STUDIES IN THE GENUS PHYTOPHTHORA—II

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In the previous article Thomas *et al.* (1947) discussed the behaviour of different isolates of *Phytophthora palmivora* in paired cultures and based on the results of their studies, all the isolates studied were brought under the same species, *viz.*, *P. palmivora* Butl. though they were being previously referred to three or more different species. Further investigations were continued with these and some more isolates belonging to *P. parasitica* and *P. colocasiæ*. The results of these investigations are described in this paper.

Materials and Methods

As mentioned in the earlier communication (Thomas *et al.*, 1947) the isolates of *Phytophthora* already available in stock collection in the section were utilised. New isolates were brought into culture from infected castor and agave leaves when infection by the fungus occurred in nature on the Central Agricultural Research Station, Coimbatore. Isolates from bread-fruit were obtained from diseased fruits got down from South Kanara. Authentic type cultures of *P. parasitica* and *P. colocasiæ* were received from the Indian Agricultural Research Institute, New Delhi, through the courtesy of Mr. Dastur. Dr. Asthana was kind enough to send us from Nagpur the culture of *P. parasitica* var. *piperina*. The paired cultures were grown on oat agar in petri-dishes or test-tubes in the months of October to January when the laboratory temperature was in the neighbourhood of 26° C.

1. *Isolate from castor* (Ricinus communis)

Castor plants growing in the experimental plots of the Oilseeds Specialist at Coimbatore were found infected during the north-east monsoon in October 1946, by a leaf-blight caused by *Phytophthora*. The fungus was isolated and brought into pure culture from single hyphal tips. A white luxuriant aerial growth developed on oat agar. Numerous ob-pyriform sporangia and intercalary hyaline to yellowish brown chlamydospores were formed. But sexual bodies did not develop even after four months.

This isolate was grown in paired cultures with other isolates and oospores were formed in the course of one week as shown in Table I.

TABLE I

Statement showing the result of growing this isolate in paired cultures

Paired with isolate from				Result
Arecanut	*P. palmivora*	plus strain	..	Oospores formed in 6 days
Clerodendron	do	do	..	do do 5 do
Agave	do	minus strain	..	do do 5 do
Hevea	do	do	..	do do 5 do
P. parasitica type culture			..	do do 4 do
P. colocasiæ			..	do do 5 do

Oospores were formed with both the plus and minus strains of *P. palmivora* and also with *P. parasitica* and *P. colocasiæ*. In single strain cultures however oospores are not developed either by this isolate or by the others with which it was paired. *P. parasitica* has been recorded on castor and the isolate under study will normally be identified as *P. parasitica* from the sporangial and chlamydospore characters though it does not form oospores in single strain cultures. But the ease with which it pairs with the plus and minus strains of *P. palmivora* raises some important doubts about the taxonomic relationship of the former species. This is discussed later in detail.

2. *Isolate from* Agave wightii

The leaf-blight on this host caused by *Phytophthora* was prevalent at Coimbatore in the months of November and December 1946. The isolate was brought into pure culture by tissue culture which was further purified by transferring single hyphal tips. On oat agar a luxuriant white aerial growth which filled the tube was formed. Profuse formation of sporangia and chlamydospores took place. No sexual bodies developed even after four months.

Paired cultures were grown using this isolate as one of the strains and one or another isolate of known performance. The results are given in Table II.

The behaviour of this isolate is identical with that of the old isolate from the same host already available in the section (Thomas *et al.*, 1947) in the formation of oospores with strains of *P. palmivora*. But the old isolate is reported (Marudarajan, 1941) to have produced oospores in single strain cultures for some time after isolation though this capacity was lost after two years' continuous culturing on agar media. The new isolate however does not form oospores in single strain cultures even after three months. The isolate readily combines with *P. parasitica* and *P. colocasiæ* also and forms oospores in paired cultures with these species.

TABLE II

Statement showing the results of growing the isolate from Agave wightii *in paired culture*

Paired with isolate from	Results
Clerodendron *P. palmivora* plus ..	Oospores formed in 5 days
Arecanut do do ..	do do 5 do
Hevea do minus ..	No oospores formed
Spondias do do ..	do
Castor *P. parasitica* ..	Oospores formed in 3 days
P. parasitica type culture ..	do do 5 do
P. parasitica var. *piperina* ..	do do 5 do
P. colocasiæ type culture ..	do do 5 do

3. *Isolate from Breadfruit* (Artocarpus incisa)

The performance of two earlier isolates from this host have been described in an earlier communication (Thomas *et al.*, 1947). This isolate was obtained from infected fruits of *Artocarpus incisa* brought from South Kanara. Its growth on oat agar was less profuse than the isolates from castor and agave. Ob-pyriform sporangia which are usually terminal and hyaline, and yellowish thick-walled spherical or subglobose intercalary chlamydospores are formed in large numbers. Sexual reproduction is not evident for the first ten days of growth. But numerous oogonia and oospores are formed in 15 days in single strain cultures. The culture was isolated from single hyphal tips and therefore this isolate is found to be homothallic and fertile. The oogonium is hyaline or light yellow and persistent. The antheridium is amphigynous. The oospore is thick walled and yellowish brown. The relative measurements of oogonia and oospores were 28·6 (20–31) μ and 27·5 (18–29) μ respectively. These are not far different from the average of the measurements obtained by Marudarajan (Thomas, 1941) for the sexual bodies of an isolate from breadfruit, *viz.*, oogonia 30·5 μ (19·3–38·5) μ and oospores 28·3 (17·5–35) μ.

This isolate from breadfruit was also grown in paired cultures with other isolates whose sexual behaviour was already known and the influence on the rapidity of oospore formation was observed.

From the results below it is found that the isolate from breadfruit forms oospores in single strain cultures in 11 days. But when paired with the plus strain of *P. palmivora* or with *P. parasitica* or *P. colocasiæ* sexual bodies begin to develop within thirty-six hours to 3 days after inoculation. On the other hand, when it is paired with the minus strains of *P. palmivora* oospore formation is visible only after ten days. In these the oospores

TABLE III

Statement showing the effect of pairing the isolate from breadfruit with other isolates of Phytophthora

Paired with isolate from				Results			
Jack	*P. palmivora*	plus strain	..	Oospores formed in		48	hours
Betelvine	do	do	..	do	do	48	do
Citrus	do	do	..	do	do	48	do
Colocasia	do	do	..	do	do	48	do
Areca	do	do	..	do	do	48	do
Clerodendron	do	do	..	do	do	36	do
Spondias	do	minus strain	..	No oospores upto		10	days
Hevea	do	do	..	do	do		
P. parasitica		type culture	..	Oospores formed in		3	do
P. colocasiæ		do	..	do	do	3	do
Isolate from breadfruit (single strain)			..	do	do	11	do

might have been formed by the breadfruit isolate itself and not by the pairing of the two strains. Thomas *et al.* (1947) have found that the first isolate of *P. palmivora* from breadfruit behaved as a minus strain. It formed oospores in single strain cultures when first isolated by Marudarajan (Thomas, 1941) but this capacity had been lost in later years, after having been grown on agar media for over four years. Thus a homothallic fertile strain has apparently changed later on into a minus strain. The present isolate also gives an indication of its probable future change. At present it is homothallic and fertile but it pairs easily with plus strains of *P. palmivora* or with homothallic non-fertile strains of *P. parasitica* or *P. colocasiæ* while there is no evidence of combination with the minus strains, thus exhibiting a tendency towards the development of the 'minus' character.

Gadd (1927) obtained an isolate from breadfruit which behaved as a member of his 'rubber' group (which is equivalent to the minus strain of *P. palmivora*). Apparently breadfruit is parasitized by both homothallic (fertile) and minus strains of *P. palmivora* in different localities. But eventually even the homothallic strain changes into the minus strain when grown on agar media for a length of time.

4. P. parasitica *Dast. var.* piperina *Dast. on* Piper betle

A type culture of this isolate was kindly supplied by Dr. Asthana, the Mycologist to the Government of Central Provinces and Berar, Nagpur. It was found to grow luxuriantly on oat agar forming a white dense aerial growth. Dastur (1935) had described this as a new variety of *P. parasitica.* His isolates were producing numerous oospores on agar media. But the culture received from Nagpur formed sporangia and chlamydospores but

not sexual bodies. It was however grown in paired cultures with other isolates of known reaction and the results are given below.

TABLE IV

Statement showing the formation of oospores in paired cultures

Paired with the isolate from			Results
Aecanut (Tyagli)	*P. palmivora*	minus strain ..	Many oospores in 8 days
Coconut	do	do ..	Less number in 6 do (Oogonia deep coloured thickened)
Hevea	do	do ..	Numerous oospores in 4 days
Jatropha	do	do ..	do do 5 do
Agave	do	do ..	do do 4 do
Spondias	do	do ..	Less number do 4 do
Tomato	do	plus strain ..	do do 8 do
Areca	do	do ..	do do 8 do
P. parasitica		..	Numerous oospores 4 do
P. colocasiæ		..	do do 7 do

This isolate combines with both the plus and minus strains of *P. palmivora*, with *P. parasitica* and *P. colocasiæ*. In this respect it is akin to the isolate from castor. The intensity of oospore formation varies in the different combinations. Oospores are formed in greater abundance with isolates recently brought into culture than with older ones.

Dastur (1935) raised this isolate to a new variety of *P. parasitica*, the main reason being the larger sizes of the oogonium and the oospore compared to those of *P. parasitica* though he acknowledges on the same page that "the size of the oogonium is not constant and is influenced by the medium". In later isolations of *P. parasitica* he had found bigger oogonia and oospores. In authentic cultures of *P. parasitica*, Tucker (1931) has found that oospores are very variable in size and exhibit a range in diameter from 12 to 35 μ. In the light of the above observations it becomes evident that this isolate is not different from the type of *P. parasitica* and there is not enough justification to classify it as a new variety.

The sexual bodies formed in some of the paired cultures were measured and the measurements are given below together with the sizes recorded by Dastur.

These measurements fall within the range of those recorded from paired cultures of *P. palmivora* strains (Thomas *et al.*, 1947).

TABLE V

Statement showing the size of sexual bodies in paired cultures

Particulars	Oogonia		Oospores	
	Mean μ	Range μ	Mean μ	Range μ
P. parasitica var *piperina* Dastur's measurements	38·4	20·4–40·8	26·1	17·8–33·1
do + *P. palmivora* (Tyagli		24 –32		22 –27
do + do Tomato		24 –33		21 –30
do + do Cocoanut	31·5	26 –43	26	20 –31
do + *P. parasitica* ..	28·0	21 –34	23	16 –25
do + *P. colocasiæ* ..	29·1	23 –33	22·5	18 –26

5. P. colocasiæ *Rac.*

A type culture of this fungus was obtained from the Indian Agricultural Research Institute, New Delhi, through the courtesy of the Head of the Division of Mycology. Its growth on oat-agar is not so luxuriant as that of the isolates from betelvine or arecanut. The cultures are in need of frequent transfers to fresh agar media in order to keep them going and to prevent them from dying out.

Raciborski (1900) was the first to describe this fungus from Java. Butler and Kulkarni (1913) conducted a detailed study of the same fungus from India. Their isolates produced sporangia, chlamydospores and oospores. The cultures now received from New Delhi were of the non-oospore forming type (non-fertile) and produced only sporangia and chlamydospores in single strain culture. The behaviour of this isolate when

TABLE VI

Statement showing the development of oospores in paired culture

Paired with	Results
P. palmivora (Tomato) plus strain ..	Oospores formed in limited numbers in 7 days
do (Jack) do ..	do do 8 do
do (Betelvine) do ..	Few oospores in 9 days
do (Coconut) minus strain ..	Numerous oospores in 5 days
do (Hevea) do ..	do 4 do
do (Breadfruit) do ..	do 3 do
do (Agave) do ..	do 4 do
do (Jatropha) do ..	do 4 do
do (Spondias) do ..	do 4 do
do (Areca-tyagli) do ..	do 9 do
P. parasitica ..	do 4 do
do var. *piperina* ..	do 6 do

grown in paired cultures with other isolates of *P. palmivora* and *P. parasitica* was studied and the results are shown above.

The behaviour of this isolate is akin to that of *P. parasitica* var. *piperina*. More oospores develop in combination with the minus strains of *P. palmivora* than with the plus strains. The studies of this fungus have shown that it closely resembles *P. parasitica* and *P. palmivora* in its morphological characters. The ease with which it pairs with these two species and forms oospores of the same type brings out the affinities between them more clearly.

The size of the sexual bodies observed by Butler and Kulkarni (1913) for *P. colocasiæ* agrees closely with those of oogonia and oospores formed in paired cultures. These are given below.

TABLE VII

Statement showing the sizes of oogonia and oospores

Combination	Oogonia		Oospores	
	Mean μ	Range μ	Mean μ	Range μ
P. colocasiæ (Butler and Kulkarni)	29·5	24–31	23	20 –28
P. colocasiæ + *P. palmivora* (tomato)	26	24–28	21	18·5–22
do + do (areca-tyagli	31·5	25–41	24	18 –34
do + do (Spondias)	27·5	21–34	22	15·5–25
do + *P. parasitica*	28	24–31	22	18 –25
do + *P. parasitica* var. *piperina*	29·1	23–33	22·5	16 –25

The measurements are comparable to those recorded for sexual bodies formed in paired cultures of *P. palmivora*. In this isolate one can however detect an indication of the weakening of the homothallic tendency since it forms larger number of oospores with the minus strains of *P. palmivora* than with the plus strains. Probably this isolate will in course of time lose its capacity to combine with the plus strains and itself may behave as a plus strain. It may be interesting to note the behaviour of an isolate of *P. palmivora* from *Colocasia antiquorum* recorded by Thomas *et al.* (1947) which had the sporangial character usually attributed to *P. colocasiæ* but was non-oospore forming and behaved as a plus strain combining with the minus strains of *P. palmivora*. All these factors indicate the necessity for merging this species with *P. palmivora*. Leonian (1925) was the first to express a similar view.

6. Phytophthora parasitica *Dast.*

Mr. Dastur, the Head of the Division of Mycology, Indian Agricultural Research Institute, New Delhi, kindly sent us an authentic type culture of *P. parasitica* for our studies. This species was first described by Dastur (1913) from India having been isolated from blighted leaves of *Ricinus communis*. Since then it has been studied by numerous workers in different parts of the world on various hosts. The original isolate has been described as forming oospores in single strain cultures. But Tucker (1931) found that the " occurrence of oogonia and oospores in cultures is uncertain. They may appear only after several months or frequently not at all." The isolate obtained from New Delhi did not produce oospores at laboratory temperature, *i.e.*, 24°–30° C. even after six months.

Paired cultures in combination with other isolates of *P. palmivora*, *P. colocasiæ* and *P. parasitica* var. *piperina* were grown and the results are recorded below.

TABLE VIII

Statement showing the development of oospores in paired cultures

Paired with isolate	Results
P. palmivora Tomato plus strain ..	Oospores numerous in 7 days
do *Colocasia* do ..	do formed in 8 do
do Jack do ..	do do 5 do
do Betelvine do ..	do do 10 do
do Citrus 1 do ..	do do 10 do
do Areca do ..	do do 10 do
do *Clerodendron* do (new) ..	do numerous in 4 do
do Coconut minus strain ..	do formed in 10 do
do Agave do (new) ..	do numerous in 4 do
do *Spondias* do (new) ..	do do 4 do
do *Hevea* do ..	do do 4 do
do Breadfruit do (new) ..	do do 4 do
P. colocasiæ ..	do many 10 do
P. parasitica var. *piperina* ..	do do 4 do

The isolate combines readily with heterothallic and homothallic isolates of *Phytophthora*. It forms oospores with fertile as well as non-fertile homothallic strains. But when grown in single strain cultures oospores are not formed. Further, when this isolate is paired with an isolate of *P. palmivora* from *Spondias mangifera* which had become neutral no oospores developed even after a month. This demonstrates the fact that oospore formation in paired cultures is governed by the biological nature of the isolates that are brought together and the neutral strains do no pair at all.

The size of the sexual bodies produced by this isolate in paired culture falls within the range recorded for *P. palmivora* or *P. parasitica* as shown below.

TABLE IX

Measurements of sexual bodies produced by P. parasitica *with other isolates of* Phytophthora

Particulars	Oogonia		Oospores	
	Mean μ	Range μ	Mean μ	Range μ
P. parasitica + *P. palmivora* (tomato) ..	26	21–31	20	15–22
do do (citrus 1) ..	27	24–34	21	15–28
do do (*Jatropha*) ..	29	24–37	22	18–29
do do (Coconut) ..	28	25–32	22	21–25
do *P. colocasiæ* ..	28	24–31	22	18–20
do *P. parasitica* var. *piperina* ..	28	21–34	23	16–25

The range of measurements of the oogonia of *P. parasitica* on agar media is 15–35 μ and of oospores 13–26 μ. In some strains the oospores "which mostly fill the oogonial cavity range from 12 μ to over 35 μ" (Tucker, 1931). The sizes of oogonia and oospores formed in homothallic or paired cultures of *P. palmivora* range from 16 to 39 μ and 12 to 28 μ respectively.

The two allegedly different species have almost identical ranges of size of sexual bodies and the oospores formed in the paired cultures included in these studies also fall within this range.

DISCUSSION

The results of the studies detailed above show the necessity for the revision of the current taxonomic classification of these isolates. The different isolates studied are at present grouped into *P. colocasiæ*, *P. palmivora*, *P. parasitica* and *P. parasitica* var. *piperina*. The criteria influencing the determination of species of *Phytophthora* include the nature of growth on culture media, temperature relations, size and shape of sporangia and chlamydospores, the readiness with which sexual bodies are formed, their size, the nature of the antheridia and pathogenicity of the isolates. We shall consider these factors with reference to the isolates under study and see how far they can be relied upon.

The nature of growth of different isolates on agar media exhibit certain differences. But these differences cannot be relied upon for specific differentiation. Some isolates of *P. parasitica* and *P. palmivora* exhibit almost

identical growths of aerial mycelium on oat agar and could not be distinguished from one another. Leonian (1925) has also found that his observations afforded no justification for the practice of making the production of aerial hyphæ a distinctly specific character. Numerous intergradations in the amount of aerial hyphæ may be produced by the strains of a single species. Hence this character cannot be relied upon. Tucker (1931) also found that the same single strain culture of *P. parasitica* may produce various types of growth on different media.

The same author has stated that the main difference between *P. parasitica* and *P. palmivora* is in their temperature relationship. The same differential behaviour is cited between *P. colocasiæ* and *P. parasitica* also. He found that *P. parasitica* grew on cornmeal agar at 35° C. while *P. palmivora* and *P. colocasiæ* did not. He further states that " the use of the ability to grow at certain temperatures as a criterion for the identification of species seems to be justified." Leonian (1934) in his studies on temperature relationships of many species of *Phytophthora* found that in both *P. parasitica* and *P. palmivora* some isolates grew at 35° C. while others did not. Mehrlich (1936) found that temperature relations for separating *P. parasitica* and *P. palmivora* do not hold good for isolates of *P. parasitica* from heart-rot of pine-apples. Six isolates of *P. parasitica* did not grow at 35° C. while four others did and all of them were morphologically alike.

In order to verify the behaviour of the local isolates one type culture of each of *P. colocasiæ*, *P. palmivora* and *P. parasitica* was inoculated in triplicate on oat agar in petri-dishes and kept in an incubator at 35° C.$\pm\frac{1}{2}$° C. When examined on the fifth day, all the three exhibited growth, the largest diameter being in *P. parasitica* and next in *P. palmivora* and still less in *P. colocasiæ*. Though there were differences in the amount of growth all of them had grown. Thus the ability to grow at 35° C. is exhibited by all the three isolates. Hence this reaction cannot be utilised for taxonomic purposes. Further the isolates under study are all tropical organisms and 35° C. is a temperature to which they will be exposed during certain parts of the year and consequently they must have become acclimatised to such high temperatures. The culture of the local isolate from castor can be kept alive for a long period. But the type culture of *P. parasitica* from Delhi died out in a few months under local conditions. It is, however, shown that the differences observed by Tucker between these three species does not always hold good.

Sporangial characters have been overemphasized by a number of mycologists in differentiating species of *Phytophthora*. *P. colocasiæ* is said to be

easily distinguished from other allied species by its elongated narrowly ovate sporangia which are shed with remnants of the pedicel attached to the base of the sporangium. When cultures of *P. colocasiæ* are examined these features are not found to be constant. Broadly oval sporangia as in *P. parasitica* or *P. palmivora* are also formed. Further some isolates of *P. palmivora* develop elongated sporangia resembling those of *P. colocasiæ* (Leonian, 1936; Thomas *et al.*, 1947). The size and shape of the sporangia in these three species are so variable and unstable that an undue emphasis should not be laid on these characters for specific differentiation. There are no constant differences between the sporangia of the three species.

The same may be said about the chlamydospores. These bodies are produced in varying numbers by the different isolates of these three species and no specific difference could be made out between them.

Considering the development of the oogonia and oospores it has been found that all the three species have been known to form these bodies in single strain cultures and no differences exist between them regarding the size attained by these bodies. The antheridium in all the three species is amphigynous. *P. colocasiæ* and *P. parasitica* were distinguished from *P. palmivora* by the readiness with which oospores were formed in single strain cultures of the two former species. Some isolates of *P. meadii* which is now considered as *P. palmivora* formed oospores readily. The studies recorded above have further shown that depending on the isolates all the three species are capable of forming oospores in single strain cultures. It has also been found that in all the three species non-oospore forming cultures are available. The isolates are non-oospore forming either soon after fresh isolation or after some generations on agar media. Other workers have also found (Tucker, 1931) that the occurrence of oogonia and oospores in culture in *P. parasitica* is uncertain. " Seldom do they appear promptly and frequently not at all." Thus this character cannot be relied upon and no difference is seen between the three species in the size or shape of oogonia, oospores or antheridia, when these are developed.

Pathogenicity has been given an undue importance in delimiting species. Though this character may be of value in obligate parasites, when dealing with organisms, like species of *Phytophthora* this method of differentiation is almost of no value for distinguishing species. *P. colocasiæ* was thought to be confined to *Colocasia antiquorium* and this phenomenon was made much of. But Thompson (1929) and Thet Su (1938) have found *P. colocasiæ* on *Piper betle.* Thomas *et al.* (1947) have isolated *P. palmivora* from *Colocasia antiquorum.* A consideration of the host range of *P. palmivora* and

P. parasitica in nature reveals that both are formed on most of the recorded host plants. Below are given some of the recorded hosts of the three species.

TABLE X

Statement showing some of the common recorded hosts of P. palmivora, P. colocasiæ *and* P. parasitica

Host	Country where recorded	Identification of pathogen	Parts affected	Isolated by
1. *Citrus* spp. ..	Bombay	*P. palmivora*	Foot rot and fruit rot	Uppal
	Madras	do	Fruit rot	Thomas *et al.*
	Philippines	*P. parasitica*		Reinking
	Porto Rico	do	do	Dreschter
2. *Cocos nucifera* ..	Madras	*P. palmivora*	Bud rot	Shaw and Sundararaman
	Philippines	*P. parasitica*	do	Reinking
	Porto Rico	*P. palmivora*	do	Tucker
3. *Colocasia antiquorum*	India	*P. colocasiæ*	Leaf spot and Blight	Butler and Kulkarni
	Madras	*P. palmivora*	do	Thomas *et al.*
	Java	*P. colocasiæ*	do	Raciborski
4. *Gossypium barbadense*	Porto Rico	*P. parasitica*	Boll rot	Tucker
	St. Vincent	*P. palmivora*	do	Ashby
	Montserrat	do	do	Wakefield
5. *Lycopersicum esculentum*	New York	*P. parasitica*	Fruit rot	Reddick
	U.S.A.	do	do	Lavelleé
	Madras	*P. palmivora*	do	Ramakrishna and Sowmini
6. *Piper betle* ..	Central Provinces (India)	*P. parasitica* var. *piperina*	Wilt	Dastur
	Bengal	*P. palmivora*	do	McRae
	Madras	do	do	Thomas *et al.*
	Malaya	*P. colocasiæ*	do	Thompson
	Burma	do	do	Thet Su
7. *Solanum melongena*	Philippines	*P. palmivora*		Reinking
	do	*P. parasitica*	Fruit rot	Ocfemia
	do	do	do	Reinking
8. *Theobroma cacao*	Java	*P. palmivora*	Pod rot	Ashby
	Ceylon	do	do	Gadd
	Surinam	*P. parasitica*	do	Stahel

The above list includes instances where the pathogen isolated from the same host affected by similar diseases has been differently named. The frequency with which *P. palmivora* and *P. parasitica* have been recorded on the same host plants denotes the identical pathogenic qualities of those two. It is surmised that the relative identification of the pathogen might have been influenced by the development of sexual bodies in cultures or their

ence. *P. colocasiæ* is however restricted in its parasitism. For a long e it was known only on *Colocasia antiquorium* but in Malaya Thompson 29) and in Burma Thet Su (1930) have recorded it on *Piper betle* also. mas *et al.* (1947) have isolated *P. palmivora* from leaves of *C. antiquorum.* tricted parasitism of certain strains of the same species is well known ungi. It is also known that the pathogenic ability of facultative suprotes can be changed by slow ' education ' of the particular strains. Therethe exclusive use of pathogenicity to distinguish species among facultasaprophytes is not a reliable guide.

The close relationship between these species is further illustrated by ease with which one is mistaken for the other. Thompson (1929) conled from his studies of a number of isolates of *Phytophthora* that *P. paraa* may develop homothallic and heterothallic strains and the latter can regarded as being atypical members of *P. palmivora.* The tobacco gus was originally described by Breda de Haan in 1896 as *P. nicotianæ.* lale (1922) observed the close similarity between this and *P. parasitica* ch was confirmed by Leonian (1925). Lester Smith (1927), however, erved that the size of the sporangium in *P. parasitica* agreed with that of *icotianæ* but considered the latter to be a strain or form of *P. palmivora* n its behaviour in paired cultures with isolates of that species. Ashby 8) included *P. nicotianæ* in *P. parasitica.* Tucker (1931) wanted to give a nguishing name to the organism responsible for black shank of tobacco named it *P. parasitica* var. *nicotianæ.* Thomas *et al* (1947) found that black shank organism could be classified as *P. palmivora* on account ts behaviour in paired cultures and the absence of any distinguishing acters to consider it as a separate species or variety. The frequent nges in the nomenclature of this fungus shows how the two species are much alike and are liable to be interchanged according to the isolate er study.

The readiness with which the isolates at present classified as *P. coloæ, P. palmivora* and *P. parasitica* combine in paired cultures and form pores is a further proof of their close specific affinity. Lenonian (1931) owed the behaviour of 85 cultures of *Phytophthora* belonging to his *nuivora* group '. The formation of oospores in paired cultures by 48 hese is considered by him and rightly too as due to heterothallism and hybridization between species. If we are to consider the pairing between *arasitica* and *P. palmivora* as one of hybridization as believed to be by asimhan (1930) there must be some features in the resulting oospores ch distinguish them from those formed when two heterothallic isolates *P. palmivora* are paired. Narasimhan took this view owing to the size

of the oospores formed when *P. parasitica* was paired with *P. palmivora* which he thought was intermediate between those of the oospores of the two species. But it is now known that the size of oospores obtained by Narasimhan in his paired cultures is even obtained in single strain cultures of *P. palmivora* or of *P. parasitica.* Therefore his reasoning that hybridization has taken place in his cultures is not tenable. The formation of oospores in paired cultures of the isolates included in these studies has to be considered as union between heterothallic forms of the same species and not as instances of hybridization between different species.

It may be mentioned here that ' plus ' and ' minus ' strains of *P. palmivora* were grown with *P. cambivora* and *P. cactorum.* Oospores did not develop in the cultures with the former species. In the cultures with the latter species oospores were formed but they were of the ' *Cactorum* ' species with paragynous antheridia in the majority of sexual bodies.

The results of these investigations point to the desirability of amalgamating *P. parasitica, P. palmivora, P. colocasiæ* and *P. parasitica* var. *piperina* into one species as there are no valid, reliable or constant differences between them to keep them separate. Leonian (1925) has already suggested the combination of all these under the binomial *P. omnivora.* This was objected to by Ashby (1928) who pointed out that the sporangia of *P. colocasiæ* are distinguishable from those of *P. parasitica* and the ready development of oospores separates it from *P. palmivora.* Later studies by various authors have shown that both these characters are not constant and are exhibited by the other species also. Another objection raised by Ashby (1928) is, in regard to the use of the binomial *P. omnivora.* The specific name ' *omnivora* ' was coined by De Bary without regard to the prior name of ' *cactorum* ' used to denote the same species (Fitzpatrick, 1930). Therefore the name *P. omnivora* becomes a synonymn of *P. cactorum* and cannot be revived to include the three species as intended by Leonian. Tucker (1931) has considered *P. omnivora* as a synonym of *P. cactorum.* In a later publication Leonian (1934) has suggested the merging of *P. parasitica* and *P. palmivora* under the latter species keeping *P. colocasiæ* as a separate species. Our studies support his original view that all the three species should be merged into one. The obvious question which arises is, which is the name to be retained for the species in which three old species are merged. The correct procedure according to the rules of nomenclature is to adopt the oldest name, *i.e., P colocasiæ.* Dr. Bisby who was consulted about the specific name to be adopted held the view that if we were satisfied about the necessity for merging all the three species into one, the specific name ' *colocasiæ* ' ought to be retained as it is the oldest and sufficiently well known. Accepting

Bisby's view it is proposed to combine *P. colocasiæ*, *P. palmivora* and *arasitica* into one species *P. colocasiæ*.

The behaviour of the isolates of this emended species in single strain paired cultures is variable. Some isolates are fertile and produce onia and oospores in single strain cultures quickly. Other isolates form e bodies very late. Both these may be described as homothallic and le. Still other isolates do not form oospores in single strains but combine lily with the plus and minus strains. These may be considered as homolic but non-fertile and require the sexual stimulation of another biologically ve isolate to form oospores. Two homothallic but non-fertile forms are capable of combination as the isolates of *P. colocasiæ* and *P. para-a* under study. Variations from this reaction are exhibted by some ates which produce more oospores with the 'plus' strain than with the nus' strain or *vice versa*. Since neutral isolates do not form oospores combination with homothallic non-fertile isolates the development of pores must be considered to be governed by biological (sexual) nature he isolate and not by the biochemical stimulation by the presence of any r isolate. Such homothallic non-fertile strains which exhibit a prefer- for the 'plus' or 'minus' strain might gradually give rise to the heterolic strains of the 'minus' or 'plus' types themselves. With continued wth on agar media some of these become neutral, and do not form pores with any combination of isolates. Thus from an original fertile othallic isolate, non-fertile homothallic or heterothallic or neutral strains be developed in course of time. This might represent the course of lopment of the sexual behaviour of this species in nature also with the lt that different isolates behave in different ways according to their genemake up. These changes can be attributed to new combinations, and egations that occur during and after the sexual reproduction in *Phytoph-a*. The germination of the oospore is usually accompanied by the otic division of the fertilised nucleus and this feature must account for segregation of factors and formation of new races and strains. Muta-s occurring during the life of the isolate in pure cultures lead to further ations.

Edgerton *et al.* (1944) have noticed during their studies on the genetics *Glomerella* that perithecia-forming strains, 'plus' strains and 'minus' ins exist in the isolates of the fungus. Perethecia-forming strains may bine with 'plus' or 'minus' strains leading to the formation of larger ber of perithecia. They have also seen that a 'plus' strain may give to a 'minus' strain or perithecia producing strain. Chilton and eler (1947) are of opinion that new strains of *Glomerella* arise by mutation

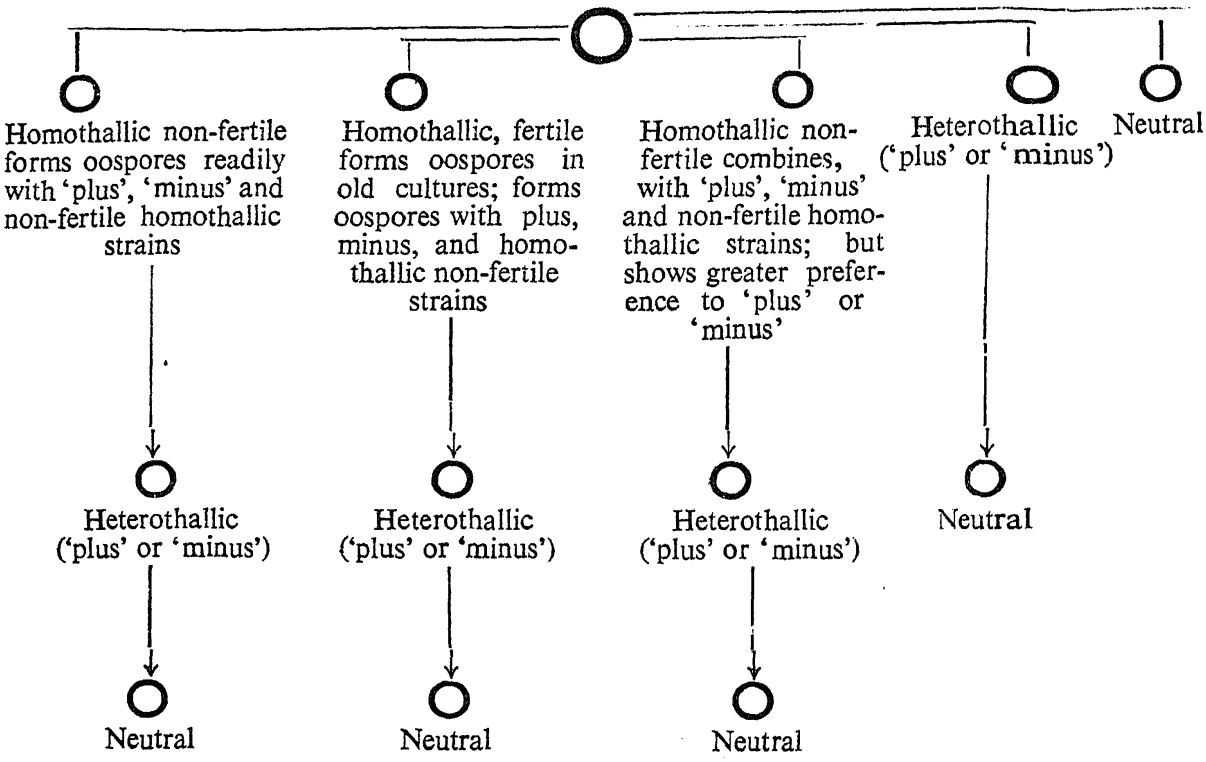
from the 'plus' strain. The above is comparable to what takes place in the cultures of *P. colocasiæ.*

Speculation on the origin of the different isolates studied is not attempted but a suggestion is put forward indicating the possible course of development of the different strains as shown below:

PARENT

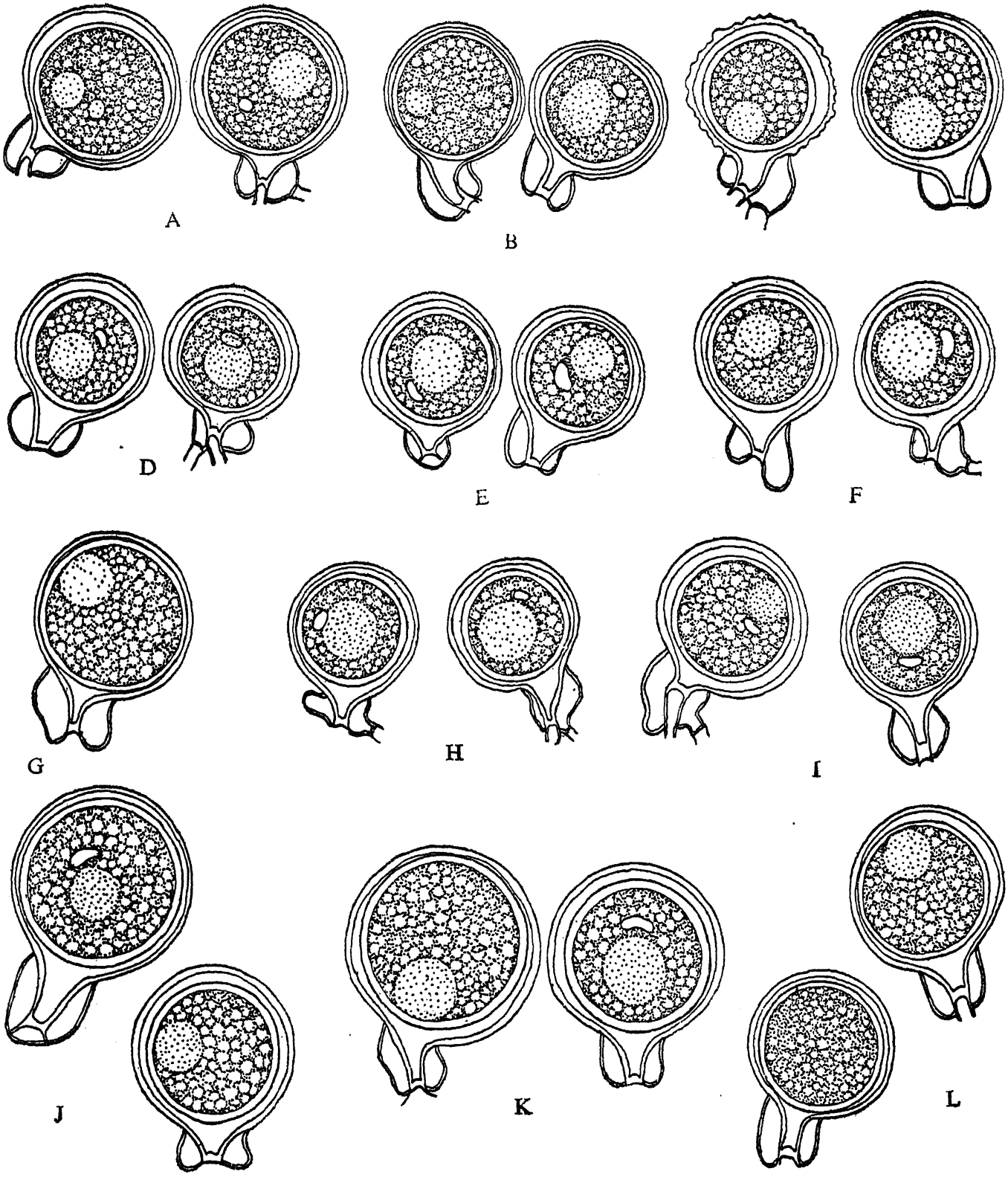
Homothallic, fertile

Forms oospores quickly



Leonian (1934) has emended the description of *P. palmivora* (including *P. parasitica* and *P. palmivora*). With slight alternations the description for the emended species of *P. colocasiæ* (Racib.) Thom. and Ram. now proposed will read as follows:—

The emended species of *Phytophthora colocasiæ* (Racib.) Thom. and Ram. (merging *P. colocasiæ*, *P. palmivora*, *P. parasitica* and its varieties) enjoys a world-wide distribution and has been recorded on numerous host plants thus exhibiting an omnivorous habit. The growths of this fungus on agar media exhibit wide variation. Aerial hyphæ may be luxuriant, scanty or sometimes absent; sub-merged hyphæ, smooth or gnarled, even or uneven; the temperature tolerance varies according to the country of origin of the isolate, from 30° C. to 37·5° C. Sporangia distinctly papillate, greatly variable in size and shape; chlamydospores spherical



The drawings of oospores have been made with the aid of an Abbe camera lucida at uniform magnification of × 680.

Oospores formed in paired cultures of different combinations :—

A.	*P. palmivora*	(plus, Tomato)	×	*P. parasitica* var. *piperina*
B.	do	(minus, Areca)	×	*P. parasitica*
C.	do	(minus, Coconut)	×	do var. *piperina*
D.	do	(plus, Tomato)	×	*P. parasitica*
E.	*P. colocasiæ*		×	do
F.	*P. palmivora*	(minus, *Jatropha*)	×	do
G.	do	(minus, Coconut)	×	do
H.	do	(plus, Citrus)	×	do
I.	do	(plus, Betelvine)	×	do
J.	do	(minus, Coconut)	×	*P. colocasiæ*
K.	do	(minus, Areca)	×	do
L.	do	(plus, Tomato)	×	do

or subspherical, light or deep coloured, terminal or intercalary; some isolates may produce more of these bodies than others. Sexual bodies present or absent: heterothallic, homothallic and neutral strains present; antheridia typically amphigynous; size of oogonia and oospores greatly variable, oogonia 13–41 μ, oospores 12–35 μ in diameter.

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Summary

Isolates of *Phytophthora* from castor, *Agave*, and breadfruit and authentic cultures of *P. parasitica*, *P. parasitica* var. *piperina* and *P. colocasiæ* were studied in detail in single strain cultures and in paired cultures in different combinations.

It was found that the isolates from the different hosts under study easily combined with *P. parasitica*, *P. parasitica* var. *piperina* and *P. colocasiæ*, forming oospores. These oospores are of the same type and fall within the range of size recorded for *P. palmivora* and *P. parasitica*. The criteria on which the species under investigation are classified are critically examined and it is found that no significant differences exist between them. The three species are able to grow at 35° C.

The readiness with which these combine to form oospores shows their specific affinity. It is argued that all the three species should be combined into one and the name *P. colocasiæ* is adopted for the emended species as it is the oldest.

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