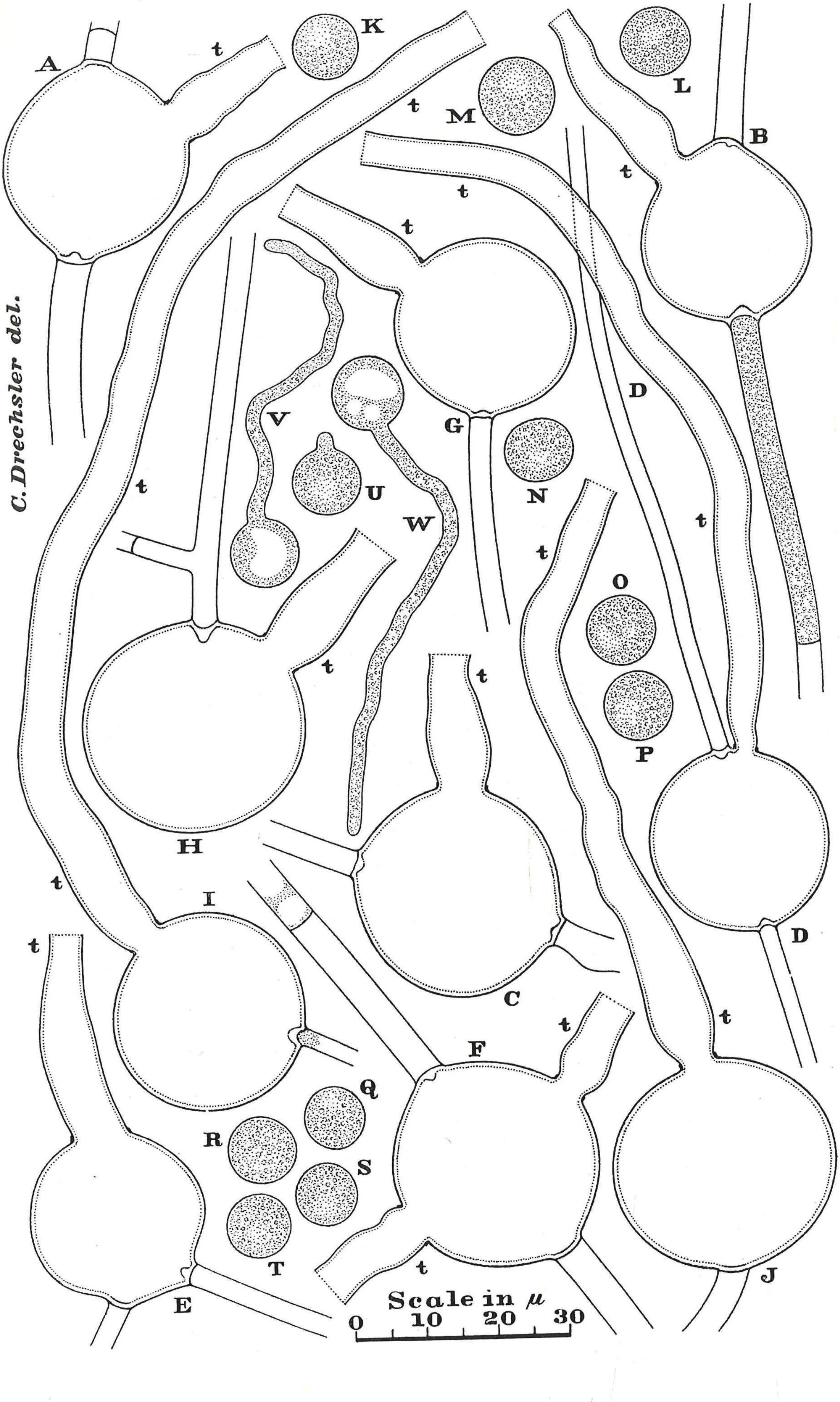
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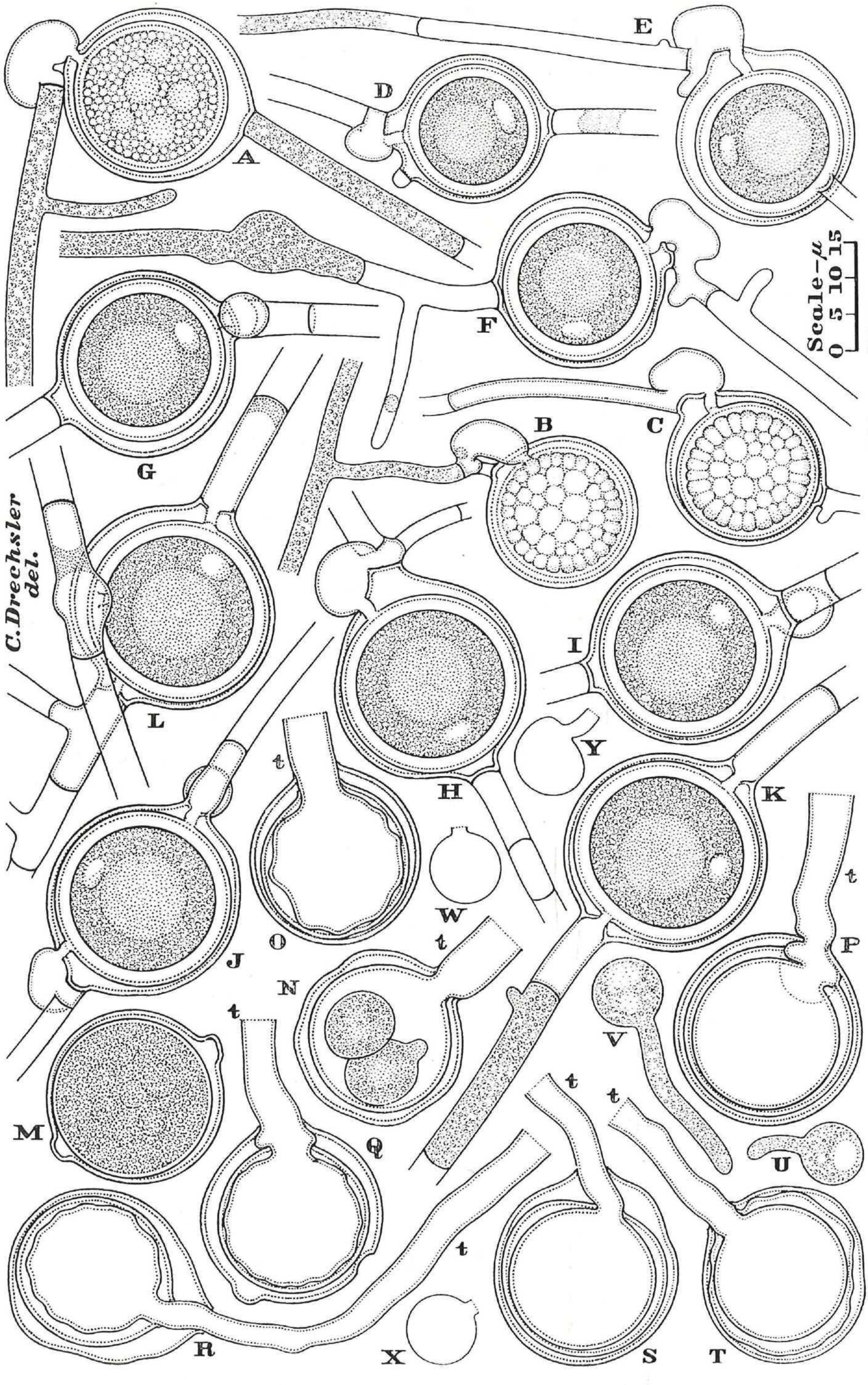
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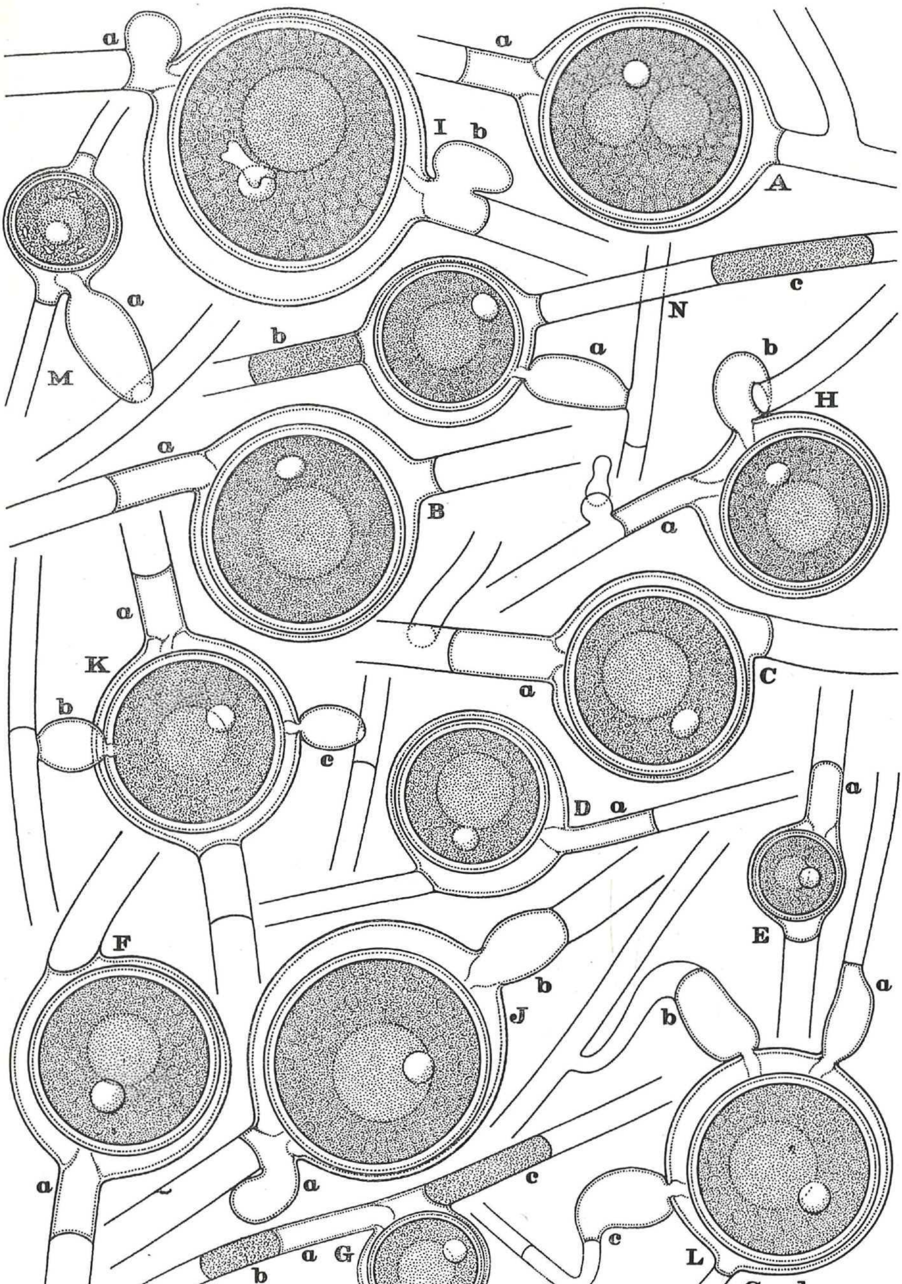

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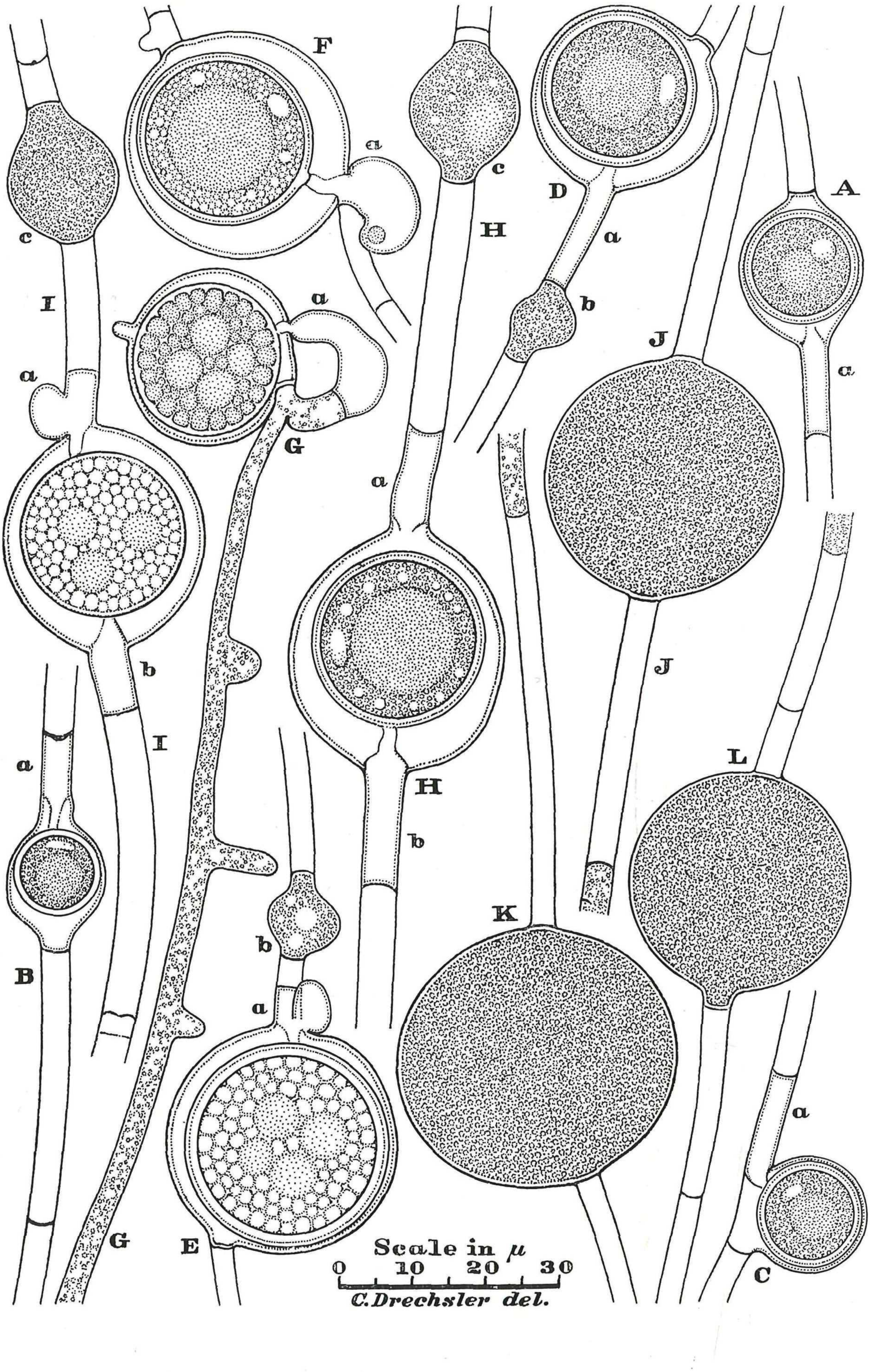

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takes place more slowly in the Washington fungus than in *Pythium ultimum* var. *ultimum*. Many days after a central reserve globule and a refringent body have come clearly into view the parietal layer may retain a more (Pl. IV, A, I; Pl. V, F) or less (Pl. IV, B—F, H, J—L, N) lumpy texture. Although the oospore of the Washington fungus is surrounded by a wall only 1 to 1.6 μ thick it has proved decidedly durable by surviving for 9 2/3 years in a maize-meal-agar tube culture (Drechsler, 1949). The longevity displayed was noteworthy especially as the substratum was in an air-dry state during approximately 8 years of this period.

In some hyphae of the Washington fungus that have become largely emptied in producing oospores, residual portions of protoplasm are found collected here and there in cylindrical segments (Pl. IV, G, b, c; N, b, c), which remain alive for many months. Globose bodies, or conidia, of small (Pl. V, D, b; E, b) or moderate dimensions (Pl. V, H, c; I, c) are also formed near sexual reproductive units. Under cultural conditions apparently more favorable for asexual reproduction many large globose conidia are formed, including some specimens between 30 and 40 μ in diameter (Pl. V, J—L). When shallowly irrigated with distilled water the conidia, whether large or small, have been observed to germinate only by the production of germ hyphae. Parallelism with *Pythium violae* is sustained in the consistent failure of the Washington fungus to produce swarmspores.

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Explanation of Plates XVI—XX

Plate XVI. Asexual reproductive apparatus of *Pythium ultimum* var. *sporangiferum* produced on slabs that after being excised from a young lima-bean-agar plate culture were shallowly irrigated with distilled water; drawn at a uniform magnification with aid of a camera lucida; × 1000. A,B, Intercalary sporangia. C,D, Sporangia that have each put forth an evacuation tube, t, provided with a hyaline cap of dehiscence. E, Newly emptied sporangium with evacuation tube, t, and vesicle, v. F, Empty sporangium with evacuation tube, t, bearing a vesicle, v, from which 7 zoospores are nearly ready to escape. G—M, Empty intercalary sporangia, each with empty evacuation tube, t, open at its tip. N—P, Empty terminal sporangia, each with empty evacuation tube, t, open at its tip.

Plate XVII. Asexual reproductive apparatus of *Pythium ultimum* var. *sporangiferum* produced on slabs that after being excised from a young lima-bean-agar plate culture were shallowly irrigated with distilled water; drawn at a uniform magnification with the aid of a camera lucida; × 1000. A—E, Empty intercalary sporangia, each with empty exit tube, t, open at its tip. F. Empty intercalary sporangium with 2 empty evacuation tubes, t, each open at its tip. G—J, Empty terminal sporangia, each with an evacuation tube, t, open at its tip. K—T, Encysted zoospores. U, Zoospore in early stage of germination. V, W, Zoospores in more advanced stage of germination.

Plate XVIII. *Pythium ultimum* var. *sporangiferum* drawn with the aid of a camera lucida at a uniform magnification; × 1000. A—C, Monoclinous sexual reproductive units produced on slabs that after being excised from a young lima-bean-agar plate culture were shallowly bathed in distilled water; in each unit the oogonium after being fertilized by a single antheridium has formed a young oospore. D—L, Fully mature sexual reproductive units from a maize-meal-agar plate culture 20 days old; in the monoclinous units J—K two adjacent antheridia are present, and in unit L two adjacent antheridia are present together with a third antheridium borne intercalarly in a neighboring hypha. M, Oogonial envelope containing an after-ripened oospore, from a maize-meal-agar plate culture 114 days old. N, Oospore that germinated by producing zoospores; the 2 encysted zoospores within the oospore were fashioned from a portion of protoplasm that failed to migrate through the open evacuation tube, t; the double-walled pouch derives entirely from the oospore as the oogonial envelope had disappeared before removal of the specimen from a maize-meal-agar plate culture 176 days old. O—T, Oogonial envelopes, each surrounding a double membrane remaining after discharge of the oospore contents through evacuation tube, t, for conversion into swarm spores; germination here had ensued when after-ripened oospores, each with oogonial envelope still intact, were removed from a 280-day-old maize-meal-agar plate culture and shallowly irrigated with distilled water. U,V, Encysted zoospores germinating by emission of a germ hypha. W—Y, Three zoospore membranes, each left empty after development of a secondary motile zoospore.

Plate XIX. Sexual reproductive apparatus produced in 30 days on moist lima-bean-agar by Washington pansy fungus probably referable to *Pythium violae;* all units drawn at a uniform magnification with the aid of a camera lucida; $\times$ 1000. A—G, Monoclinous units in each of which the intercalary oogonium was fertilized by an adjacent cylindrical antheridium, a; b and c (in G), hyphal cells, H—J. Monoclinous units in which the intercalary oogonium is supplied with 2 adjacent antheridia, a and b. K,L, Intercalary oogonia, each supplied with 1 adjacent antheridium, a, and with 2 other antheridia, b and c, contributed by neighboring hyphae. M, N, Diclinous reproductive units in which an intercalary oogonium is fertilized by an antheridium, a, sessile on a neighboring hypha; b and c (in N), hyphal cells.

Plate XX. Washington pansy fungus probably referable to *Pythium violae;* all parts drawn at a uniform magnification with the aid of a camera lucida; $\times$ 1000. A—D, Monoclinous sexual reproductive units formed in 30 days on moist lima-bean-agar; each oogonium here is supplied with a single cylindrical adjacent antheridium, a, and contains a fully mature oospore; b (in D), small conidium. E, F, Monoclinous sexual reproductive units from 2 maize-meal-agar plate cultures 8 and 14 days old, respectively; in each unit the oogonium was fertilized by a laterally protuberant adjacent antheridium, a; b (in E), small conidium. G, Terminal monoclinous sexual reproductive unit formed on moist lima-bean agar; the single antheridium, a, here is borne terminally on a short branch given off close to the oogonium. H,I, Two monoclinous sexual reproductive units from separate maize-meal-agar plate cultures 14 and 4 days old, respectively; the oogonium in each unit is attended by 2 adjacent antheridia, a and b; c, small conidium. J—L, Large intercalary conidia produced on moist lima-bean agar.

Correction:

References to plates No. I—V in the text should be replaced by numbers XVI—XX. (XVI instead of I; XVII instead of II etc.)!

The references in the explanation to the plates however are correct!