# DESCRIPTIONS OF THE SOUTH AFRICAN PYTHIACEAE WITH RECORDS OF THEIR OCCURRENCE.

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### INTRODUCTION.

The fungi belonging to the Pythiaceae had received little attention from plant patho logists in South Africa before the writer (25) became interested in this group. Until then, only three species had been recorded, namely, Phytophthora infestans on potatoes (late blight), *Ph. parasitica* on rhubarb (crown rot), and *Ph. citrophthora* on citrus (brown rot). During the writer's investigation of root-rot diseases of vegetable and garden plants, Pythiaceae species were encountered more and more frequently, showing that this group of fungi is fairly common, and widely distributed in South Africa. They have been isolated on more than one hundred occasions from forty-four different host plants. They have been isolated from roots and stems of wilting plants, from bark or trunk lesions, from rotting fruits and from many dying and rotting succulent plants. More often than not they were associated with other wilt-producing fungi, more especially species of Fusarium, Rhizoctonia solani, or Sclerotium rolfsii. In large numbers of instances, these latter fungi were probably responsible for the disease in the affected plants, the Pythiaceae being secondary, or living saprophytically in the decaying tissues. Some of them, however, are solely responsible for serious diseases, for instance, Pythium ultimum or P. aphanidermatum for the foot-rot of papaws (26), and the latter fungus for "leak" disease of potatoes (27). That these fungi have a wide distribution may be shown by the fact that in 1925 the first record of *Ph. citrophthora* was made by Doidge (10) when the fungus appeared in epidemic form causing a brown-rot of oranges in most areas where oranges were grown. Also in 1934 Ph. parasitica was recorded by the writer (29) for the first time as a serious disease of tomato fruits, when the trouble occurred in epidemic form over a large area in the eastern Transvaal.

All the Pythiaceae fungi collected have been allotted to 10 known species of *Pythium* and seven known species of *Phytophthora*.\* In some cases there are slight differences between these fungi and the original descriptions, but such differences have not been considered sufficiently great to justify making new species.

In the following pages all the fungi mentioned were isolated by the writer unless where otherwise stated, and when localities are not mentioned, they should be understood as meaning the Transvaal.

The writer wishes to thank Mr. S. F. Ashby and his staff at the Imperial Mycological Institute, and Dr. C. M. Tucker of the University of Missouri, for their kind assistance in determining the identity of these organisms. He was also fortunate in meeting Dr. J. T. Middleton at the University of California who is monographing the genus *Pythium*, and is greatly indebted to him for examining the cultures and confirming their identity, and for reading the manuscript. As Dr. Middleton is also including all known records of the host plants and distribution of the species of *Pythium* in his monograph, information on this point is not included in this paper.

For the sake of convenience the words Pythium and Phytophthora have, in this paper, been abbreviated to P. and Ph. respectively.

\* All the cultures have been lodged in the American Type Culture Collection, Washington, D.C.

### Pythium ultimum Trow.

Hyphae are from 3 to 9  $\mu$  in diameter, much branched, and septate in old cultures.

Oogonia are smooth, terminal or rarely intercalar, spherical, or slightly irregular in shape. The diameter ranges from 13.5 to 29.3  $\mu$ , the average diameter from different strains being from 18.9 to 23.2  $\mu$ .

Oospores are spherical with a smooth, thick wall. The diameter ranges from 11.3 to  $23.4 \mu$ , the average diameter from different strains being from 16.0 to  $18.9 \mu$ . They germinate after a period of rest, producing one or more germ tubes.

Antheridia are generally one to each oogonium, rarely two; the antheridium has a very short, or practically no stalk; it arises immediately below the oogonium, very rarely from a neighbouring hypha; is more or less horn-shaped, and curves around sharply so that its tip is applied to the oogonium.

Sporangia are mainly terminal and spherical, sometimes intercalar and lemon-shaped; they vary in diameter from 12 to 31  $\mu$ , the average diameter in different strains being from 20.6 to 24.2  $\mu$ ; they germinate by the production of from one to three germ tubes.

Strains of this fungus isolated from various hosts may differ to a slight extent from one another. In culture media, some produce more aerial mycelium than others; some produce sporangia sparsely and oogonia in abundance, while in others the opposite is the case. There is also some variation in the average size of the oospores, oogonia, and sporangia in the different strains. In all, however, the antheridium is typical and characteristic. The fungus grows well on prune and oatmeal agars. The optimum temperature for the growth varies from 25 to 30°C. in most of the strains, but 35°C. for a few. The maximum temperature is above 37°C. and the minimum is from 4 to 7°C.

The fungus differs very little from that originally described by Trow (22). His average measurements for the oogonia and oospores are 20.6 and  $16.3 \mu$  in diameter respectively. A distinctive character of the fungus is the fact that the production of zoospores has never been observed. One difference is that Trow states his fungus to be saprophytic, while here it is parasitic and responsible for numerous diseases.



FIG. 1.—P. ultimum. (a) and (b) Terminal, and (c) intercalar oogonia and antheridia, (d) intercalar and (e) terminal sporangia.

A culture labelled P. debaryanum Hesse was obtained from the Centralbureau, Holland, and grown in parallel series with a typical culture of P. ultimum. The two fungi were found to be similar in all respects, both having the same type of antheridium, and neither producing zoospores when grown in suitable water cultures, including insects. This fungus from Holland was undoubtedly a typical culture of P. ultimum and it is quite likely that this same mistake in identity has been made before by other writers. Drechsler (11) also drew attention to this fact and mentioned the difference between the two species.

### HOSTS.

*P. ultimum* appears to be the commonest species of the *Pythiaceae* encountered in South Africa and has been isolated from a large number of plants. It may cause a disease of papaws known as "foot-rot", where the base of the trunk becomes soft and rotten, and the plant collapses (26). It has been isolated from this host on 11 occasions from the eastern, northern and western Transvaal, from Natal and the Cape.

It has also been isolated from the following plants, often along with *Rhizoctonia solani* Kuhn, or species of *Fusaria*, and all from the Transvaal except where otherwise stated :

From wilted bean, peanut, tomato, pea (six occasions), tobacco collar-rot and wilt (E. S. Moore), sweet potato infected with soft-rot, rhubarb infected with crown-rot and associated with *Ph. parasitica* from Balfour, Cape, from cabbage infected with soft heart-rot from Port Elizabeth, Cape, and from the navel-end of young Washington navel oranges. From wilted asters (twice), delphiniums (twice), gillias from Natal, nasturtium, pink, sweet peas (four times), witchweed (*Striga lutea*), Iceland poppies (twice) and from damped-off seedlings of Iceland poppy, dahlia, and pine trees.

From the following succulents all infected with a soft-rot, Dinteranthus microspermus, Fenesturia aurantiaco, Duvalia parvifolia, Delosperma sp., Stapelia sp. Tavaresia sp., Aloe variegata and Mesembryanthemum sp.

Hopkins (15) from Rhodesia reports *P. ultimum* on damping-off seedlings of Clarkia elegans, Cupressus sp., Coleus sp., Pinus sp., Carica papaya, and Nicotiana tabacum.

In inoculation experiments *P. ultimum* has been found capable of producing a foot-rot of papaws, soft-rots of potatoes, sweet-potatoes and oranges, and also a rapid wilting of asters when the plants were inoculated through wounds. It caused only the slow wilting and death of a small percentage of Iceland poppies inoculated with it. It is probable that in some cases the fungus is only a weak parasite, but may hasten the wilting when associated with more virulent pathogens, or if the host is weakened through some cultural fault. An interesting case of the longevity of the fungus in the soil was observed. In an experiment, papaws were inoculated with *P. ultimum*, and one plant partially wilted but recovered. It continued growing in the tin in the greenhouse for eight years. At the end of one year a few particles of the soil were removed from the tin and plated, and cultures of *P. ultimum* were obtained. This was repeated after the fifth year, and again after the eighth year, and in each case the fungus was recovered, showing that it was capable of living in the soil without being in the tissue of a plant during this period of time.

#### Pythium aphanidermatum (Eds.) Fitz.

Hyphae are much branched and non-septate except in fructifications; vary in diameter from 2 to 10  $\mu$ , commonly about 6  $\mu$ .

Observation O are smooth, spherical and terminal, sometimes intercalary; range in diameter from 18 to  $31 \cdot 5 \mu$  with an average of  $25 \cdot 3 \mu$ .

Oospores are spherical with smooth, thick walls, and do not fill the oogonia; range in size from 15.8 to  $22.5 \mu$  with an average of  $21.3 \mu$  in diameter.

Antheridia are sub-orbicular and broadly clavate, being closely appressed to the oogonium; generally one to each oogonium, sometimes two; may arise from the oogonial hypha, more usually from another; may be terminal or intercalary and about  $11 \mu$  in size.

Sporangia.—A terminal hypha becomes swollen and usually produces lobulate outgrowths; a septum is formed cutting off this portion which may be up to  $150 \,\mu$  in length, from the rest of the hypha. Usually from the tip, more rarely from one of the lobulate outgrowths, the vesicle is produced, and may be up to  $50 \,\mu$  or more in diameter. From 8 to 40 zoospores are produced in the vesicle depending on its size. The zoospores are  $9 \times 12 \,\mu$  in average size, and are bi-ciliate.

The fungus grows well on prune and oatmeal agars forming profuse white, cottony, aerial mycelium. The optimum temperature for growth is approximately 34°C., maximum is above 37°C. and no growth takes place at 7°C. The average size, both of the oogonia and oospores, varies only slightly in different cultures from different hosts. The zoospores have been noticed to conjugate, usually in pairs, but as many as 11 have become fused to form a spherical body, which subsequently germinated in a similar manner to a single zoospore. This occurrence does not appear to have been observed by other writers.



FIG. 2.—P. aphanidermatum. (a) Intercalar and (b) terminal antheridium and oogonium, (c) lobulate sporangium, and (d) the vesicle and developing zoospores produced at the tip of (c).

HOSTS.

*P. aphanidermatum* is responsible for a serious disease of potatoes known as "Soft-rot" or "Leak", which was described in a previous paper (27). It was also found on two occasions to cause a foot-rot disease of papaws in the same manner as does *P. ultimum*. It was isolated from rotting tomato fruits from the northern Transvaal, and from the stems of wilted tomatoes sent from Windhoek, S.W. Africa, and also from wilted squash (*Cucurbita pepo*) from the same locality. It was isolated from the rotting fruits of the chou-chou (Sechium edule) and brinjal or egg-plant (twice). It was obtained from damping-off tobacco seedlings from Balfour, Cape, and from a wilted tobacco plant from the western Transvaal (E. S. Moore). It was isolated from a wilting brachen plant (*Pteridium aquilenum*) and also caused serious destruction in young transplanted tomatoes by rotting away the stems (28).

Hopkins (15) reports it on Nicotiana tabacum in Rhodesia.

### Pythium irregulare Buisman.

Hyphae are commonly  $4.5 \mu$  in diameter, seldom more but may be less; much branched, and non-septate except in older cultures.



F10. 3 – P. irregulare. (a), (b), (c) and (d) Antheridia and oogonia, (e) an intercalar sporangium, (f), (g), (h) and (i) a terminal sporangium showing stages in the production of zoospores.

Oogonia are mostly intercalar, but sometimes terminal on short lateral branches; may be spherical or irregularly lobed or sometimes with definite narrow processes; vary somewhat in size, but are commonly 22  $\mu$  in diameter.

Oospores are spherical with a smooth, thick wall, not filling the oogonium, 13 to 20  $\mu$  in diameter.

Antheridia are club-shaped to cylindrical, straight or curved; usually one, sometimes two and rarely three to an oogonium; the antheridial stalk is fairly long and usually arises from the same hypha that bears the oogonium.

Sporangia may be terminal or intercalar, more often the latter; they are spherical, or lemon- or barrel-shaped, and from 13 to 28  $\mu$  in diameter. They may germinate by one or more germ tubes, or may produce zoospores. In the latter case, an evacuation tube about  $4.5 \mu$  in diameter, and from 15 to  $22.5 \mu$  in length is produced; the tip of the tube swells out into a vesicle which is spherical and thin-walled.

Zoospores.—From three to nine zoospores have been observed in a vesicle; they are approximately  $13.5 \times 9 \mu$  in size and vigorously motile at first, later becoming spherical, about 10  $\mu$  in size, and germinate, sending out one germ tube.

The fungus grows well on prune and oatmeal agar, and conidia and sexual organs are readily produced in large numbers. The fungus could only be induced with difficulty to form its zoospores. This was accomplished by growing it on sterilised locusts in water incubated at 27°C., frequent changes of water being made. The optimum temperature for growth was 22°C. for one strain and 28°C. for the other, with maximum 37°C. and minimum 4°C.

The above description agrees fairly closely with that of Buisman (6).

### Hosts.

*P. irregulare* has been isolated from a young papaw plant infected with foot-rot in the northern Transvaal, and from a rotting citrus fruit (E. M. Doidge) from the western Transvaal.

In inoculation experiments it was found that the fungus was unable to produce a rot of citrus fruits when introduced through wounds.

#### Pythium vexans de Bary.

Hyphae are much branched, most of the branches being very fine, the main branches commonly  $4.5 \mu$  in diameter.

Organia are smooth and spherical, often with a widened base, usually terminal, occasionally intercalary; range in size from  $15\cdot8$  to  $22\cdot5 \mu$  in diameter, with an average (of 50) of  $19\cdot4 \mu$ .

Obspores are spherical, with a smooth, thick wall which is generally yellow in colour; range from 13 to 18  $\mu$  in diameter with an average of 16.2  $\mu$ .

Antheridium is broad and clasping, about  $5 \mu$  in thickness, and covering about one-third of the surface of the oogonium; may arise from a separate hypha, or from just below the oogonium on the oogonial stalk.

Sporangia are commonly spherical and terminal, but may be pear-shaped and intercalar; vary in size from 13.5 to  $22.5 \mu$  in diameter, with an average of  $17.3 \mu$ . They may germinate by producing one germ tube, or may produce zoospores. In the latter case the contents of the sporangium pass through an evacuation tube into a vesicle; the evacuation tube is most commonly about  $7 \mu$  in length and  $4.5 \mu$  in diameter. When the zoospores emerge, the vesicle wall disappears, but the evacuation tube persists.

Zoospores. In different cases under examination, the numbers of zoospores produced were 11, 7, 10, 11, 10. They are elongate and about  $11.5 \times 9 \mu$  in size; they round off to about  $9 \mu$  in diameter, and germinate by one germ tube.

The appearance of the culture on Petri dishes poured with agar is distinctive, the fungus making a fine radial growth, and, as Braun (4) suggests in his description of *P. complectens*, having the appearance of combed silk. Sporangia are produced abundantly on most media, but oogonia are at first very scarce. They may be obtained fairly readily in the aerial fluffy mycelium of a culture on oatmeal agar three to four weeks old. Zoospores were obtained in large numbers when portions of a three-week culture on oatmeal agar were transferred to watchglasses containing Petri's solution, or dilute bean broth, and left in the dark for 15 to 20 minutes. The whole process of zoospore formation is extremely rapid; in one case only 14 minutes elapsed from the moment the vesicle was produced until the zoospores escaped. The temperatures for growth are optimum 28 to  $31^{\circ}$ C., maximum 37 and minimum  $13^{\circ}$ C.



FIG. 4.—P. vexans. (a), (b) and (c) Antheridium and oogonium, (d) sporangium and evacuation tube, (e) formation of vesicle, and (f) after the escape of the zoospores.

The above description of the fungus agrees very closely with that of *P. complextens* and *P. vexans.* The sporangia, however, are somewhat smaller, the average diameter being about 4  $\mu$  less than those described for both these species. Middleton (17) suggests dropping the name *P. complextens* in favour of the earlier *P. vexans*, stating that in his opinion the differences between the two species are not sufficiently great to justify the retention of the two species.

#### HOSTS.

**P.** vexans has been isolated from two different plants; in the first instance, along with **P.** aphanidermatum from a papaw infected with foot-rot, and secondly, along with species of *Fusarium*, from a perennial statice plant infected with wilt or crown-rot.

### Pythium myriotylum Drechsler.

Hyphae are much branched, the main branches being up to  $9 \mu$  in diameter; the side branches are variable in thickness, sometimes being thin, 2 to  $3 \mu$ , or are swollen out into clavate, lobulate-like processes often in groups and usually in contact with the glass of the culture vessel—the appressoria.

Organia are smooth and spherical, usually terminal on short thin branches but may be intercalar; range in size from 22.5 to  $28.9 \mu$ , with an average of  $25.5 \mu$  in diameter.

Obspores are smooth and spherical with a thick wall; occasionally two in one obsorbing; range in size from 13.5 to  $22.5 \mu$  with an average of  $18.5 \mu$  in diameter.

Antheridia commonly three to six to each oogonium, but may be more; appear like undifferentiated hyphae about  $4.5 \mu$  in thickness; may clasp the oogonium closely or only at the tip; the hypha bearing the antheridium may arise from the oogonial branch, or from a neighbouring hypha; the antheridial branch may divide, producing two or more antheridia.



FIG. 5.—P. myriotylum. (a) and (b) Oogonia and antheridia, (c) a lobulate sporangium and vesicle.

Sporangia are irregular in shape, usually being formed of the end portion of a hypha with lobulate and rounded outgrowths, very variable in shape and size; the vesicle is produced from one of the lobulate outgrowths, or from the tip of the hypha, and is up to  $40 \mu$  in diameter, depending on the size of the sporangium; up to 40 zoospores are produced in the vesicle.

Zoospores are vigorously motile, 9 to 11  $\mu$  in size before they round off and germinate.

The fungus grows well on various agars, forming abundant aerial mycelium. Oogonia are readily produced on oatmeal agar after three weeks, and sporangia are produced when portions of a culture on plain water agar are placed in Petri's solution and left in the dark for a number of hours. The above description agrees closely with that of Drechsler (12).

The temperatures for growth are optimum 34, maximum about 37, and minimum 7°C. Hosts.

*P. myriotylum* has been isolated only once, and that, along with *P. aphanidermatum* and *P. vexans* from papaw plants infected with "foot-rot".

### Pythium splendens Braun.

Hyphae are very much branched, the main branches being commonly  $6 \mu$  in diameter, but may be as much as  $9 \mu$ ; sickle-shaped bodies or appressoria, often in chains, may develop on the medium in contact with the glass.



FIG. 6.—P. splendens. (a), (b) and (c) Antheridia and oogonia, (d) and (e) sporangia.

Oogonia are smooth, spherical, and terminal; from  $27 \cdot 2$  to  $35 \mu$ , commonly  $33 \mu$  in diameter.

Oospores were not seen by the writer, the contents of the oogonium remaining undifferentiated.

Antheridia one to three to each oogonium, clavate, 8 to 15  $\mu$ , usually 10  $\mu$  long by 5 to 6  $\mu$  wide, the blunt end being applied to the oogonial wall; produced on a hypha adjacent to that producing the oogonium.

Sporangia spherical, smooth, thin-walled, and terminal; vary from 19.8 to 49.5, commonly 33  $\mu$  in diameter. Germinate readily producing one or more germ tubes.

The fungus forms profuse aerial mycelium on most culture media. Sporangia are produced after two days and appear in very large numbers. It was some years before the writer was able to obtain any oogonia. They were finally discovered on a potato dextrose culture some three months old, and about a dozen were seen. The contents of the oogonium remained undifferentiated, and oospores were not produced. Braun (5) had a similar difficulty in obtaining oogonia; his figures are, oogonia  $25 \cdot 5$  to  $34 \cdot 7$ , average  $31 \cdot 7 \mu$  in diameter, and oospores, spherical, with thick walls,  $21 \cdot 3$  to  $29 \cdot 8$ , average  $26 \cdot 6\mu$ ; antheridia were three to eight to each oogonium, and he also stated that the fungus does not produce zoospores. The S. African fungus thus agrees fairly closely with the description by Braun except in the matter of the number of antheridia produced.

Temperatures for growth are optimum 31, maximum 37 and minimum 7°C.

This fungus was mentioned in a previous publication Wager (25) under the name of *P. cf. splendens.* 

#### Hosts.

*P. splendens* was isolated only once, and that, along with *P. ultimum*, from a papaw tree infected with "foot-rot" from the eastern Transvaal.

### Pythium spinosum Sawada.

Hyphae may range from 2 to 8  $\mu$  in diameter, much branched, and septate in old cultures.



FIG. 7.—P. spinosum. (a) and (b) Antheridium and oogonium, (c) intercalar and (d) terminal sporangium. Organia are spherical and covered with spines; they are commonly produced terminally on short lateral branches, but may be intercalar; range from 13.5 to  $23.4 \mu$  in diameter, with an average (of 50) of  $17.2 \mu$ .

Spines are blunt, narrow, finger-like processes; they are about 4 to 8  $\mu$  long by 1.5  $\mu$  wide; from 10 to 21 spines being visible laterally on the organium.

Oospores are spherical and smooth, and practically fill the oogonial cavity.

Antheridia are usually one to each oogonium, sometimes two or even three; each is borne on a fairly long, slender branch from the same hypha that produced the oogonial branch, or from a neighbouring hypha; it is cut off by a septum from the antheridial branch, and is sub-cylindrical or club-shaped.

Sporangia are produced abundantly in water cultures; they may be terminal and spherical, or intercalary and lemon-shaped or cylindrical; they are smooth but occasionally may have a few spines; they vary greatly in size from 9 to 27  $\mu$  in diameter, and germinate, producing one to three germ tubes.

Temperatures for growth are optimum 25 to 28, maximum 37 and minimum 4°C.

This fungus differs from Sawada's description (19, 20) in the fact that multiple antheridia are common whereas he described only single. In correspondence with the writer, E. J. Butler stated that he had examined a culture of *P. spinosum* from the Centraalbureau, Holland, and found that it also had multiple antheridia, a fact that Sawada had evidently overlooked. In the original description the oogonia are given as ranging from 17 to  $24 \mu$  in diameter, with  $19.7 \mu$  the average, being thus somewhat larger than those described above. According to the original description this fungus does not produce zoospores, and none has been observed.

### HOSTS.

*P. spinosum* has been isolated only once from a young papaw plant infected with footrot. The plant had been sent in from a plantation which had just been badly frosted, and as a result nearly all the plants died; the fungus was thus probably not responsible. *P. irregulare* was isolated from an adjacent plant.

### Pythium acanthicum Drechsler.

Hyphae are generally very slender, wavy and branched. The mycelium develops successive ridges or scalloped frills as the culture in a tube of oatmeal agar gets old, in a very characteristic manner.

Organia are spherical and covered with spines; terminal on short slender branches, occasionally intercalar; vary in size from 18 to 27  $\mu$  with an average of  $22 \cdot 3 \mu$  in diameter, exclusive of spines.

Spines are conical with blunt points, slightly longer than broad at the base, and about  $2\mu$  in length.

Oospores are smooth and spherical, nearly filling the oogonium, and thin-walled; vary from 15.8 to 22.5 with an average of 19  $\mu$  in diameter; may germinate, producing one or numerous germ tubes, or may develop immediately into a sporangium.

Antheridia are commonly one to each oogonium, sometimes two, rarely three; subspherical or clavate, 7 to 10  $\mu$  in size, making a broad contact at the tip with the oogonial wall; borne on a short branch usually arising from the same hypha as the oogonium, or from a neighbouring hypha. Sporangia are smooth, thin-walled, spherical, ovoid, or irregular in shape; terminal or intercalar; range in diameter up to 31.5, but commonly  $22 \mu$ ; germinate with the production of numerous, slender germ tubes, or may produce an evacuation tube 30 to  $85 \mu$  in length, and from 2.5 to  $4 \mu$  in diameter; the vesicle is produced at the end of the evacuation tube, is spherical and its contents are rapidly divided up into zoospores.

Zoospores. From 8 to 30 zoospores have been observed in a vesicle; they are about  $11 \times 7 \mu$  in size and vigorously motile at first.



FIG. 8.—P. acanthicum. (a), (b) and (c) Antheridia and oogonia, (d) and (e) sporangium, evacuation tube, and vesicle produced directly from the oospore.

The fungus grows well on prune or oatmeal agars. Oogonia are produced readily but sporangia are scarce. They were formed when portions of a Petri-dish culture eight weeks old were transferred to Petri's solution. In liquid cultures it was noticed that oospores often germinated, producing a single tube from 10 to 90  $\mu$  in length, the tip of which swelled out to form a sporangium. This sporangium might be up to twice the size of the oospore, and spherical, ovoid or irregular in shape ; it produced an evacuation tube and vesicle in the manner described above. Drechsler (12) mentions this fact in his description of this fungus.

Temperatures for growth are optimum 25, maximum 37, and minimum 10°C.

### Hosts.

*P. acanthicum* has been isolated twice; from wilted peas, and from damping-off dahlia seedlings. In each case *P. ultimum* was isolated at the same time.

### Pythium oligandrum Drechsler.

Hyphae are generally slender, but up to 7  $\mu$  in diameter, much branched; the fungus produces little aerial mycelium on culture media.



FIG. 9.—P. oligandrum. (a) Oogonium and antheridium, (b) parthenogenetic oogonium, (c) sporangium and vesicle produced directly from oospore, and (d) ditto produced in ordinary manner on a hypha.

Oogonia are spherical and covered with spines; terminal on short slender branches, rarely intercalar; size exclusive of spines varies from 18 to  $27.4 \mu$  in diameter, with an average of  $23.4 \mu$ , on oatmeal agar.

Spines are sharp-pointed, conical, about twice as long as broad at the base, vary from 3.4 to  $7.7 \mu$ , commonly  $5.0 \mu$  in length.

Obspores are smooth, spherical, and thin-walled; range from  $15 \cdot 8$  to  $22 \cdot 5 \mu$  in diameter, with an average of  $20 \cdot 5 \mu$  on oatmeal agar; germinate readily, producing either numerous slender germ tubes or sporangia.

Antheridia are rare; when present are closely pressed to the oogonium; are semicircular or clavate, about  $9\mu$  wide, borne on a slender branch which arises from the same branch as the oogonium, or a neighbouring one, the branch twining around the oogonium; usually one, very seldom two to one oogonium; most oospores appear to develop parthenogenetically.

Sporangia are readily produced on plain water agar; large, ellipsoid, spherical, elongate or irregular in shape, sometimes with lobulate processes; usually terminal, but may be intercalar; range in size up to 90  $\mu$  in length, but commonly about 50  $\mu$ ; may germinate producing numerous germ tubes, or may form zoospores, in which case the evacuation tube is usually  $4.5 \mu$  thick, wavy, and from 36 to 72  $\mu$  long; the vesicle is spherical at first, later irregular in shape, and from 27  $\mu$  in diameter to 67.5 by 36  $\mu$ ; the number of zoospores produced in four cases observed were 5, 5, 6, and 19.

Zoospores vary in size from 12 to  $14 \times 9\mu$ , vigorously motile at first, later become spherical and germinate.

The four cultures obtained behave in the same manner and differ only slightly from each other in their measurements. In two of them, however, antheridia have not been observed, and are rare in the other two; the oospores appear to develop parthenogenetically. On oatmeal agar, oogonia are produced in profusion, but very few sporangia. On plain water agar, both oogonia and sporangia are numerous. Zoospores are not readily obtained; they were observed in one case where a portion of a culture on plain agar was placed in Petri's solution for four days, and then transferred to tap water for a few hours. Sometimes the contents of a sporangium pass along the evacuation tube into a vesicle, and no further change takes place. This vesicle may later act as a secondary sporangium and produce another evacuation tube and vesicle in a normal manner.

Temperatures for growth are optimum 25 in one strain and 31 in another, maximum 37 and minimum 10°C.

It was also observed that when placed in water culture, the oogonia germinate and their contents develop immediately into a sporangium which in turn gives rise to an evacuation tube and vesicle as shown in figure 9. This phenomenon is not mentioned by Drechsler (12). The above description of this fungus agrees fairly well with that of Drechsler except that his oogonia are some 3  $\mu$  larger in average diameter.

#### HOSTS.

*P. oligandrum* has been isolated from shirley poppy, antirrhinum, marrow and cabbage plants, all suffering from wilt. In a previous paper (Wager, 25) this fungus was mentioned under the name of *Pythium sp. cf. artotrogus*, as isolated from the first two host plants mentioned above. In inoculation experiments with iceland poppies and asters, the fungus was unable to produce any wilt symptoms. It is probably a weak parasite attacking plants weakened through faulty cultural practices, or plants already wilting due to the attack of some other more virulent pathogen.

### Pythium debaryanum Hesse (= P. fabae Cheney).

Hyphae are usually slender, up to 6  $\mu$  thick, commonly 3  $\mu$ , much branched.

Oogonia are commonly intercalar and sub-globose to lemon-shaped, or terminal and spherical, variable in size from 12 to 25  $\mu$ , commonly 16  $\mu$  in diameter.

Oospores are spherical, thick-walled, and practically fill the oogonia.

Antheridia are tubular, making contact at narrowed tip of enlarged apical portion; fairly long antheridial branch which is usually curved or crook-necked; one to three to each oogonium, frequently two, especially on intercalar oogonium when one arises from each side of it; the antheridial branch may arise near the base of the oogonium or some way back along the oogonial branch, or occasionally from a separate hypha.



FIG. 10.—P. debaryanum (=P. fabae.) (a), (b) and (c) Variable-shaped intercalar sporangia, (d) terminal sporangium, evacuation tube, vesicle, and developing zoospores, (e) sporangium, cld evacuation tube and new evacuation tube and developing vesicle, (f) sporangium and vesicle and zoospores produced in sporangium, (g), (h) and (i) oogonia and antheridia.

Sporangia may be terminal and spherical and from 10 to 30, commonly  $21.5 \mu$  in size; they are more generally intercalar and irregular in shape, from barrel-shaped, ovoid, elongate or sausage-shaped, and may be very small—like fragments of a hypha—or up to  $60 \times 20$ , commonly about 20  $\mu$  in size; all have a large and pronounced vacuole within. They germinate rarely, usually with the production of one germ tube. Zoospores may be produced in liquid cultures; the evacuation tube is produced laterally, is thick, and is one to three times the length of the sporangium, commonly 30  $\mu$  long, and is quite commonly curved or bent; an evacuation tube may be produced but not used, and later another one may be formed or the old one may produce a branch; the contents of the sporangium pass very rapidly into the forming vesicle; sometimes not all the contents of the sporangium pass into the vesicle and thus a few spores may develop within the sporangium as well as in the vesicle; zoospores are 7 to 8  $\mu$  in size, and 12 and 14 were seen produced in various vesicles.

Sporangia are produced in abundance on all media, but oogonia are very scarce, only a few being seen on an old culture. Temperatures for growth are optimum 22, maximum 28, minimum 7°C.

In correspondence with the writer, S. F. Ashby suggested that this fungus might possibly be *P. fabae*. Cheney's (8) description of her fungus, *P. fabae*, isolated from wilting broad bean plants, is very similar to the above, although there is no mention of any production of zoospores; her details are—conidia sparse, 13 to 26, average  $21.5 \mu$  in size, oogonia 13 to 23, average  $19.7 \mu$  in diameter. Middleton (17) is of the opinion that the differences between this species and *P. debaryanum* are not sufficient to justify retaining a separate species, and would rather consider it a strain of *P. debaryanum*.

HOSTS.

This fungus has been isolated only once, and that from a succulent (Stapelia sp.) that was infected with a soft-rot.

### Pythium debaryanum Hesse. (= P. debaryanum var. pelargonii Braun.)

Hyphae are slender, 3 to 4 but sometimes up to  $6.5 \mu$  in thickness, and much branched.

Oogonia are smooth-walled, spherical when terminal, or somewhat oval when intercalar; vary in size from 18 to 33, commonly 21  $\mu$  in diameter.

*Oospores* are smooth and spherical, and range from 16 to 26, commonly 19  $\mu$  in diameter.

Antheridia are one to two to each oogonium; the antheridial branch commonly coils around the oogonium for as much as half its circumference; the antheridium usually arises from a different hypha from that of the oogonium, but both have been seen on the same.

Sporangia are very variable in size, ranging from 9 to 30.6, commonly 20 to 23  $\mu$  in diameter, usually terminal and spherical, but often intercalar and oval shaped; germinate by the production of 1 to 8 germ tubes.

Sporangia are produced in abundance, but only rarely were oogonia seen. Although a variety of culture solutions was tried, and at different temperatures, it was not possible to induce the formation of zoospores.

The temperatures for growth are optimum 25, maximum 28 and minimum 10°C. Both this fungus and the previous one listed under the name of *P. debaryanum* (= P. fabae), after having been kept for a few years in culture tubes, suddenly developed a growth rate of less than half of that which they used to have. They are thus both omitted from Table 1.

The above description agrees very closely with that of *P. debaryanum* var. *pelargonii*. Braun (5) states that oogonia were 17.4 to 21.9, average  $20.1 \mu$  in size, antheridia 1 to 4, often adhering to the oogonium along the entire length, sporangia 12.8 to 27.7, average  $20.1 \mu$  in size. Sporangia were also produced in abundance, and sexual organs were very scarce. He also states that his fungus is characterised by its minimum growth temperature of 6° C.



FIG. 11.—P. debaryanum (= P. debaryanum var. pelargonii.) (a) and (b) Oogonia and antheridia, (c) (d) and (e) sporangia.

Middleton (17) suggests that the name P. debaryanum var. pelargonii should not be retained as he regards this fungue as a minor variant of the somewhat variable species P. debaryanum.

### HOSTS.

This fungus was isolated once only, along with P. ultimum, from a wilting bean plant.

### TABLE 1.-TEMPERATURE RELATIONS OF THE PYTHIUMS.

Showing the average amount of growth in mm. made by cultures of the various fungi which had been allowed to grow for two days at room temperature, and then placed in the various controlled temperature chambers for a further period of two days.

D	Degrees Centigrade.												
FUNGUS AND HOST.	1	4	7	10	13	16	19	22	25	28	31	34	37
P. ultimum from papaw	0	2	5.5	17	31	42	51	59	67	<b>69</b> • 5	64	34	3
P. ultimum from aster	0	0	6.5	19.5	32	42	50	61	70	74	73	48	6
P. ultimum from mesembryanthemum	0	2	7.5	16.5	28	35	46	54	63.5	60	58.5	39.5	5
P. aphanidermatum from papaw	0	0	0	3	18	31	45.5	60	77	86	99	99	98
P. aphanidermatum from potato	. 0	0	0	1	7	25	35	45	62	67	82	91	90
P. irregulare from citrus	0	9	13	20	29	36	42.5	50	55	57	47.5	21	2
P. irregulare from papaw	0	0	6	9	15	24	29	39	33	31.5	26	15.5	1.5
P. vexans from papaw	0	0	0	0	10	18	24	32	36	37	37	30	3
P. vexans from statice	0	0	0	0	9	18	25	30	36	37	37	30.5	3
P. myriotylum from papaw	0	0	1	8	19	31.5	44	54	65 • 5	71	81	84	83
P. splendens from papaw	0	0	1	8	19.5	34·5	41	57	61	61 • 5	63	42	5
P. spinosum from papaw	0	4	11	19.5	29	<b>37</b> · 5	43.5	52.5	56	56	42.5	12	3
P. acanthicum from pea	0	0	0	2	11.5	19.5	$23 \cdot 5$	<b>3</b> 0	3 <mark>5</mark>	34.5	34.5	28.5	17
P. oligandrum from antirrhinum	0	0	0	4	15	25	32	42	51	<b>56</b> ·5	47.5	47	25
P. oligandrum from cabbage	0	Q	0	4	14.5	25	32	44	53	54	59	49	26

### Phytophthora infestans de Bary.

Hyphae in plant tissues are 3 to 5  $\mu$  in thickness, and much branched. The sporangiophores are from 200 to 500, or even up to 1000  $\mu$  in length, and 5 to 10  $\mu$  thick, and often have three or more side branches.

Sporangia are ovoid in shape, and range from 25 to  $45 \times 15$  to 26, with an average of  $30 \times 17.5 \mu$  in size. They readily become detached from the sporangiophores. Four to eight spores are produced in a sporangium; they are 8 to 10  $\mu$  in size, vigorously motile before rounding off and germinating.

Cultures from fresh material were made only with great difficulty. No sexual organs were seen by the writer. Tucker (23) gives the size, as reported by various workers, as cogonia ranging in average size from 27.9 to  $38 \mu$ , and cospores 23.6 to  $35 \mu$ ; antheridia are amphigynous.



FIG. 12.—Ph. infestans. Sporangiophore and suorangia.

Late Blight was first recorded by E. M. Doidge on potatoes in South Africa in 1913. Since then it has occurred sporadically in certain areas of the northern Transvaal, Natal and Cape, when wet seasons occur and the temperature is low. Under such conditions, infection may be severe, and heavy losses result. It was recorded on tomatoes (9) in Natal in 1922.

#### Phytophthora parasitica Dast.

Hyphae are commonly about 5  $\mu$  in diameter, much branched, and with numerous, short, thin side branches and projections; very much septate in old cultures; large, coiled, lobulate processes are sometimes formed.

Oogonia are spherical and terminal, range from 21.6 to 32  $\mu$ , average 24 to 27.7  $\mu$  in diameter in various strains.

Oospores are spherical, thick-walled and yellow to brown in colour in old cultures; range from 17.1 to  $29.5 \mu$ , average 21.5 to  $24.8 \mu$  in diameter in various strains.

Antheridia are invariably amphigynous, and commonly  $13.5 \mu$  in size.

Chlamydospores are spherical, terminal; very seldom intercalary,  $16 \cdot 2 \text{ to } 45 \mu$ , commonly 30  $\mu$  in diameter; thick-walled and yellow-brown in colour in old cultures where they are produced abundantly.

Sporangia are produced on the ordinary mycelium, not on special sporangiophores; terminal, seldom intercalary; normally ovate and prominently papillate; vary greatly in size from  $31 \times 27$  to  $64 \times 46$ , in water were commonly  $50 \times 38 \mu$ , but the average size

was much less when produced on solid media being about  $40 \times 30 \mu$ ; ratio of length to breadth 1.3 to 1.4; zoospores are produced in the sporangia and escape through the papilla, being 8 to 11  $\mu$  in size; germinate usually with one germ tube.

All the isolations mentioned below were grown in parallel series on various culture media. Variations were noted in the form of aerial mycelium produced, rate of growth, development of certain reproductive bodies readily in some and reluctantly in others, size of reproductive bodies, etc., but these variations were considered not of significant difference. Sporangia are produced abundantly, especially in water culture; chlamydospores on solid media and usually in old tubes. The sexual organs are often restricted to a few opaque white patches in which they are abundant. The optimum temperature for growth was 25°C. for the rhubarb strain, and 28°C. for the tomato strain, with a maximum of 37°C. and minimum of 13°C.



FIG. 13.—*Ph. parasitica.* (a) Thick-walled chlamydospore, (b) and (c) oogonia and amphigynous antheridia, (d) papillate sporangium, (e) sporangium and escaping zoospores.

Hosts.

(a) Abroad.—Ph. parasitica has a wide host range and world-wide distribution. Tucker (24) has listed the published records of its occurrence, and from this it is seen that the fungus has been found on most vegetable and field crops associated with the wilting of the plants, on the roots and trunk lesions or in rotting fruits of a wide range of fruit and other trees, and in connection with root and stem rots of a large variety of garden, ornamental and greenhouse plants.

(b) In South Africa.—Under the name of *Ph. parasitica* var. *rhei*, which Tucker (23) suggests should be eliminated in favour of *Ph. parasitica*, the fungus has been known for many years as the cause of crown-rot of rhubarb. It has recently been isolated from infected rhubarb plants from all areas where this crop is grown in the Cape and Transvaal. Inoculation experiments on rhubarb have shown that the fungus is a virulent parasite.

In 1934 a serious outbreak of brown-rot in tomato fruits occurred in widelyseparated localities in the eastern Transvaal, causing considerable damage. The responsible pathogen was identified as *Ph. parasitica* and the trouble was described by Wager (29). This fungus has been found as the cause of a "purple-rot" of a succulent plant (Cotyledon sp.) in which the thick, fleshy leaves successively turned purple and rotten, Wager (25). It was also identified as being the cause of the rotting of another succulent (Trichocaulon sp.)

It was isolated (A. M. Bottomley) from a Delphinium plant which wilted suddenly.

Hopkins (15) in Rhodesia reports this fungus on Antirrhinum majus, Clarkia elegans, Nicotiana tabacum, Cotyledon sp., Godetia sp., Rheum rhaponticum and Lilium phillippinense.

### Phytophthora citrophthora (Sm.) Leon.

Hyphae are much branched, with numerous irregular-shaped projections; commonly 5  $\mu$  in diameter; may become septate in old cultures; sterile in fruit, but may form sporangia readily in cultures and moist soil.

Oogonia are not known to occur for this fungus.

Sporangia are usually ovate but may sometimes be rounded or irregular in shape; usually one pronounced papilla, sometimes two or three; on oatmeal agar the size ranged from 22.5 to  $56.2 \times 20.2$  to  $40.5 \mu$  with an average of  $40.6 \times 31.3 \mu$ , giving a ratio of length to breadth of 1.3. On plain water agar the average was slightly greater, and the ratio was 1.55. Smith (21) gives the size as 30 to  $90 \times 20$  to  $60 \mu$  with an average of  $50 \times 35 \mu$ , giving a ratio of 1.43. The sporangia produce zoospores, usually about 20, which are discharged through the papilla. They are vigorously motile, become spherical when at rest and commonly  $9 \mu$  in diameter, and germinate by one germ tube.



FIG. 14.-Ph. citrophthora. Sporangia and zoospores.

The fungus grows well on culture media. It is difficult to isolate from trunk lesions unless very fresh infections are obtained, and the inoculum taken from the junction of discoloured and healthy tissue. The isolations obtained from time to time from infected fruits or bark lesions differed only slightly from one another. The fungus isolated from grapefruit trunk made optimum growth at 25 to 28, while that from orange brown-rot was at 22 to 25, and the maximum and minimum temperatures for growth were 34 and 10°C. respectively.

### Hosts.

(a) Abroad.—As a disease of citrus the fungus has a world-wide distribution. Tucker (24) records that it has been isolated from bark cankers and trunk lesions, and dying seedlings from walnut varieties, avocado, apricot, sweet cherry, almond, peach, pear, spruce and pine trees. It has also been recorded from watermelon, honey-dew melon, squash and pumpkin.

(b) South Africa.—Ph. citrophthora, as the brown-rot disease of citrus fruits, first appeared in epidemic form in the western, eastern, and northern Transvaal, and two localities in the Cape, in 1925, being induced by an exceptionally wet season, and caused severe losses, Doidge (10). Since then it has appeared sporadically in the citrus areas during wet periods, especially if weeds are left standing close to the trees, thus reducing ventilation and increasing the humidity. In severe storms, the spores may splash quite high up in the tree and produce infections.

In 1930 the fungus was isolated from a grape-fruit tree infected with gummosis and collar-rot, Wager (25). This trouble occurs frequently in grape-fruit and orange trees in areas where there is a tendency for water-logging of the soil to occur. Experiments in treatment of infected trees by injecting with methylene blue were carried out by Hector and Loest (14).

It has also been recorded by Hopkins (15) and Bates (2) on citrus in Rhodesia.

### Phytophthora cactorum (L. & C.) Schroet. ( $= Ph. \ citricola \ Sawada$ ).

Hyphae are 4 to 5  $\mu$  in thickness, much branched, with numerous, short, side branches or projections.

Obgonia are terminal and spherical, or may have a bulbous or tubular base; vary in size from 18 to 29  $\mu$ , with an average of 23  $\mu$  in diameter.

Oospores are spherical and practically fill the oogonium; they have a thick, yellow wall.

Antheridia are 6 to 8  $\mu$  in size, and paragynous; usually one to each oogonium, rarely two.

Chlamydospores are terminal and spherical and have thin hyaline walls; vary from 14 to 31  $\mu$ , commonly 26  $\mu$  in size.

Sporangia are ovoid; in some the papilla is inconspicuous, generally it is prominent; range in size from  $28 \cdot 8$  to  $48 \times 12 \cdot 8$  to  $25 \cdot 6 \mu$ , average  $32 \times 19 \mu$ ; are smaller when produced on solid media; may germinate directly with one or more germ tubes, or even forming other sporangia, or may produce zoospores which are actively motile and 8 to  $12 \mu$  in size.

The fungus grows well on solid media and oogonia are rapidly produced in abundance. Chlamydospores occur in old cultures. Sporangia are rare on solid media, but develop abundantly in liquid cultures.

The above description is of a fungus isolated from a wilted antirrhinum. *Ph.cactorum* was also isolated in South Africa by Mes (16) from the same host, and by Wijers (30) from carnation, verbena and sweet sultan. Mes gives oogonia ranging from 18 to 28 with an average of 23  $\mu$ , and sporangia of 26-88  $\times$  18-37, commonly 42-49  $\times$  25-33  $\mu$ ; Wijers states that the average diameter of oogonia of her various cultures ranged from 20.7 to  $25 \cdot 3 \mu$ , and gives sporangia considerably smaller than those of Mes. It is evident that there can be a variation of the size of the reproductive organs in different strains of the fungus. Tucker (23) lists a considerable range in the size of oogonia as recorded by various workers, from 24 to 36  $\mu$  in diameter, commonly 26 to 28  $\mu$ ; and of sporangia as ranging from 15 to 120  $\mu$  in length, commonly 50 to 60, and an average for 10 strains of  $30 \times 23 \mu$ .

A fungus referable to *Ph. citricola* was isolated by E. M. Doidge from a rotting grape-fruit. Its hyphae do not have so many short side branches or projections as that described above. Its oogonia are consistently some  $6 \mu$  larger, averaging  $29 \cdot 3 \mu$ , with a range of  $27 \cdot 7$  to  $32 \cdot 6 \mu$ . Chlamydospores range from 16 to 33, commonly  $28 \mu$ . Sporangia in liquid culture were very irregular in shape, elongated, and prominently papillate, and ranged in size from  $42 \cdot 9$ - $72 \cdot 6 \times 19 \cdot 8 - 36 \mu$ , with an average of  $58 \cdot 4 \times 30 \cdot 7 \mu$ . On solid media, sporangia were smaller, ranging from  $26 - 49 \cdot 5 \times 18 - 36$ , with an average of  $39 \times 28 \mu$ . When grown in parallel series with *Ph. cactorum* from antirrhinum, both show approximately the same rate of growth, and both develop sexual organs rapidly and abundantly. The latter does not produce sporangia so readily as the former. Ashby in correspondence with the writer suggests that, although it does not fully agree with Sawada's isolation, it is a strain of *Ph. citricola*. Tucker (23) however, is of opinion that there are no significant differences between *Ph. citricola* and *Ph. cactorum*, so that the former name should be dropped. This strain from grape-fruit is thus included as *Ph. cactorum*.



F10. 15.—Ph. cactorum (= Ph. citricola.) (a) and (b) Sporangia from antirrhinum strain, (c) ditto from grape-fruit strain, (d) and (e) oogonia and paragynous antheridium from antirrhinum strain, and (f) ditto from grape-fruit strain.

Both cultures were grown in a series of controlled temperature incubators, and the antirrhinum strain gave minimum 4°, optimum 22°, maximum 34°, while the grapefruit fungus gave minimum 7°, optimum 19°, and maximum between 31° and 34°, which agrees with Sawada's findings of maximum of 33°C.

#### HOSTS.

(a) Abroad.--From Tucker's (24) list of records of this fungus it is seen that it has a large range of host plants. It has been obtained from stem rots of a large variety of garden and ornamental plants, from vegetable roots and fruits, and from numerous rotting succulents. It has also been obtained frequently from roots and trunk cankers of a large variety of trees, and from wilting seedlings of a number of forest trees. Sawada (20) records his strain (= Ph. citricola) on fruits of Citrus sinensis var. Sekkar and Citrus tanka in Formosa.

(b) South Africa.—As mentioned above, Ph. cactorum was isolated by the writer and Mes from wilting antirrhinum plants, and by Wijers from carnation, verbena and sweet sultan. Doidge isolated a strain of Ph. cactorum (= Ph. citricola) from a grapefruit affected with a kind of brown-rot from the Cape, and reported that the fungus reproduced the rot when inoculated into grapefruit.

### Phytophthora cinnamomi Rands.

Hyphae are up to 10  $\mu$ , commonly 6.5  $\mu$  in thickness, and much branched; often irregular-shaped protrusions are formed on the hyphae in masses; older hyphae may become brown in colour and septate; the aerial mycelium, especially in older cultures, becomes very tough and wiry.

*Oogonia* are terminal and spherical, each with a broad, funnel-shaped base within the antheridium, varying in size from 30 to 52, being commonly 42  $\mu$  in diameter, (average size of 50 was 41.4  $\mu$ ); are a brilliant brown in colour.

Oospores are spherical and thick-walled, and fill the oogonia completely.

Antheridia are amphigynous, one to each oogonium, somewhat spherical in shape being about 15  $\mu$  in size, or may be oblong and 24  $\times$  12  $\mu$  in size; may be transparent or opaque, and also stained the same brilliant brown colour as the oogonium.

Chlamydospores are spherical, thin-walled, may be borne singly, more usually in groups or bunches of 3 to 12; they range from 26 to 43, commonly 32  $\mu$  in diameter.

Sporangia are borne on very thin hyphae; are oval or elongate in shape, and have no papilla; range in size from 39 to 66 by 26 to 40, commonly 50 by  $32 \mu$ ; may germinate by one or more germ tubes, and may proliferate, the contents of one sporangium passing up a tube to form another; zoospores may also be produced.

The fungus is characterised by its peculiar irregular or knobby hyphae, the fact that chlamydospores are produced abundantly, usually in grape-like clusters, and by the complete absence of oogonia in ordinary cultures. The fungus was grown for many years on all varieties of culture media without any oogonia ever being produced. They were finally obtained in large numbers in a few oatmeal agar and watermelon-seed agar tubes that were left standing during autumn on a shelf in the laboratory. The oogonia were numerous in some areas on the cultures, especially at the top end of the tube, both in the aerial mycelium and in the agar where it was about  $\frac{1}{8}$ -inch thick.

Sporangia were obtained when portions of a culture were placed either in Petri's solution, or soil-extract solution.

The fungus has minimum 10, optimum 25, and maximum 34°C. temperatures for growth.



Fig. 16.—*Ph. cinnamomi.* (a) Sporangia, (b) proliferating sporangium, (c) showing the knobby nature of the mycelium, (d) a bunch of chlamydospores, (e), (f) and (g) cogonia and amphigynous antheridia.

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Rands (18) in the original description of this fungus gives the chlamydospores as being somewhat larger than those described above, namely 26 to 60, commonly 31 to 50, average 41  $\mu$  in diameter, but sporangia more or less the same as above, being 38 to 84  $\times$  27 to 39, average 57  $\times$  33  $\mu$ . He was unable to find oogonia. Ashby (1) obtained oogonia on an old culture of commeal agar, average 32 $\mu$  in diameter. Tucker (23) induced the development of oogonia, 28.1  $\mu$  in diameter, when mycelium was placed in M/100 potassium nitrate.

This fungus was mentioned by Wager (25) under the name of *Ph. cambivora* as isolated from rotting roots of the avocado. More recently Ashby is of opinion that the fungus goes better into *Ph. cinnamomi* than *Ph. cambivora*, and Tucker confirms this.

### Hosts.

(a) Abroad.—From Tucker's list (24), *Ph. cinnamomi* is noted to have been reported from pineapple stems and leaves, erica, rhododendron, and from the bark cankers and rotting roots of numerous species of chestnut, walnut, cinnamon, and on the blackened feeding roots of avocado.

(b) South Africa.—Ph. cinnamomi has been isolated once only (E. M. Doidge) from decaying avocado roots.\*

#### Phytophthora cryptogea Pethyb. and Laff.

Hyphae are branched, commonly 5  $\mu$  thick; may develop circular or irregular-shaped vesicles, often in groups.

Organia are pherical and terminal, with a narrow, funnel-shaped base within the antheridium; vary in size from 24 to 54  $\mu$  in diameter, commonly 40 (average of 50 being  $38 \cdot 4 \mu$ ); they are light-brown in colour.

Obspores are spherical and thick-walled, and some 3 to 4  $\mu$  less in diameter than the obsporia.

Antheridia are amphigynous, one to each oogonium, somewhat spherical or oblong in shape, commonly 12 to 15  $\mu$  in size.

Sporangia are usually oval in shape, may be irregular or elongate, and are non-papillate; they range from 22.8 to 68.5 by 16.3 to 35.8, commonly 35 by 23  $\mu$  in size; the sporangia may germinate directly with the production of a germ tube, or the contents of one may pass out to form another, or a sporangiophore may grow up through the old sporangium; zoospores may be produced, they are large, 13 to 15  $\mu$  in size, and from 3 to 15 are produced in each; they are vigorously motile at first, then round off to about 12  $\mu$  and germinate.

The fungus makes profuse mycelial growth, filling the aerial portion of the Petri dish or tube, and is characterised by the absence of all types of reproductive organs in ordinary cultures.

Sporangia were formed in abundance after six days in Petri's solution, or in non-sterile soil extract. Tucker (23) states that his culture of this fungus produced sporangia 25 to 49 by 16 to 29, average 36.7 by  $21.9 \mu$  in size.

Oogonia and antheridia were at last found in a tube of oatmeal agar which had been subjected to varying temperatures, such as a few months in an ice-box, then room temperature, the ice-box again, and finally three months on a shelf in the laboratory. In the

<sup>\*</sup> Foot note.—Since going to press, *Ph.cinnamomi* has been found by the writer on avocado roots both from the western Transvaal and Natal, where the trees were suffering from die-back or decline. Experiments have shown that where excessive water was present, the fungus was rapidly able to kill off the plants-

original description of this fungus, oogonia averaging 30  $\mu$  in diameter were found in an old culture of oatmeal agar. Tucker obtained oogonia averaging  $25 \cdot 8 \mu$  in diameter in an old oatmeal culture subjected to winter temperatures.

The fungus makes good growth at 4°C., not below, optimum 22, and good growth up to 34, but none at 37° C.



Fig. 17.—*Ph. cryptogea.* (a) Sporangia, (b) irregular-shaped processes occurring on the hyphae, (c), (d) and (e) cogonia and amphigynous antheridia.

HOSTS.

(a) Abroad.—According to Tucker's list (24), *Ph. crytogea* is a fairly common parasite in decayed or discoloured roots and stems of garden and ornamental flowers, and of a few vegetables, namely, aster, cineraria, wallflower, lupine, iceland poppy, gilia, antirrhinum, petunia, gladiolus, tulip, turnip, strawberry, tomato and celery.

(b) South Africa.—This fungus has been obtained once only (A. M. Bottomley) from a wilting godetia plant.

Phytophthora syringae Kleb (= Ph. hibernalis Carne).

Hyphae are much branched, commonly  $4.5 \mu$  in thickness or less, and septate in old cultures.

*Oogonia* are terminal and spherical; commonly  $35 \cdot 2$ , ranging from 26 to 40  $\mu$  in diameter.

Oospores are spherical and almost fill the oogonium; are slightly tinged with a yellow or brown colour.

Antheridia are both amphigynous and paragynous, although the former type predominates.



FIC. 18.—Ph. syringae (= Ph. hibernalis) (a) Paragynous and (b) amphigynous antheridium and oogonium, (c) and (d) sporangia with persistent pedicels.

Sporangia are formed on very slender branches of the mycelium; they are elliptical and vary from 26 to 57 by 15 to 25, commonly 37.5 by  $20 \mu$  in size. The sporangium has a broad and pronounced papilla; the sporangium readily becomes detached from the mycelium, but retains a portion of the pedicel which may be from 20 to  $50\mu$  in length, more commonly about the same length as the sporangium; the sporangium may germinate with the production of a germ tube, or zoospores may be formed; these are approximately  $10 \mu$ in length, and after moving vigorously for a time come to rest and germinate.

The fungus grows very slowly on culture media; oogonia are formed readily on most agars, and sporangia were produced on Petri's agar. The optimum temperature for growth was 13 to 16, minimum 7 and maximum 19°C.

The above description agrees fairly closely with that of *Ph. hibernalis* by Carne (7), except that the oogonia are on the average somewhat smaller. Carne's figures are sporangia average  $34 \cdot 6$  by  $16 \cdot 1$ , range of 17 to 56 by 10 to  $21 \mu$ , and oogonia average  $40 \cdot 8$ , ranging from  $22 \cdot 4$  to  $56 \mu$  in diameter. Bensaude (3) gives the following figures : sporangia 41 by 19, range of  $25 \cdot 2$  to 54 by  $12 \cdot 6$  to 27 (smaller when grown on solid media), oogonia  $35 \cdot 17$ , range of  $19 \cdot 8$  to  $44 \mu$  in diameter; he also states that the optimum temperature is 18 to 20, minimum 12, and maximum  $24^{\circ}$ C.

Tucker (23) includes *Ph. hibernalis* in the species *Ph. syringae*, but the former name appears to be the one commonly used by citrus pathologists.

### Hosts.

(a) Abroad.—Ph. syringae has been isolated from common lilac (Syringa vulgaris) and and pear and apple fruits in Europe; under the name of Ph. hibernalis it has been recorded as a serious fruit-rot, leaf-blight and twig die-back of citrus in Australia, Portugal and California, Tucker (24).

(b) South Africa.—This fungues has been isolated only once (Doidge), from oranges showing brown-rot symptoms from the Fish River Valley in the eastern Cape.

#### TABLE 2.-TEMPERATURE RELATIONS OF THE PHYTOPHTHORAS.

Showing the average amount of growth in mm. made by cultures of the various fungi which had been allowed to grow for four days at room temperature and then placed in the various controlled temperature chambers for a further period of four days.

Furgue AND Host	Degrees Centigrade.												
FUNGUS AND HUST.	1	4	7	10	13	16	19	22	25	28	31	34	37
Ph. parasitica from rhubarb crown-rot	0	0	0	0	5.5	23.5	31.5	40	44	43.5	42	28	6
Ph. parasitica from tomato fruit brown-rot	0	0	0	0	7	13	24.5	26	36	37.5	34	<b>29·5</b>	5
Ph. citrophthora from grapefruit trunk gummosis	0	0	0	5	13	20	22	25.5	32	31·5	27.5	2	0
Ph. citrophthora from orange fruit brown- rot	. 0	0	0	5.5	13.5	19	27	29	28.5	25	20	2	0
Ph. cactorum from antirrhinum wilt	0	2.5	5.5	10	16	23	35	<b>39</b> .5	36.5	35	15	3.5	0
Ph. cactorum from orange fruit rot	0	0	4	10	15	22	27.5	26.5	24	23.5	5	1.5	0
Ph. cinnamomi from avocado root rot	0	0	0	2.5	11	$22 \cdot 5$	30.5	38	41	37	$22 \cdot 5$	2	0
Ph. cryptogea from Godetia wilt	0	3	8.5	13.5	17	23	<b>3</b> 0 · 5	39	36.5	35.5	32·5	28.5	1
Ph. syringae from grapefruit brown rot	0	0	4	8	11	11	1	0	0	0	0	0	0

#### ANNOTATED HOST INDEX.

Aster (Callistephus chinensis Nees.) WILT. P. ultimum. Avocado (Persea americana Mill.) DECAYED ROOTS. Ph. cinnamomi. Bean (Phaseolus vulgaris L.) WILT. P. ultimum. P. debaryanum (= P. debaryanum var. pelargonii.) Brachen (Pteridium aquilenum) WILT. P. aphanidermatum. Brinjal (Solanum melongena L. var. esculentum Nees.) FRUIT ROT. P. aphanidermatum. Cabbage (Brassica oleracea L.) WILT. P. olijandrum. HEART ROT. P. ultimum. Carnation (Dianthus caryophyllus L.) WILT. Ph. cactorum. Chou-Chou (Sechium edule Sw.) FRUIT ROT. P. aphanidermatum. Dahlia (D. variabilis Des.) DAMPING-OFF. P. acanthicum. P. ultimum. Delphinium (D. sp.) WILT. P. ultimum. Ph. parasitica. Gilia (G. rubra Heil). WILT. P. ultimum. Godetia (G. sl.) WILT. Ph. cryptogea. Grapefruit (Citrus grandis Os.) FRUIT ROT. Ph. cactorum, (= Ph. citricola.) TRUNK GUMMOSIS, Ph. citrophthora, Iceland Poppy (Papaver nudicaule L.) WILT. P. ultimum. DAMPING-OFF. P. ultimum. Marrow (Cucurbita peppo L.) WILT. P. oligandrum. Nasturtium (Tropaeolum majus L.) WILT. P. ultimum. Orange (Citrus sinensis Os.) FRUIT ROT. P. irregulare. Ph. citrophthora. Ph. syringae (= Ph. hibernalis). TRUNK GUMMOSIS. Ph. citrophthora. WITHIN NAVEL-END OF YOUNG FRUIT. P. ultimum. Papaw (Carica papaya L.) FOOT ROT. P. ultimum. P. aphanidermatum. P. splendens. P. myriotylum. P. vexans. P. irregulare. P. spinosum. Pea (Pisum sativum L.) WILT. P. ultimum. P. acanthicum. Peanut (Arachis hypogea L.) WILT. P. ultimum. Pine (Pinus sp.) DAMPING-OFF. P. ultimum. Pink (Dianthus plumarius). WILT. P. ultimum. Potato (Solanum tuberosum L.) LEAF BLIGHT AND TUBER ROT. Ph. infestans. TUBER SOFT-ROT OR "LEAK". P. aphanidermatum. Rhubarb (Rheum rhaponticum L.) CROWN ROT. Ph. parasitica. P. ultimum. Shirley Poppy (Papaver Rhoeas L.) WILT. P. oligandrum. Snapdragon (Antirrhinum majus). WILT. Ph. cactorum. P. oligandrum. Squash (Cucurbita pepo). WILT. P. aphanidermatum. Statice (Armeria sp.) WILT. P. vexans. Succulents-producing rots of Aloe variegata. P. ultimum. Cotyledon sp. Ph. parasitica. Delosperma sp. P. ultimum. Dinteranthus microspermus. P. ultimum. Duvalia parvifolia. P. ultimum. Fenesturia aurantiaco. P. ultimum. Mesembryanthemum sp. P. ultimum. Stapelia sp. P. ultimum. P. debaryanum (= P. fabae). Tavaresia sp. P. ultimum. Trichocaulon sp. Ph. parasitica. Sweet Pea (Lathyrus odoratus L.) WILT. P. ultimum.

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Sweet Potato (Ipomoca batatas Poir.) TUBER ROT. P. ultimum. Sweet Sultan (Centaurea moschata). WILT. Ph. cactorum. Tobacco (Nicotiana tabacum L.) WILT. P. ultimum.

P. aphanidermatum. DAMPING-OFF. P. aphanidermatum.

Tomato (Lycopersicum esculentum Mill.) LEAF BLIGHT. Ph. infestans. WILT. P. aphanidermatum. P. ultimum. WILTING TRANSPLANTS. P. aphanidermatum. FRUIT ROT. Ph. parasitica. P. aphanidermatum.

Verbena (V. hybrida Voss.) WILT. Ph. cactorum.

Witchweed (Striga lutea.) WILT. P. ultimum.

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