

## KEY TO THE SPECIES OF *PHYTOPHTHORA* DE BARY

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**D**ESPITE Fitzpatrick's statement (1930, p. 204) concerning *Phytophthora* that 'the identification of an unknown form is often difficult if not actually impossible,' there has been a demand for some time that a bold attempt should be made to formulate a key to the known species. It is only when such a key is available that it is possible for workers to assess more precisely the similarities and differences between closely related taxa.

This key is put forward very much as a first effort, to be tested and moulded by use. It is only thus that a more 'perfect' key will eventually emerge. It will undoubtedly be found wanting, but the idea of publishing it is to encourage workers to use it on such isolates as they find, to look for species that have been inadequately described or have not been seen since the first descriptions, and to compare 'species' that are close together and might possibly be merged. I have decided to keep, for the present, several names for taxa which may turn out to be not very good species, in order that they may be thus tested. The worker is warned that when an identification is finally tracked down to a name, this is something which has been described as a species (or variety), but by present-day standards may not now be worthy of that rank, but type or authentic material should be examined before any decision is made. Reproductions of the diagnoses and figures from the original publications will be found in a previous paper (Waterhouse, 1956). There is still much information needed concerning many of the species, in particular chromosome numbers and mating type relationships, and it would be wise to defer further name changes until more is known.

A few of the species (mainly Sawada's) are known only from the original descriptions—most of these have been omitted because the descriptions do not give enough data to find them a place in the key. These inadequately described species are placed in a list at the end (p. 17). Also listed are many epithets rejected on nomenclatural grounds (invalidly published or illegitimate) and those regarded as unnecessary.

With the exception of one or two species with very characteristic features, most can be identified only if both sporangia and sex organs have been obtained. It is necessary at the outset to induce sporangial production and zoospore emission in order to make certain that a species of *Phytophthora* (and not *Pythium*) is being dealt with. This is usually fairly easily done by transferring small (a few sq. mm.) pieces of infected tissue or agar culture to autoclaved Petri solution or water (pond:distilled, 1:2). For sex organs, if



these are not present in the original tissues or agar cultures (oat, corn meal, etc.), it may be necessary to grow the isolate with an oospore-inducing strain of the same or another species. Where this is necessary an indication is given in the key.

Cultures were always on oat or corn meal agar. Permanent preparations were always made with lacto-phenol cotton blue or lacto-phenol alone if it was desirable to see the colour of chlamydospores or oogonia. Measurements were always taken from these preparations because some parts, particularly the apical thickening of the sporangium and thickened walls of other spores, would swell slightly and this emphasized differences difficult to measure in fresh material. Sporangia were measured in fresh cultures in the first flush of growth wherever possible, since continued culturing often causes them to become distorted and dwarfed or brings about a thickening of the apex as a prelude to germination. For terminology and illustrations of organs see Blackwell (1949).

Dual cultures to secure oospore production were also on oat or corn meal agar. Their induction by the growing together of two different isolates does not mean that the isolates must be of the same species or even of nearly related ones. Merging of taxa on these grounds alone is not acceptable.

### KEY

For convenience of identification the taxa are segregated into six groups, but the grouping is not necessarily intended to imply that this is a 'natural' classification.

- I Apex of sporangium markedly papillate; hyaline apical thickening hemispherical or at least  $4\mu$  deep, exit pore narrow ( $7\mu$  or less). Sporangia abundant on solid substrata, usually deciduous, not proliferating internally. Oospores always formed in the host and in culture. Antheridia all or nearly all paragynous.
- II Sporangium as in I. Oospores often not formed in single-strain culture. Antheridia all amphigynous.
- III Apex of sporangium less protuberant than in I and II, sometimes scarcely papillate; hyaline thickening evident but less than hemispherical (up to  $3.5\mu$ ), exit pore narrow ( $7\mu$  or less). Sporangia deciduous or not, not proliferating internally. Oospores always present in the host or in culture. Antheridia predominantly or all paragynous.
- IV Apex of sporangium as in III. Sporangia usually deciduous, not proliferating internally. Oospores not always present in single-strain culture. Antheridia predominantly or all amphigynous.
- V Apex not protruding beyond the general contour of the sporangium (i.e. non-papillate); very thin apical thickening, scarcely detectable without staining, exit pore broad,  $12\mu$  or more. Sporangia non-deciduous, rarely or never produced on agar media without placing in water, proliferating internally. Oospores always produced in the host and/or in agar culture. All, or the majority, of the antheridia paragynous.
- VI Sporangium as in V. Oospores not always produced in single-strain culture. Antheridia all or mostly amphigynous.

### I

Only *P. cactorum* (syn. *fagi*, *paeoniae*) falls in this group.



## II

1. Sporangia mostly or often much longer than broad, l:b ratio c. 1.5:1 or more; not developing in a regular sympodium, the branching of the sporangiophore being rather irregular . . . . . 2
1. Sporangia generally broadly ovoid or almost spherical, l:b ratio usually 1.2:1 but may be up to 1.4:1; usually develop in a regular sympodium . . . . . 5
  2. Growth on agar at 35° C. slight or nil . . . . . 3
  2. Several mm. growth at 35° in 24 hr.; sporangia often very elongated (over 100 $\mu$ ) . . . . . *capsici* (syn. *hydrophila*)
3. Sex organs abundant in single-strain culture; oogonium 28 $\mu$  diam., tapering markedly to the stalk; antheridial cell small and spherical (9  $\times$  9 $\mu$ ); chlamydospores none . . . . . *heveae*
3. Sex organs not of this type or infrequent or absent . . . . . 4
  4. Sporangia up to over 90 $\mu$  long, rounded at the base, deciduous, with a narrow pedicel up to 6 $\mu$  long; chlamydospores abundant; sex organs not formed in single-strain culture . . . . . *palmivora*
  4. Sporangia (max. length 80 $\mu$ ), tapering to the base, not deciduous, sporangiophore widening below the sporangium to 8–10 $\mu$ ; no chlamydospores; sex organs usually formed but not abundant . . . . . *mexicana*
  4. Sporangia rarely over 70 $\mu$ , very irregular in shape but usually rounded at the base; sporangiophore not widening below the sporangium; chlamydospores sparse or nil; sex organs sometimes frequent in culture, sometimes absent . . . . . *meadii*
5. Growth on agar at 35° slight or nil . . . . . 6
5. Growth 3–15 mm. in 24 hr. . . . . 7
  6. Sex organs develop promptly and abundantly in single-strain culture . . . . . *boehmeriae*
  6. No sex organs in single-strain culture nor in dual cultures with *palmivora* or *nicotianae*; colonies on c.m.a. with a fine radiate growth . . . . . *citrophthora arecae*
  6. Sex organs abundant in dual cultures . . . . . *nicotianae* var. *nicotianae* (syn. *allii*, *melongenae*, *parasitica* var. *rhei*, *terrestris*)
7. Not this combination of characters . . . . . *nicotianae* var. *parasitica* (syn. *formosana*, *lycopersici*, ? *ricini*, *parasitica*, *parasitica* var. *piperina*, ? *tabaci*)

## III

1. On aerial parts of Gramineae . . . . . *macrospora* (and other species that have been put in *Sclerophthora*)
1. On aerial parts of Cyperaceae . . . . . 5
1. Not so . . . . . 2
  2. Grows well on agar at 25–27° C. . . . . 3
  2. Growth slow (5–6 mm. in 24 hr.), little, or nil . . . . . 4
3. Antheridial branches coiled and contorted, up to 50 $\mu$  long . . . . . *inflata*
3. Antheridial branches not coiled or contorted . . . . . *citricola* (syn. *cactorum* var. *applanata*, *pini*, *pini* var. *antirrhini*)
  4. Sporangia in regular sympodia and of a regular, broadly ovoid shape, av. 55  $\times$  35 $\mu$ ; antheridium small (c. 10 $\mu$  diam., rarely more), paragynous, very rarely amphigynous . . . . . *syringae*
  4. Sporangia in aerated soil extract very elongated (up to 165 $\mu$ ) often in series; antheridia always paragynous . . . . . *primulae*
  4. Sporangia not in regular sympodia, often of irregular shape, av. 40  $\times$  30 $\mu$ ; antheridia av. 12.5 (max. 19)  $\mu$  long, often amphigynous . . . . . *porri*
5. Oogonium wall reticulate . . . . . *cyperi-bulbosi*
5. Oogonium wall smooth . . . . . 6
  6. Sporangium nearly twice as long as broad (52  $\times$  30 $\mu$ ); oogonium 25–50 $\mu$  diam. . . . . *cyperi* (syn. *cyperi-rotundati*, *cyperi-iriae*)
  6. Sporangium broader (40–64  $\times$  26–52 $\mu$ ); oogonium 40–52 $\mu$  diam. . . . . *leporinae*



## IV

On Solanaceae . . . . .	<i>infestans</i> f. sp. <i>infestans</i>
On <i>Thalictrum</i> . . . . .	<i>infestans</i> f. sp. <i>thalictri</i>
On <i>Phaseolus</i> . . . . .	<i>phaseoli</i>
On <i>Citrus</i> and related genera . . . . .	<i>hibernalis</i>
On <i>Ilex</i> . . . . .	<i>ilicis</i>
On <i>Colocasia</i> and related genera . . . . .	<i>colocasiae</i>

## V

1. Oogonial wall irregularly thickened, the outer surface verrucose . . . . . *verrucosa*
1. Oogonial wall smooth . . . . . 2
  2. Oogonia very large, 67–82 $\mu$  diam. . . . . *quininea*
  2. Oogonia less than 60 $\mu$  diam. . . . . 3
3. Sporangia large (av. 60  $\times$  38 $\mu$ ), many up to 90 $\mu$  long; oogonia av. about 40 $\mu$  . . . *fragariae*
3. Sporangia av. less than 55  $\times$  35 $\mu$ , rarely exceeding 60 $\mu$  long (*megasperma*) . . . 4
  4. Oogonia av. over 45 $\mu$  diam. often up to 60 $\mu$  . . . *megasperma* var. *megasperma*
  4. Oogonia av. under 40 $\mu$ , diam., rarely over 45 $\mu$  . . . *megasperma* var. *sojae*  
(syn. *sojae* and *miyabeana*, an epithet which  
must be used if this taxon is considered  
to be a species distinct from *megasperma*)

## VI

1. Sporangia average 55 $\mu$  or more long . . . . . 2
1. Sporangia average 34–45–50 $\mu$  long . . . . . 5
  2. Young mycelium on malt agar coralloid, older mycelium on most media  
bearing abundant botryose usually spherical swellings (av. 41 $\mu$  diam.); oogonia  
and oospores, formed in dual culture with *P. cryptogea*, with smooth walls  
*cinnamomi* . . . . . 3
  2. Young mycelium fairly uniform, hyphal swellings if present not botryose . . . 3
3. Sporangia broad (av. 47 $\mu$ ); oogonia rarely formed in single culture but produced  
in dual cultures with *P. parasitica*; wall has rounded protuberances (warts) . . . *cambivora*
3. Sporangia much narrower, av. 30–40 $\mu$  broad . . . . . 4
  4. Sex organs abundant . . . . . *erythroseptica* var. *pisi*
  4. No sex organs . . . . . *oryzae*
5. Abundant yellow to brown chlamydospores . . . . . *lateralis*
5. No true chlamydospores, only hyphal swellings . . . . . 6
  6. Sex organs absent or rare and late . . . . . 7
  6. Sex organs develop promptly and abundantly in single-strain culture . . . 8
7. Sporangia up to 55  $\times$  30 $\mu$ ; sex organs abundant in dual cultures with *P. cinnamomi*  
or with an 'opposite' strain of *cryptogea* . . . . . *cryptogea*
7. Sporangia up to 70  $\times$  32 $\mu$ ; no sex organs with *cinnamomi* . . . . . 9 or *gonapodyides*
  8. Antheridia large, 18(–23)  $\times$  14–15 $\mu$ , often extended into a short hyphal  
outgrowth . . . . . *richardiae*
  8. Antheridia large, 16(–25–30)  $\times$  15–18 $\mu$ , but without hyphal extensions . . . *vignae*
  8. Antheridia smaller (14–16  $\times$  13 $\mu$ ) . . . . . 9
9. Growth at 34–36° 5 mm. or more in 24 hr.; sex organs often absent, but abundant  
in dual culture with an 'opposite' strain . . . . . *drechsleri*
9. No growth at 34°; sex organs abundant in culture . . . *erythroseptica* var. *erythroseptica*  
(syn. *himalayensis*)

## GENERIC DESCRIPTION

*Mycelium* colourless, aerial hyphae white in the mass; in the host inter- or intracellular, often with haustoria.

*Hyphae* 3 $\mu$  (when young) to 8 $\mu$  (when mature) wide; in some species or under certain conditions irregularly swollen up to 12 $\mu$ , or undulate, or even



gnarled. Sometimes broadening into swellings which may be of a characteristic shape in particular species; branch hyphae grow out initially at right angles to the parent hypha and are often swollen for a short distance, thus giving the appearance of a constriction at the point of origin. Hyphal wall rarely up to  $0.5\mu$  thick, staining various shades of violet with a cellulose reagent (Iodine + 72% sulphuric acid); transverse septa formed only to delimit chlamydospores, sporangia, antheridia, and oogonia and empty parts of the hyphae; plane or curved, often with a central plug.

*Hyphal swellings* usually intercalary but occasionally terminal, not delimited by transverse septa; spherical (single or in clusters), ellipsoidal (singly or at regular short or long intervals along the hypha), or when at the origin of branch hyphae appearing angular (singly or in clusters). Wall and contents not appearing different from those of the hyphae.

*Chlamydospores* usually intercalary but sometimes terminal, always completely delimited by a smooth wall becoming up to  $2\mu$  thick by the deposition of an inner layer of cellulosic material; spherical or more rarely ellipsoidal, hyaline at first but often becoming yellowish or brownish on certain media; contents dense, sometimes with a large central globule.

*Sporangiophores* usually no different from other hyphae (except in breadth and for the presence of occasional swellings) apart from the few species that have a branched sporangiophore reminiscent of *Peronospora* but with nodal swellings; proliferating by branching from below the sporangium or from within an empty one; branching sympodial or irregular.

*Sporangia* colourless, usually terminal but sometimes intercalary, especially in species with a papillate sporangium; single on long hyphae, in sympodia (close or lax), or within (or just beyond) a previously evacuated sporangium; broadly or elongated ellipsoid (to almost fusiform), ovoid, obpyriform, or limoniform (when shed), or occasionally spherical; apex differentiated by an internal hyaline thickening of the inner wall of a depth (constant for the species) up to  $6\mu$  and protruding, in some species, to form a more or less well-defined papilla; wall smooth, unthickened or with an internal deposition of cellulosic substance up to  $2\mu$  thick. The septum delimiting the sporangium may be confluent with the base or a few  $\mu$  down the sporangiophore. Non-caducous or shed with a portion of hypha (pedicel)  $2-55\mu$  long. Germination by (1) zoospores matured within the sporangium and emerging individually on the dissolution or inflation of the apex and either free at once or held momentarily in an evanescent vesicle; or (2) a germ tube or tubes.

*Zoospores* hyaline, ovoid to phaseoliform, tapering slightly to the anterior end, but able to change in shape, biflagellate with a shorter anteriorly directed, tinsel-type flagellum and a longer posteriorly directed whiplash-type flagellum. Usually uninucleate. On ceasing to be motile, forming a spherical cyst which may exhibit repetitional emergence but not diplanetism.

*Oogonium* usually terminal on a lateral hypha, occasionally intercalary, spherical or tapering to the stalk, delimited by a thick septum (sometimes with a plug); wall thin and hyaline at first, becoming thicker and often coloured (yellow to brown) with age, smooth in most species, tuberculate in a few, and reticulate in one.



*Antheridium* usually single, monoclinal or declinal on a very short to very long lateral hypha, spherical, oval, clavate or short cylindrical, often angular, sometimes with a short terminal hyphal prolongation, amphigynous or paragynous or both; if paragynous, applied to the oogonium close to the stalk, occasionally between the stalk and the equatorial region, rarely elsewhere.

*Oospore* characteristically single, more or less filling the oogonium, spherical, smooth, hyaline or sometimes faintly yellow, outer wall very thin, inner wall 0.5 to 6  $\mu$  thick, when mature enclosing fine protoplasm with a large central globule.

### DESCRIPTIONS OF THE TAXA INCLUDED IN THE KEY

These notes are not intended to be formal descriptions but to give additional data that might help to confirm the identification secured from the key.

**arecae** (Type or authentic cultures not seen; Uppal's Tyagli and Nilekani strains examined)

*Sporangiophores* about 2.5  $\mu$  wide, irregularly sympodial; *sporangia* broadly ellipsoid or obturbinate to nearly spherical, mostly in the range 40–50  $\times$  35–40 (max. 70  $\times$  48)  $\mu$ , ratio 1.1–1.4:1, deciduous, pedicel 1–6  $\mu$ , papilla and apical thickening hemispherical or slightly less; *chlamydospores* variable in numbers, sometimes absent or rare, never abundant, 35–40 (max. 60)  $\mu$  diam., wall 1  $\mu$  thick; *sex organs* rare in single culture, abundant in paired culture with an opposite strain, with *P. meadii*, 'cacao' strains of *P. palmivora* or certain strains of *P. nicotianae* and var. *parasitica*; *oogonia* 30  $\mu$  diam., rarely over 35 (max. 40)  $\mu$ , wall smooth; *oospore* nearly filling the oogonium, 28  $\mu$  diam., wall 3  $\mu$  thick; *antheridia* always amphigynous, frequently broader than long, 14  $\times$  15  $\mu$ .

*Culture* fairly fluffy, slightly radiate.

*Cardinal temps.*: min. 10–12°; opt. 27–30°; max. c. 35°.

**boehmeriae** (Type culture examined)

*Sporangiophores* 2.5  $\mu$  wide, sympodial (close or lax); *sporangia* broadly ellipsoid to nearly spherical or obturbinate to obpyriform, mostly 50  $\times$  35–40 (max. 70  $\times$  45)  $\mu$ , ratio 1.25–1.4:1, deciduous, pedicel up to 3  $\mu$ , papilla and apical thickening hemispherical or deeper; *chlamydospores* 40 (max. 50)  $\mu$  diam., wall 2  $\mu$  thick, variable in numbers; *sex organs* abundant in the host and in single-strain culture; *oogonia* 27 (max. 40)  $\mu$  diam., wall smooth, colourless at first, slightly yellowish later; *oospore* 24  $\mu$ , nearly filling the oogonium, wall up to 2  $\mu$  thick; *antheridia* always amphigynous, 14 (up to 21)  $\times$  13  $\mu$ , often with a residual oil globule.

*Culture* uniform, with dense aerial mycelium.

*Cardinal temps.*: min. 5–6°; opt. 25°; max. 32.5°.



**cactorum** (see Blackwell, 1943; no type or authentic cultures in existence; Miss Blackwell's culture examined)

*Sporangiophores* 2–2.5 $\mu$ , regularly sympodial (close or lax); *sporangia* broadly ellipsoid or ovoid to obpyriform, commonest dimensions 36–50  $\times$  28–35 (max. 55  $\times$  40) $\mu$ , ratio 1.3–1.4:1, deciduous, pedicel up to 4 $\mu$ , papilla and apical thickening hemispherical; *chlamydospores* variable in numbers not produced by all strains, 33 (max. 53) $\mu$  diam., wall 1–1.5 $\mu$  thick; *oogonia* mostly 25–32 (rarely up to 40) $\mu$ ; *oospore* fairly loose in the oogonium, 20–26 $\mu$ , wall 2 $\mu$  thick; *antheridia* ranging from nearly spherical to irregularly club shaped, 15 (–21)  $\times$  13 $\mu$ , always applied close to the oogonial stalk, often obscured in a knot of hyphae.

*Culture* when typical, uniformly slightly fluffy and slightly radiate (but see Stamps, 1953).

*Cardinal temps.*: min. c. 2°; opt. (20–) 25 (–28)°; max. c. 30°.

**cambivora** (Type culture examined)

*Hyphae* on malt agar fairly uniform to slightly undulate (cf. *cinnamomi*), when old rather broad (7 $\mu$ ) and thick-walled; *hyphal swellings* (in some strains and only in rich media) with rounded irregular contours, never botryose; *sporangiophores* 3–4 $\mu$  diam., usually unbranched, except by internal proliferation; *sporangia* formed only in liquid media, broadly ellipsoid or ovoid, 55–65  $\times$  40–45 (up to 85  $\times$  60) $\mu$ , ratio 1.4:1, no papilla, slight apical thickening; *sex organs* rare in single strain culture; produced in about 10 days when grown with certain strains of *P. nicotianae* and var. *parasitica*; *oogonia* yellow to brown, 43 (up to 62) $\mu$  diam., wall 2 $\mu$  thick and with irregularly disposed bullate protuberances; *oospore* 36 $\mu$  diam., wall 3 $\mu$  thick; *antheridia* amphigynous, often very long, av. 25 (often up to 35) $\mu$  long.

*Culture* moderately to profusely fluffy and fairly uniform.

*Cardinal temps.*: min. about 2°; opt. (18–) 22–24°; max. 32°.

**capsici** (Type culture examined)

*Hyphae* fairly coarse (5–7 $\mu$ ); *sporangiophores* rather narrow (1.5–2 $\mu$ ) but sometimes widening slightly at the base of the sporangium, irregularly branched; *sporangia* very variable in size and shape, from nearly spherical through broadly ovoid or obturbinate to elongated, av. 30–60  $\times$  25–35 $\mu$ , but may be up to over 100 $\mu$ , often distorted and developing asymmetrically on the sporangiophore, many with two papillae; papilla and thickening hemispherical; not readily deciduous but some do break off with rather a long stalk (more than 10 $\mu$ ); *chlamydospores* absent (or rare); *oogonia* frequent in culture, av. 30 (max. 39) $\mu$  diam., wall yellowish, becoming increasingly yellowish brown but not much thicker (cf. *mexicana*) with age; *antheridia* very variable in shape and size (av. 17  $\times$  15 $\mu$ ); *oospores* nearly filling the oogonium, wall thin (1 $\mu$ ).

*Culture* finely radiate, fluffy.

*Cardinal temps.*: min. c. 11°; opt. (26–) 28 (–32)°; max. over 35°.



**cinnamomi** (Type culture examined)

*Hyphae* on malt agar coralloid (i.e. with frequent rounded nodules, cf. *cambivora*), becoming broad ( $8\mu$ ) and very tough; *hyphal swellings* typically spherical (av.  $42\mu$ , max.  $60\mu$  diam.) and in clusters, wall not much thickened; *sporangiophores* thin ( $3\mu$ ), occasionally branched (externally), more often proliferating internally; *sporangia* formed only in liquid media, broadly ellipsoid or ovoid  $57 \times 33$  (up to  $100 \times 40$ ) $\mu$ , non-papillate, apical thickening very slight; sporangium partially collapsing after dehiscence; *sex organs* rarely produced on agar media, but abundant when grown with *P. cryptogea*; *oogonia* av.  $40$  (max.  $58$ ) $\mu$ , wall smooth, becoming yellow but not much thicker with age; *oospore* nearly filling the oogonium, wall  $2\mu$  thick; *antheridia* long,  $21-23 \times 17\mu$ .

Culture with profuse tough aerial mycelium, sometimes in a rosette pattern.

Cardinal temps.: min. c.  $5^\circ$ ; opt.  $24-28^\circ$ ; max.  $32-34^\circ$ .

**citricola** (Culture which probably represents the type examined)

Description, see Waterhouse (1957).

Culture 'chrysanthemum' pattern, fairly fluffy.

Cardinal temps.: min. about  $3^\circ$ ; opt.  $25-28^\circ$ ; max.  $31^\circ$ .

**citrophthora** (No type or authentic cultures available; Fawcett's isolates examined)

*Hyphae* fairly coarse (up to  $7\mu$ ); *sporangiophores*  $2.5\mu$ , irregularly branched; *sporangia* often intercalary, very variable in shape and size; on agar rather like those of *P. nicotianae* and var. *parasitica* (q.v.), in water cultures of bizarre shapes, often with 2 papillae, av.  $45 \times 27\mu$ , but may be up to  $90 \times 60\mu$ ; papilla hemispherical or slightly less ( $5\mu$  deep); *chlamydospores* may be abundant, few, or absent, av.  $28\mu$  diam., wall medium ( $1.5-2\mu$  thick); *sex organs* unknown.

Cultures have a very characteristic finely radiate growth, especially on corn meal agar.

Cardinal temps.: min. below  $5^\circ$ ; opt.  $24-28^\circ$ ; max.  $32^\circ$ .

**colocasiae** (It is probable that other *P.* species are able to attack *Colocasia* and they may in the past have been identified as *P. colocasiae*, when in fact they were of the 'parasitica-palmivora group'. Hence possible confusion in the descriptions. No type or authentic cultures available)

*Sporangiophores* slender ( $2-4\mu$ ), on the leaf rather short, sometimes scarcely longer than the sporangia, and unbranched; in culture branching is irregular to sympodial with a swelling at the point of branching; *sporangia* elongated ellipsoidal, sometimes almost fusiform, mostly  $45-60 \times 23\mu$ , but may be up to  $70 \times 28\mu$ , ratio  $1.6:1$ ; papilla projecting but the apical thickening is less than hemispherical, often only  $3\mu$  deep, at the most  $3.5\mu$ ; deciduous, pedicel slender,  $3.5-10\mu$  long; *chlamydospores* usually produced in culture, sometimes abundantly, usually  $26-30$  (up to  $39$ ) $\mu$ , wall up to  $3\mu$  thick, yellow;



*oogonia* usually develop in culture, av. 29 (up to 35)  $\mu$  diam., becoming yellow; *antheridia* 11–13  $\times$  11  $\mu$ ; *oospore* loose in oogonium, wall up to 2.5  $\mu$  thick.

*Culture* uniformly fluffy.

*Cardinal temps.*: min. over 10°; opt. 27–30°; max. c. 35°, probably always below this.

**cryptogea** (Type culture examined)

*Hyphae* of very uneven width (up to 8  $\mu$ ); *mycelium* in water cultures with groups of angular swellings (av. 11  $\mu$ , max. 20  $\mu$ ), with 2 or 3 branch hyphae which soon swell in their turn and branch giving a 'net-like' appearance; *sporangiophores* 2–3.5  $\mu$ , proliferating through the empty sporangium, occasionally sympodially from below; *sporangia* not formed in agar culture but only in liquid media; regularly ovoid or obpyriform, non-papillate, without obvious apical thickening, apex flattening on mounting; often with a conspicuous central vacuole; av. 37–40  $\times$  23 (max. 55  $\times$  30)  $\mu$ , ratio 1.7:1; *oogonia* formed only rarely in agar culture, then only sparingly in the richer media (oat, bean maize, etc.) and after a few weeks, but develop promptly and abundantly when grown with a complementary str. or with *cinnamomi*, av. 30–32 (max. 38)  $\mu$ , wall becoming yellow but not much thicker with age; *antheridia* spherical, 10  $\mu$  diam. (max. 16  $\mu$ ) or occasionally oval or short cylindrical; *oospore* nearly filling the oogonium, wall 3.5  $\mu$ .

*Culture* uniform and fairly fluffy.

*Cardinal temps.*: min. under 1°; opt. 22–25°; max. 31–33°.

**cyperi**

Has not been grown in culture. Known only on *Cyperus*. (Type material, if in existence, not seen)

*Sporangiophores* sympodially branched, 4–10  $\mu$  wide; *sporangia* ovoid, pyriform, or elongate ellipsoid, av. 52  $\times$  30 (max. 130  $\times$  44)  $\mu$ , papillate with a flattened apex and shallow apical thickening, deciduous with a pedicel about 4  $\mu$  long; *oogonia* av. 42 (up to 48)  $\mu$ ; *antheridia* 20  $\times$  12  $\mu$ ; *oospore* nearly filling oogonium, wall 3  $\mu$ .

**cyperi-bulbosi**

Has not been grown in culture. Known only from the original description (see Waterhouse, 1956).

**drechsleri** (Type culture not seen; a culture ex Tucker (No. 113) examined, but this is not mentioned in his monograph (Tucker, 1931) in which he described the species)

*Hyphae* fairly uniform, not often over 5  $\mu$  wide; *mycelium* in liquid cultures sometimes forming groups of swellings similar to those of *P. cryptogea*; *sporangiophores* narrow (1–2  $\mu$ ), sometimes widening slightly below the sporangium; *sporangia* very variable in shape from broadly obpyriform to elongated obpyriform, sometimes asymmetrical and sometimes tapering at



the base; av.  $36-50 \times 26-30$  (max.  $70 \times 40$ ) $\mu$ ; non-papillate, apical thickening barely detectable or a narrow crescent, apex often flattening on mounting; collapsing somewhat after dehiscence; *oogonia* sometimes formed promptly and abundantly in single culture, but if not, will produce them if grown with an 'opposite' strain, but not with *cinnamomi*;  $36$  (max.  $53$ ) $\mu$  diam., wall smooth and slightly yellow, becoming darker with age; *antheridia* oval or cylindrical,  $14-15 \times 13$  $\mu$ ; *oospore* nearly filling the oogonium, wall  $3\mu$  thick.

*Cultures* very fluffy, slightly rosette-like.

*Cardinal temps.*: min.  $5^{\circ}$ ; opt.  $28-31^{\circ}$ ; max.  $36-37^{\circ}$ .

***erythroseptica* var. *erythroseptica* (Type culture examined)**

*Hyphae* fairly uniform and fine (max.  $7\mu$  thick) occasionally with angular swellings in water culture; *sporangiophores*  $1-2\mu$  diam., widening slightly beneath the sporangium; more often branching sympodially (laxly) from immediately below the sporangium, but under certain conditions proliferating through the empty sporangium; *sporangia* very varied in shape, ellipsoid or obpyriform, often constricted distal to the middle, sometimes tapering to the sporangiophore; non-papillate, apical thickening inconspicuous or a narrow crescent; apex flattening on mounting;  $43 \times 26$  (max.  $69 \times 47$ ) $\mu$ ; *oogonia* always formed in culture,  $30-35$  (max.  $46$ ) $\mu$  diam., wall smooth,  $1\mu$  thick, may turn faintly yellow with age; *antheridia* ellipsoid or angular,  $14$  ( $-16$ )  $\times 13\mu$ ; *oospore* nearly filling oogonium, wall  $2.5\mu$  thick.

*Cultures* stellate or rosette pattern, fairly fluffy.

*Cardinal temps.*: min. under  $2.5^{\circ}$ ; opt.  $27.5$ ; max.  $34^{\circ}$ .

***erythroseptica* var. *psi* Hickman & Bywater (*Trans. Brit. mycol. Soc.* 42, 522-523, 1959. Authentic culture seen)**

*Hyphae*, lateral ones tortuous in growth and uneven in diam. ( $2-14\mu$ ); *hyphal swellings* spherical, angular or irregular, av.  $20\mu$  diam.; *sporangia* variable and irregular in shape and size, obpyriform to elongate often with a median constriction,  $63 \times 29$  (max.  $91 \times 40$ ) $\mu$  on pea roots in 5% peat percolate and  $86 \times 35$  (max.  $171 \times 40$ ) $\mu$  on bean agar in peat percolate, proliferating, non-papillate, apex flattening; *sex organs* abundant; *oogonia* spherical  $37$  ( $28-44$ ) $\mu$  diam. with a pale straw coloured to brownish yellow smooth wall  $0.7-2.7\mu$  thick; *antheridia* very pale straw colour, rounded isodiametric,  $19 \times 18$  (max.  $22 \times 26$ ) $\mu$ , often without a delimiting septum; *oospores*  $26$  ( $14-34$ ) $\mu$  diam. with a slightly coloured wall up to  $5.3\mu$  thick, loose in oogonium.

*Cultures* entirely non-fluffy.

*Cardinal temps.*: min.  $? 6^{\circ}$ ; opt.  $24^{\circ}$ ; max.  $30+^{\circ}$ .

***fragariae* (see original description, reproduced in Waterhouse, 1956. Type culture examined)**



**gonapodyides** (see Waterhouse, 1958)

*Hyphae* irregular, (3-) 8-9 (-12)  $\mu$  diam. without true hyphal swellings; *sporangiophores* more slender than other hyphae; *sporangia* broadly or elongated obpyriform, base rarely tapering, 42-70  $\times$  20-32  $\mu$ ; *sex organs* not known with certainty.

*Culture* not known.

*Cardinal temps.* not known.

**heveae** (Authentic culture examined)

*Hyphae* fairly uniform, mostly not more than 5  $\mu$  diam., though occasionally up to 7  $\mu$ ; *chlamydospores* none; *sporangiophores* 3.5  $\mu$  wide, branching irregular; *sporangia* very irregular in shape and size, ellipsoid or broadly obpyriform, often asymmetrical and laterally placed on the stalk, base rounded (never tapering), 46  $\times$  29 (max. 66  $\times$  48)  $\mu$ , ratio 1.4-1.5:1, deciduous, pedicel up to 10  $\mu$ ; *sex organs* abundant on agar, often in close groups with the oogonial stalks radiating from one point; *oogonia* spherical above, but usually tapering to the stalk, colourless, thin-walled, 25  $\times$  28 (up to 32  $\times$  35)  $\mu$  diam.; *antheridia* spherical, 9  $\mu$  diam. or slightly ellipsoid, 10.5  $\times$  9  $\mu$ ; *oospore* loose in oogonium, 21  $\mu$  diam., wall 3  $\mu$ .

*Cultures* with very little aerial mycelium.

*Cardinal temps.*: min. c. 11.5°; opt. c. 25°; max. 31°.

**hibernalis** (No type or authentic culture available; culture ex Baarn examined)

*Hyphae* av. 4  $\mu$ , but may be up to 7  $\mu$ , rather undulate, without hyphal swellings or chlamydospores; *sporangiophores* very slender, 1-1.5  $\mu$ , bearing sporangia singly or in very lax irregular sympodia, not proliferating internally; *sporangia* formed on some solid media; characteristically long and narrow, elongated ellipsoid or ovoid to nearly fusiform, often with the broadest part nearer the apex, scarcely papillate, apical thickening evident but shallow (1-2  $\mu$ ); 36  $\times$  19 (max. 56  $\times$  28)  $\mu$ , deciduous with a long pedicel (up to 55  $\mu$  long); after dehiscence a translucent globule is often left in the sporangium; *oogonia* readily produced on agar, av. 35 (max. 56)  $\mu$ , sometimes slightly elongated to the stalk, wall colourless or faintly yellow with age, but not much thickened; *antheridia* usually amphigynous, but sometimes paragynous, or there may be both to one oogonium, 12 (-14)  $\times$  10  $\mu$ , shape various but usually oval; *oospore* nearly fills the oogonium, 30  $\mu$ , wall 3  $\mu$ .

*Culture* rosette-like, fairly fluffy.

*Cardinal temps.*: min. under 5°; opt. 20°; max. 25°.

**ilicis** Buddenhagen & Young in *Phytopathology*, 47, p. 100, 1957.

(Authentic culture examined)

*Sporangiophores* unbranched or sympodially branched; *sporangia* sparse



on agar but abundant in liquid cultures, ovoid to obpyriform,  $26-50 \times 18-30$  (av.  $39 \times 24-29$ ) $\mu$ , ratio 1.3-1.6:1, non-papillate, non-proliferating, apical thickening shallow; deciduous, with a pedicel 5-15 $\mu$  long; *oogonia* abundant in the host (av. 21 $\mu$ ) and on agar, av. 27 (up to 32) $\mu$ , often tapering to the stalk, wall smooth, colourless and unthickened; *antheridia* amphigynous,  $13 \times 11\mu$ , oval; *oospores* nearly filling the oogonium, wall may become slightly yellow on some media.

*Culture* irregular and only slightly fluffy.

*Cardinal temps.*: min. below 5°; opt. 20°; max. c. 25°.

***infestans*** f. sp. *infestans* and f. sp. *thalictri* comb. nov., syn. *Phytophthora thalictri* Wilson & Davis in *Bull. Torrey bot. Cl.* 34, p. 392, 1907. (No type or authentic culture available; type material—slides—examined)

*Sporangiophores* differentiated from the mycelium (in the host) by being broader and having a small swelling at the point of formation of each sporangium; *chlamydospores* not formed; *sporangia*  $29 \times 19$  (max.  $59 \times 31$ ) $\mu$ , abundant on the host and on solid media, ellipsoid, ovoid or, when shed, limoniform, with a tendency to taper to the base; deciduous, pedicel short (up to 3 $\mu$ ); papilla not very protuberant, apical thickening less than hemispherical, usually about 3-3.5 $\mu$ ; *sex organs* rare in host and in culture unless 'opposite' strains are grown together; *oogonia* 38 (max. 50) $\mu$  diam., spherical to obpyriform, wall smooth, 1-2 $\mu$  thick, becoming reddish brown and thicker by an accretion from the medium; *antheridia* not always present but always amphigynous when they are,  $17$  (max. 22)  $\times 16\mu$ ; *oospores* 30 $\mu$  diam., loose in oogonium, wall colourless, up to 3-4 $\mu$  thick.

*Culture* slow growing (4 mm. per day at the opt.), fairly fluffy.

*Cardinal temps.*: min. c. 4°; opt. 20°; max. 26°.

***inflata*** (Not seen. No type or authentic culture available)

*Description*, see original (reproduced in Waterhouse, 1956).

*Culture* not reported.

*Cardinal temps.*: min. ?; opt. 25°-30°; max. under 35°.

***lateralis*** (information additional to the original description, reproduced in Waterhouse, 1956. Type culture examined)

*Sporangiophore* sometimes proliferating through the base of the empty sporangium.

*Culture* with little or no aerial growth.

*Cardinal temps.* min. under 2°; opt. ? 20°; max. under 30° (near 25°).

***lepironiae*** (known only from the original description, reproduced in Waterhouse, 1956)



**macrospora** (No type material available. Known only in the host)

*Hyphae* rather thick; *sporangiophores* 1.25–3.75 $\mu$  wide, emerging through the stomata, branched in a close unilateral or bilateral sympodium; *sporangia* av. 85  $\times$  50 (max. 112.5  $\times$  65) $\mu$ , narrowly to broadly obpyriform, ovoid, or ellipsoid; papillate, apical thickening scarcely hemispherical; deciduous, pedicel up to 14 $\mu$  long; *oogonia* numerous in the tissues of the host, av. 50–65 (max. 100) $\mu$ , wall slightly irregular, thickening to 3–6.5 $\mu$  and becoming yellowish or brown; *antheridia* paragynous, 27  $\times$  15 $\mu$ ; *oospore* filling the oogonium, colourless or pale or dark amber, wall 3–6.5 $\mu$  thick.

NOTE

This species was made the type of the genus *Sclerophthora* by Thirumalachar *et al* (1953) on the grounds of the thick oogonial wall, the union of the oogonial wall with the oospore wall, the multinucleate oospore, and the production of a sporangium on the germ tube from the oospore. A thick oogonial wall is known in *Phytophthora*, e.g. in *P. lepironiae* (4 $\mu$  thick), *P. palmivora* (cacao strain), *P. erythroseptica* var. *pisi* (up to 2.7 $\mu$ ), *P. infestans* (1–2 $\mu$ ), *P. mexicana*, and in *P. cambivora* and *P. verrucosa* where the wall becomes warted. In Herb. I.M.I. material the oogonium wall of *P. macrospora* is not always thick; the thickness seems to vary with the host and, possibly, the conditions. Nor is the wall fused to the oospore wall, it is quite easy to get the oospore out of the oogonium. The production of a sporangium on the germination of the oospore is not unusual in *Phytophthora* and has been figured more than once, e.g. in *P. cyperi-bulbosi* and *P. cactorum*. This leaves only the multinucleate condition of the oospore as the sole feature distinguishing *Sclerophthora*. But since the oospores of so few species of *Phytophthora* have been investigated, this differentiating criterion cannot yet be accepted with confidence. In view of this, it seems better to leave this species in *Phytophthora*. *S. cryophila* Jones could equally well be accommodated in *Phytophthora*.

**meadii** (See p. 21).

*Cultures* with variable aerial mycelium.

*Cardinal temps.*: min. over 5°; opt. 25–30°; max. over 33° (after Tucker).

**megasperma** var. **megasperma** (see original description; a shortened version is reproduced in Waterhouse, 1956. Type culture examined)

*Cultures* slightly radiate and fluffy.

*Cardinal temps.*: min. c. 2°; opt. ? 15–27.5°; max. 30°.

**megasperma** var. **sojae** Hildebrand, in *Canad. J. Bot.* 37, p. 954, 1959.

Differs from the species in the consistently smaller oogonia, rarely over 45 $\mu$ , av. under 40 $\mu$  diam., and in the cardinal temps.: min. 5°, opt. 25°, max. 33–35°.

**mexicana** (Type culture examined)

*Hyphae* up to 6 $\mu$ , rather gnarled and irregular, the finer hyphae often growing spirally round the wider ones; *sporangiophores* rather wide in comparison with the mycelial hyphae, widening noticeably to 8–10 $\mu$  or more immediately beneath the sporangium; unbranched or sparingly branched with a few short widely-spaced laterals; *sporangia* elongated ovoid to fusiform,



often distorted in shape, many with two apices,  $46 \times 24$  (max.  $77 \times 33$ ) $\mu$ , but many about  $60\mu$  long; papilla prominent, apical thickening hemispherical or less; not shed; *chlamydospores* none or rare ( $22-44\mu$  in original diagnosis); *oogonia* usually frequent in culture, but there may be occasional strains which do not produce them, av.  $30$  (up to  $37.5$ ) $\mu$  diam., wall becoming increasingly golden yellow or yellowish brown and thick with accretion; *oospores* nearly filling the oogonium, wall  $2\mu$  thick; *antheridia* always amphigynous,  $15.5 \times 14\mu$ .

*Culture* with moderate aerial growth, surface slightly 'frosty'.

*Cardinal temps.*: min. over  $10^\circ$ ; opt.  $27.5^\circ$ ; max. near  $35^\circ$ .

**nicotianae** var. **nicotianae** (No type material available; culture from type host in type locality examined).

*Hyphae* fairly uniform in diam., up to  $5\mu$ ; hyphal swellings frequent, especially in water cultures and on the sporangiophores, spherical, oval, or angular, all sizes up to chlamydospore size; as soon as the swellings are formed, four to five hyphae grow out in all directions; *chlamydospores* frequent, forming very early on the new mycelium,  $20-40\mu$ , wall  $1.5\mu$  thick, not turning brown; *sporangiophores* thin ( $2\mu$ ), closely or sparsely branched, the branches often arising from a hyphal swelling; *sporangia* terminal or less frequently intercalary, broadly turbinate, the basal part often nearly spherical with the apical third or quarter narrowed and prolonged into a 'beak', apical thickening hemispherical; av.  $45 \times 36\mu$ , often up to  $60-70\mu$  long; not usually shed; *oogonia* formed promptly by some isolates in single culture, but those that form them sparsely or not at all after some weeks produce them abundantly in dual culture with an 'opposite' strain; mostly  $28-30$  ( $-32$ ) $\mu$  diam., wall becoming slightly thicker with age and acquiring a golden brown accretion; *antheridia* always amphigynous, but the oogonial stalk is sometimes very eccentric so that the antheridium appears to be not amphigynous at first sight,  $10-16 \times 10\mu$ , rounded, not angular; *oospore* not filling the oogonium,  $24\mu$  diam., wall  $1\frac{1}{2}-2$  ( $-3$ ) $\mu$  thick.

*Culture* diaphanously fluffy with no zones or striations.

*Cardinal temps.*: min.  $12^\circ$ ; opt. ( $25^\circ-$ )  $30^\circ$ ; max. c.  $36.5^\circ$ .

**nicotianae** var. **parasitica** (Dastur) comb. nov. (syn. *P. parasitica* Dastur *sensu stricto* in *Mem. Dep. Agric. India. Bot. ser.*, 5, 4, p. 226, 1913) (No type culture available)

*Hyphae* tough, up to  $9\mu$  wide, irregular in width; *sporangiophores* more slender than the mycelial hyphae, irregularly or sympodially branched, sympodia close in moist air; *sporangia* broadly ovoid or pyriform to spherical, not noticeably narrowed in the apical part, av.  $38 \times 30$  (max.  $50 \times 40$ ) $\mu$ , l:b ratio 1.4 or less, sometimes intercalary, dropping off with a very short pedicel ( $2\mu$ ), apical thickening hemispherical; *chlamydospores* up to  $60\mu$ , forming rather tardily (1-2 weeks), wall  $3-4\mu$ , terminal or intercalary, becoming yellowish brown with age; *oogonia* usually produced in single culture, though



often very sparsely or not until after some weeks, but readily produced when grown with an 'opposite' strain; sparsely produced with some strains of *palmivora*; av. 24–26 (max. 31) $\mu$ , wall becoming thick and yellowy brown with age; *antheridia* spherical or oval, 10  $\times$  12 (–16) $\mu$ ; *oospores* aplerotic, wall thick (2 $\mu$ ) compared with the small size.

*Culture* variable (see Leonian, 1925) but commonly irregularly fluffy in an irregular rosette pattern.

*Cardinal temps.*: min. about 10° C., probably less; opt. 30–32°, max. 37° or over.

**oryzae** (Ito & Nagai) Waterhouse

(Type culture examined)

Description reproduced in Waterhouse (1956, 1958). The following additional features may be noted:

*Hyphal swellings* knob-like on some agar media; in liquid media spherical, ellipsoid, or irregular-shaped, up to 43 $\mu$  in length or diam.

NOTE.—In 1939 Hara is reported to have transferred *Sclerospora oryzae* Brizi to *Phytophthora* in 'Ine no Byogai' [Rice plant diseases]; I have not been able to obtain this publication. If the transfer is validly published then a new name must be given to *Phytophthora oryzae* (Ito & Nagai) Waterhouse (1958).

**palmivora** sensu stricto

(No type culture or material available)

*Hyphae* fairly uniform, undulating, rarely over 5 $\mu$ ; *sporangiophores* thin (1 $\mu$ ); *sporangia* various shapes, but many elongated ellipsoid or elongated ovoid, mostly 50–60  $\times$  31–35 (max. 93  $\times$  43) $\mu$ , l:b ratio over 1.4, usually 1.7, may be up to 1.8:1; tapering slightly to the stalk, deciduous, pedicel 2–10 $\mu$ ; *chlamydospores* up to 55 $\mu$ , mostly 30–35 $\mu$ , forming promptly in a few days, wall thin (1–2 $\mu$ ), terminal or intercalary; *oogonia* never (? or very rarely) formed in single culture, produced readily when grown with an 'opposite' strain and sometimes (sparsely) with certain strains of *nicotianae* and var. *parasitica*; av. 30 (max. 42) $\mu$ ; wall colourless at first, becoming thicker and yellower with age; *antheridia* 15  $\times$  14 $\mu$ , spherical or oval; *oospores* nearly filling the oogonium, wall 2 $\mu$ .

*Culture* uniform and slightly radiate

*Cardinal temps.*: min. 11°; opt. 27.5–32°; max. 35°, usually less.

NOTE.—The str. on the type host, Palmyra palm (*Borassus flabellifer*), is the 'cacao' str. The 'rubber' str., of 'opposite' compatibility, is slightly different morphologically.

**phaseoli** (Type or authentic material not seen)

This species is very near *infestans*, differing only in host range, the longer sporangiophores, the larger sporangia, 32  $\times$  22 (max. 50  $\times$  27) $\mu$ , the rather smaller oogonia, 30 (max. 38) $\mu$  diam., oospores, and antheridia 15  $\times$  10 (max. 17  $\times$  11.5) $\mu$ .



*Culture* slow growing but fairly fluffy.

*Cardinal temps.*: min. 5°; opt. 15–20°; max. 25–30°.

**porri** (Authentic material examined)

*Hyphae* very irregular in thickness, often growing in coils in culture; *hyphal swellings* single or in chains, spherical, ellipsoid, or irregular; *sporangiophores* no different from the mycelial hyphae; *sporangia* produced fairly freely on solid media, long ellipsoid or obpyriform or sometimes rather distorted and tapering to the stalk where there is a conspicuous septum and plug, not proliferating, mostly 35–40 (–50) × 29–35 (max. 80 × 50)μ; apex scarcely protruding, apical thickening shallow (up to 3μ) dipping into protoplasm; *oogonia* abundant in agar culture, 36 (max. 45)μ diam., wall thin at first and rather undulate, becoming thicker and yellowish (2μ); *antheridia* paragynous and amphigynous, usually single, sometimes two, large, av. 12 × 12 (max. 24 × 15)μ; *oospore* fairly loose in the oogonium or nearly filling it, wall up to 4.5μ thick.

*Cultures* slow growing (4–7mm.day at 25°), radiate, aerial mycelium dense.

*Cardinal temps.*: min. under 5°; opt. c. 25°; max. 33–35°.

**primulae** (Authentic culture seen)

See original description (reproduced in Waterhouse, 1956). This species is very close to *P. syringae*, differing only in the more elongated and serial sporangia produced in aerated soil extract and the larger, never amphigynous antheridia.

**quininea** (Type culture examined)

See original description (reproduced in Waterhouse, 1956).

**richardiae** (Culture which is probably authentic for the name examined)

*Hyphae* very irregular and tortuous with frequent *hyphal swellings* which are spherical, ellipsoid or angular, all sizes up to 25μ, strung out along the hyphae and having two or three germ tubes; *sporangiophores* variable in width with occasional swellings, broadening immediately below the sporangium, proliferating through the empty sporangium, rarely branched; *sporangia* very variable in size and shape but average 50 × 30μ; *oogonia* variable in size, 24–38 (av. 32)μ, spherical, wall smooth, colourless, thin; *antheridia* the majority amphigynous (about a quarter paragynous), variable in shape but often with a hyphal prolongation, 18 × 14 (max. 23 × 15)μ; *oospore* nearly filling the oogonium, colourless, wall variable in thickness up to 4μ.

*Cultures* medium fluffy.

*Cardinal temps.*: min. 3–4°; opt. 24°; max. under 32°.

**syringae** (No type or authentic culture available; De Bruyn culture ex Baarn and others examined)

*Hyphae* rather irregular in width, up to 6μ; *hyphal swellings* spherical to



ellipsoid, monilioid or catenulate, rare in some isolates common in others; *chlamydospores* none; *sporangiophores*  $2\mu$  wide, branching closely sympodial on agar media, more lax in water; *sporangia* broadly ovoid or obpyriform, on short stalks,  $57 \times 36$  (max.  $75 \times 42$ ) $\mu$ ; non-deciduous; scarcely papillate, apical thickening shallow (up to  $3.5\mu$ ); *sex organs* usually abundant in culture and in host tissues; *oogonia* spherical, av.  $33\mu$  diam. (max.  $46\mu$ ), wall at first thin and colourless becomes thicker and yellower after the oospore is mature; *antheridia* small,  $10 \times 7\mu$  usually paragynous (rare amphigyny has been reported); *oospore* almost or quite filling the oogonium, wall  $2\mu$  thick.

Culture 'rose' shaped growth zones.

Cardinal temps.: min. under  $5^\circ$ ; opt.  $20^\circ$ ; max.  $23^\circ$ .

**verrucosa** (Authentic material examined)

Has not been grown in culture. See original description (reproduced in Waterhouse, 1956).

**vignae** Purss (taken from Purss, G.S. in *Qd J. agric. Sci.* **14**, pp. 125–154, 1957; with additional information from the type culture)

*Hyphae* undulating, but fairly uniform in thickness, av.  $4.5$  (up to  $7.5$ ) $\mu$  thick; *hyphal swellings*, mostly spherical, terminal or intercalary,  $12$ – $21$  (av.  $17$ ) $\mu$ , abundant in Petri solution, sparse in water and on solid media; *chlamydospores* not formed (those described as such in the original diagnosis were hyphal swellings); *sporangiophores* like the mycelial hyphae, widening slightly at the base of the sporangium, unbranched or in lax sympodia; *sporangia* ellipsoid, ovoid, or obpyriform, often tapering somewhat to the base, formed only in liquid culture, average  $48 \times 27$  (max.  $72 \times 54$ ) $\mu$ , proliferating, non-papillate, apical thickening inconspicuous; *sex organs* abundant in the host tissues and in culture; *oogonia* spherical,  $32$  (max.  $46$ ) $\mu$  diam., wall colourless at first, becoming light brown and up to  $2\mu$  thick with age; *antheridia* all amphigynous, very variable in size and shape, av.  $16 \times 15$  (max.  $27 \times 18$ ) $\mu$ ; *oospore* loose in the oogonium,  $26$  (max.  $32$ ) $\mu$  diam., colourless (? faint brown), wall up to  $3\mu$  thick.

Cultures with a medium amount of loose aerial mycelium.

Cardinal temps.: min.  $10$ – $12^\circ$ ; opt.  $28$ – $30^\circ$ ; max.  $34.5^\circ$ .

### INSUFFICIENTLY DESCRIBED TAXA

*canavaliae* Hara—no sex organs described; sporangia and chlamydospores would place it in group II near *palmivora*.

*carica* (Hara) Hori (syn. *P. carica* (Hara) Hara)—the sex organs described were probably chlamydospores; most likely this belongs in group II near *palmivora*.

*cinchonae* Sawada—no sex organs described; possibly the same as *P. cinnamoni*. Probably not validly published as it was described after 1 Jan., 1935 and no Latin diagnosis has been found.



*persica* Sawada—description not seen.

*polygoni* Sawada—no sex organs described.

*taihokuensis* Sawada 1959—no sex organs described—said by Sawada to be near *melongenae*. No Latin diagnosis has been found and so it may not be validly published.

## REJICIENDA

### GENERIC NAMES

(the combinations in which they appear (Waterhouse, 1956) are also rejected)

*Blepharospora* Petri—type species, *B. cambivora* Petri—erected on the character of proliferating sporangia, but *Pythiomorpha* Petersen already existed (1909) for proliferating species. This character is not considered sufficient to warrant generic distinction.

*Kawakamia* Miyabe—type species, *K. cyperi* (Miyabe & Ideta) Miyabe—erected on the character of the pedicel-like appendage to the conidium (but *P. infestans*, the type species, has a pedicel) and on the shape of the conidia and conidiophores, differences not sufficient for generic distinction to be maintained.

*Mycelophagus* Mangin—type species, *M. castaneae* Mangin, producing chestnut ink disease, most probably *Phytophthora* sp. but impossible to tell from the description.

*Nozemia* Pethybridge—type species, *N. cactorum* (Leb. & Cohn) Pethyb.—erected on the character of paragynous antheridium. Since many species of *Phytophthora* have both amphigynous and paragynous antheridia, this generic distinction is not acceptable and was rejected later by Pethybridge himself.

*Phloeophthora* Klebahn—type species, *P. syringae* Kleb.—reduced later (1909) by Klebahn himself to synonymy with *Phytophthora*.

*Pseudopythium* Sideris—type species, *P. phytophthoron* Sideris—nomen nudum (no description) based on *Phytophthora cinnamomi* (see Waterhouse, 1956, p. 3).

*Pythiacystis* Smith & Smith—type species, *P. citrophthora* Sm. & Sm., not distinct from *Phytophthora*, *vide* Leonian.

*Pythiomorpha* Petersen—type species, *P. gonapodyides* Petersen—based on the character of red-violet coloration of the mycelium with chlor-zinc iodide, not an acceptable distinguishing character.

### SPECIFIC EPITHETS

*agaves* Villada apud Gandara—nomen nudum (no description)

*allii* Sawada—not seen, probably the same as *nicotianae* var. *nicotianae*



- cactorum* var. *applanata* Chesters—the same as *citricola*  
*cactorum* var. *arecae* (Colem.) Sacc. & Trotter—a synonym of *arecae*  
*cactorum* subvar. *syringae* (Kleb.) Sarej.—a synonym of *syringae*  
*carica* (Hara) Hara (Nov., 1916)—antedated by *carica* (Hara) Hori (Nov., 1915)  
*castaneicola* Goicoechea (1949)—not seen  
*citri* Venkata Rau—nomen nudum (no description)  
*cryptogea* var. *richardiae* Ashby—a synonym of *richardiae*  
*cyperi-iriae* Sawada—not seen; probably the same as *cyperi*  
*cyperi-rotundati* Sawada—not seen; probably the same as *cyperi*  
*devastatrix* (Lib.) Puttemans—an earlier epithet for the potato blight fungus (*P. infestans*), not validly published  
*erythroseptica* var. *atropae* Alcock—not significantly different from var. *erythroseptica*  
*erythroseptica* var. *drechsleri* (Tucker) Sarej.—a synonym of *drechsleri*  
*erythroseptica* var. *pisi* Bywater & Hickman 1959—type specimen not cited (invalidly published)  
*faberi* Maublanc—the same as, and antedated by, *palmivora*  
*fagi* (Hartig) Hartig—the same as *cactorum*  
*fagopyri* Takimoto—*Pythium* sp. probably *P. oedochilum* Drechs.  
*fici* Hori—based on *carica* (Hara) Hori *fide* Hori (1915) who reverted back to *carica* later  
*fici* Venkata Rau (June, 1916)—nomen nudum (no description) and antedated by *fici* Hori (1915)  
*fischeriana* (Höhnk) Sparrow (1960)—probably the same as *syringae*  
*formosana* Sawada—not seen; probably the same as *nicotianae* var. *parasitica*  
*himalayensis* Dastur—the same as *erythroseptica*  
*hydrophila* Curzi—the same as *capsici*  
*imperfecta* Sarejanni—not validly published (after 1935 and no Latin diagnosis) and no adequate description  
*imperfecta* var. *citrophthora* (Smith & Smith) Sarej.—not validly published (see above); a synonym of *citrophthora*  
*imperfecta* var. *nicotianae* (van Breda da Haan) Sarej.—not validly published (see above); a synonym of *nicotianae*  
*infestans* var. *phaseoli* (Thaxter) Leonian = *phaseoli*  
*jatrophae*—name only published  
*leersiae* Sawada 1941—not validly published (no Latin diagnosis); no sporangia described  
*lycopersici* Sawada—not seen; probably the same as *nicotianae* var. *parasitica*



- manoana*—the name appears only in the Baarn list; the culture at Baarn labelled *manoana* Sideris probably belongs in the *nicotianae* group
- meadii* var. *ananaphthoros*—the name appears only in the Baarn list
- melongenae* Sawada—the same as *nicotianae* var. *nicotianae*
- melongenae* var. *ananaphthoros*—the name appears only in the Baarn list
- miyabeana* Ito & Nagai (*Pythiomorpha*)—falls into *megasperma*
- murrayae* Sawada—not validly published (after 1935 and no Latin diagnosis); no oospores described
- omnivora* de Bary—an illegitimate (superfluous) new name for *cactorum*
- omnivora* var. *arecae* Coleman—a var. of an illegitimate specific name (see above)
- omnivora parasitica* f. *eriobotryae* Dufrénoy—illegitimate (see above); a trinomial is also illegitimate
- oryzae* Brizi (*Sclerospora*)—probably the same as *macrospora*
- paeoniae* Cooper & Porter—is the same as *cactorum*
- palmivora* var. *heveae* (Thomps.) Orellana, applied by Orellana to the 'rubber' strain of *P. palmivora*; *heveae* appears to be a good species and is not the same as the 'rubber' strain of *palmivora*
- palmivora* var. *theobromae* (Colem.) Orellana, for the 'cacao' strain—*theobromae* Coleman is antedated by *faberi* Maublanc for the cacao black pod pathogen; both are usually regarded as synonyms of *palmivora*; the 'cacao' str. is nearest to the type description and if a varietal name is needed it should be *palmivora* var. *palmivora*
- palmivora* var. *piperis* Muller—based on growth temperature difference and host specificity, therefore unacceptable as a variety; no Latin diagnosis given (after 1 Jan., 1935), therefore invalidly published
- parasitica* Dastur—does not appear to be specifically different from *nicotianae*, which has priority
- parasitica* var. *capsici* (Leonian) Sarejanni—*capsici* Leonian seems to be a good species
- parasitica* var. *colocasiae* (Racib.) Sarejanni—as *colocasiae* antedates *parasitica* this comb. is illegitimate; *colocasiae* Racib. appears to be a good species
- parasitica* 'macrospora group and microspora group' Ashby, sometimes referred to as sect. or var. *macrospora* and *microspora*
- parasitica* var. *nicotianae* (van Breda da Haan) Tucker—*nicotianae* antedates *parasitica*; therefore, this comb. is illegitimate
- parasitica* var. *piperina* Dastur—published after 1 Jan., 1935 without a Latin diagnosis, therefore not validly published; a synonym of *nicotianae* var. *nicotianae*
- parasitica* var. *rhei* Godfrey—the same as *nicotianae* var. *nicotianae*
- parasitica* var. *sabdariffae* Mukerjee—nomen nudum—not published
- parasitica* var. *sesami* Prasad—based solely on host specificity; therefore unacceptable as a var.



- pini* Leonian—the same as *citricola*  
*pini* var. *antirrhini* Sundar. & Ramarkr.—the same as *citricola*  
*ricini* Sawada—published after 1 Jan., 1935 without a Latin diagnosis, therefore not validly published, probably a strain of *nicotianae* var. *parasitica*  
*sabdariffae* ex Thung—nomen nudum. Thung thought this name had been published when he used it (personal communication)  
*sempervivi* (Schenk) ? De Bary—the same as *cactorum*  
*sojae* Gerdeman *et al.*—not sufficiently distinct from *P. megasperma*  
 'speciosa' Mehlisch—probably was not intended as an epithet but as *Phytophthora* species  
*stellata* Shanor—is *Pythium* sp. (*fide* many authors)  
*symmetrica* Sideris—nomen nudum—not published  
*tabaci* Sawada—not seen; probably the same as *nicotianae* var. *parasitica*  
*terrestris* Sherbakoff—the same as *nicotianae* var. *nicotianae*  
*terrestris* var. *rhei* ? Drechsler apud Tucker—nomen nudum  
*theobromae* Colem.—the same as and antedated by *faberi*; now accepted to be the same as *palmivora*  
*viticola* Reichelt—a synonym of *Plasmopara viticola* (Berk. & Curt.) Berl. & de Toni

## ADDENDUM

***Phytophthora meadii***

*Hyphae* fairly uniform (up to  $6\mu$ ) in diam.; *chlamydospores* none or rare; *sporangiophores* slender (up to  $3\mu$ ) with nodal swellings from which the long or short branches (1–3) arise; *sporangia* variable in shape, mostly ellipsoid or elongated ellipsoid, sometimes obpyriform, often asymmetrical, rounded at the base, av.  $48 \times 24$  (max.  $67 \times 30$ ) $\mu$ , 1 : b ratio up to 2 : 1; deciduous, pedicel slender, 10–20 $\mu$  long; papilla and apical thickening scarcely hemispherical (4 $\mu$  deep); *sex organs* formed in single culture or, if not, when grown with *arecae* or *palmivora*; *oogonia* spherical to somewhat pyriform, 33 (max. 49) $\mu$  diam., wall smooth or wrinkled, becoming honey or tawny coloured; *antheridia* amphigynous, rounded,  $12 \times 13$  (up to  $16 \times 16$ ) $\mu$ ; *oospore* 23 (up to 32) $\mu$  diam., wall yellowish, 4 $\mu$  thick.

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