GENERIC CONCEPTS IN THE PYTHIACEAE

BY

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The family Pythiaceae was created by SCHRÖTER (1897) to embrace the genera *Pythium*, described by PRINGSHEIM (1858), and *Nematosporangium*, originally described by FISCHER (1892) as a subgenus of *Pythium*. SCHRÖTER considered the Pythiaceae to be one of three families of the Saprolegniales while FISCHER considered that *Pythium* should be assigned to the single family Peronosporaceae of the Peronosporales. DE BARY (1863) founded the Peronosporaceae for a group of parasitic fungi of the genus *Peronospora*, to which he (1876) later added the genus *Phytophthora*. The similarity of *Peronospora*, *Phytophthora*, and *Pythium* led DE BARY (1881) to conclude that they all should be contained within the Peronosporaceae. Various authors concurred in this placement for the genera until FITZPATRICK (1923) proposed that *Phytophthora*, *Pythium*, and related genera which display successive development of sporangia, the absence of well-defined sporangiophores, and, less typically, deciduous sporangia, be maintained as congeners of the Pythiaceae. *Plasmopara*, *Peronospora*, and related genera which produce their typically deciduous sporangia simultaneously on well-defined sporangiophores were separated from the Pythiaceae and were maintained as congeners of the Peronosporaceae. Both families were treated as subdivision of the Peronosporales. This scheme of classification is employed by the writer and has been adopted by BUTLER and JONES (1949), GWYNNE-VAUGHAN and BARNES (1927), MATTHEWS (1931), TUCKER (1930), and others.

PYTHIUM

The genus *Pythium* was characterized by PRINGSHEIM as producing its swarmspores from the contents of the sporangium outside the sporangial opening and forming a single oospore within each oogonium. The type species, *P. monospermum* Prings., was described as possessing filamentous sporangia not unlike the hyphae. A single thick-walled oospore was formed that filled the spherical oogonium. The antheridia described and figured were all paragynous. Species have subsequently been described which resemble the type in having filamentous sporangia that are undifferentiated from the vegetative hyphae as in *P. gracile* Schenk, others in which the sporangia are filamentous but inflated as represented by *P. indigoferae* Butler, still others in which the sporangia are spherical and proliferous as in *P. proliferum* de Bary, and yet others with obovoid, conspicuously papillate sporangia as found in *P. helicoides* Drechs. All of these species with various sporangial forms possess spherical oogonia, paragynous antheridia, and typically contain a single oospore in each oogonium.

The mode of zoospore formation in these several examples is likewise similar. The production of zoospores is admirably described by BUTLER (1907) in his excellent account of the genus *Pythium*. He shows that the sporangia of both filamentous and spheroidal species germinate by the production of a discharge tube or beak that forms at some distance from the supporting sporangiophore from a swelling of the sporangial wall and the protrusion of the endosporangial lining. This hyaline cap or papilla continues to elongate and finally at its apex swells into a more or less spherical, thin-walled, evanescent vesicle into which the contents of the sporangium flow and where the final fashioning of the laterally biflagellate zoospores occurs. The length of the discharge tube varies greatly not only within a single species but between different species, and may even be absent and result in a sessile vesicle as in *P. proliferum*, or be long and tenuous and form the apical vesicle as much as 500 μ from the sporangium as in *P. gracile*. The similarity in oospore production and zoospore formation in these diverse sporangial types precludes dividing the genus into *Nematosporangium* and *Pythium* as advocated by SCHRÖTER, FITZPATRICK, and SIDERIS (1930). Further evidence for maintaining all these sporangial forms within the genus *Pythium* is given by MIDDLETON (1943).

EDSON (1915) described *Rheosporangium aphanidermatus* Eds. as the cause of seedling disease of *Beta vulgaris* L. COKER (1923) reported that this fungus should be considered a species of *Pythium*. FITZPATRICK concurred in this opinion and after comparing it with *Pythium* placed the fungus under the binomial *P. aphanidermatum* (Eds.) Fitz. SPARROW (1931) suggested that *Rheosporangium* may be a suitable name for species of *Pythium* with inflated filamentous sporangia. Since the fusion organs and mode of zoospore formation are similar in noninflated and inflated filamentous and spheroidal sporangial types, nothing is to be gained by placing noninflated filamentous sporangial species in *Nematosporangium* and inflated filamentous sporangial species in *Rheosporangium*. These genera should be abandoned in favor of *Pythium*.

The Pythiaceae bear many resemblances to the Lagenidiaceae both in respect to fusion organs and the formation of the laterally biflagellate zoospores. The Lagenidiaceae differ markedly from the Pythiaceae in that they are endobiotic and holocarpic. The site of zoospore formation in *Myzocytium* is variable. SPARROW (1936) reported that in *M. zoophthorum* Sparrow the zoospores are partially or wholly delimited within the sporangium, discharged through the emission tube, and mature at its apex in the absence of a vesicle. In *M. proliferum* Schenk, SPARROW (1943) showed that the zoospores mature in the evanescent vesicle. In *Lagenidium marchalianum* de Wildeman the zoospores are delimited within the sporangium and complete their maturation at the orifice of the discharge tube concurrent with the disintegration of the vesicle. In *L. entophytum* (Prings.) Zopf zoospores are formed in the vesicle.

The site of zoospore formation is also variable in *Pythium*. MIDDLETON indicated that sometimes the contents of the vesicle in *Pythium* was discharged in an undifferentiated state and that zoospores were delineated exogenously. Further study has revealed that zoospores may be formed within the sporangium in *P. irregulare* Buis. and *P. vexans* and that they escape through the orifice of the sporangial apex into the vesicle which disintegrates prior to the complete emptying of the sporangium. Occasionally the sporangial contents of *P. indigoferae* and *P. mamillatum* Meurs have been observed to spew out through the discharge tube into the surrounding water without being contained in a vesicle and to subsequently form zoospores. In other instances the contents have been partially delineated in the sporangium and are discharged through a short, stout, emission tube and complete their formation within the vesicle, then being released by rupture of the containing wall.

The sporangia of some *Pythium* species, such as *P. splendens* Braun, rarely germinate by production of zoospores but renew growth through the formation of from one to several germ tubes. The sporangia of *P. ultimum* Trow were described as germinating only by germ tubes. ANGELL (1950) indicated that the generic name of *P. ultimum* apparently needs revision since the sporangia of the genus are typified by the production of zoospores. ARK and MIDDLETON (1949) reported the sporangia of *P. ultimum* commonly germinated by production of zoospores rather than germ tubes and although this mode of germination is unusual it cannot be considered phenomenon alien to the species. It is perhaps appropriate to report here that a number of single sporangial cultures out of several hundred made from *P. ultimum* yielded lines that germinated by formation of zoospores. Similar handling of *P. splendens* likewise yielded lines that readily produced zoospores. It is interesting to note that in this species a few lines were also secured that readily formed fusion organs, whereas the occurrence of these structures is usually rare. The variation in the shape of the sporangia, the variation in type of germination and site of zoospore formation, and the regulation of these processes by environmental conditions suggest that these features have limited value as taxonomic criteria.

The sporangiophores in *Pythium* are characteristically poorly defined and usually support a single sporangium either as an intercalary or as an acrogenous structure. A few, such as *P. splendens*, bear their sporangia on a simple sympodial sporangiophore, but without nodal swelling at the point of sporangial attachment. Others, such as *P. intermedium* de Bary, produce catenulate sporangia at the tip of a simple, unbranched sporangiophore. Still others, such as *P. proliferum*, show proliferation of the sporangiophore.

Pythium spp. can usually be recognized by the appearance of their fusion organs. Although the oogonia may be echinulate or smooth, they rarely contain more than a single oospore. The antheridia are typically paragynous and never amphigynous. A very few species, such as *P. hypogynum* Middleton, exhibit antheridial cells enclosed within the oogonial stalk. It may be that *Pythium* is most readily distinguished from *Phytophthora* on the basis of these antheridial habits and the occurrence of filamentous and generally inconspicuously papillate spheroidal sporangia.

PHYTOPHTHORA

The genus *Phytophthora* was established by DE BARY following his research into the life history of the potato fungus. He described it as having acrogenous, obovoid, papillate sporangia borne on branched sporangiophores, with sporangia successively produced by continued growth of the branches. As the branch elongates the sporangium is pushed more or less to one side by an unequal swelling of the point to which it is attached. The node-like swellings of the sporangiophore are a conspicuous feature of the type species, *P. infestans* (Mont.) de Bary. The sporangia abstrict, and when lodged in water, germinate by the production of zoospores within the sporangium which are discharged through the disruption of the apical papilla. DE BARY did not observe oogonia, antheridia, or oospores. CLINTON (1910) discovered these structures in culture, but it remained for PETHYBRIDGE and MURPHY (1913) to demonstrate the origin and disposition of the oogonium and antheridium. They found the fusion organs in *P. infestans* were similar to those described by PETHYBRIDGE (1913) for *P. erythroseptica* Pethy. in which the oogonial incept grew up through the antheridial incept with the result that the basal part of the oogonium was within and surrounded by the antheridium. This type of antheridium is termed amphigynous as opposed to paragynous in which the antheridium is applied to the side of the oogonium and does not encircle its base.

The discovery of amphigyny in the type species *Phytophthora infestans* led PETHYBRIDGE to conclude that species with amphigynous antheridia, such as *P. erythroseptica*, *P. infestans*, and *P. phaseoli* Thax., should only be placed in the genus *Phytophthora*, and that other species described as *Phytophthora* but possessing paragynous antheridia, such as *P. cactorum* (L. and C.) SCHRÖT. and *P. syringae* Kleb., should be withdrawn and assigned to the newly created genus *Nozemia*. WILSON (1914) favored this separation of species and showed that the genus *Phloeophthora*, proposed by KLEBAHN (1905) for the incompletely described fungus that KLEBAHN (1909) later found to be *Phytophthora syringae*, had priority over *Nozemia*. *Nozemia* was discarded by LAFFERTY and PETHYBRIDGE (1922) after discovering that amphigynous antheridia sometimes occurred in cultures of *P. cactorum* and *P. syringae*. Other species, such as *P. hibernalis* Carne and *P. porri* Foister, also exhibit both amphigynous and paragynous antheridia.

A number of other genera have been described which would appear inseparable from *Phytophthora*. FITZPATRICK (1930) considers the genus *Kawakamia* described by MIYABE to be synonymous with *Phytophthora*. The presence of a pedicel attached to the abstricted sporangium characterizes *Kawakamia*, the fungus in other respects resembles *Phytophthora*. BLACKWELL (1949) described and illustrated the form and nature of the pedicel in her unusually definitive treatise on terminology in *Phytophthora* and conclusively demonstrated the pedicellate nature of the sporangia in *P. infestans*. Since pedicels are common to the type species there is no basis for retention of the genus *Kawakamia*.

Pythiacystis was created by SMITH and SMITH (1906) with the type *P. citrophthora* representing a parasite of citrus fruit. BARRETT (1917), FAWCETT (1920), and FITZPATRICK (1923) all indicated that *Pythiacystis* should apparently be merged with *Phytophthora* since the sporangiophores, sporangia, and production of zoospores were features common to both genera. Their synonymity was finally described by LEONIAN (1925).

PETERSEN (1909) described *Pythiomorpha* as a new genus on the basis of the production of zoospores within the sporangium and their liberation in the absence af a vesicle. The type species, *P. gonapodyides* Petersen, produced ovoid, proliferating sporangia, and was found on decaying organic material in water. The features which distinguish this fungus from *Phytophthora* are not obvious. BUISMAN (1927), a student of Prof. Dr JOHANNA WESTERDIJK, demonstrated in her discerning study of root rots incited by Phycomycetes, that the proliferous nature of the sporangia of *Pythiomorpha* was insufficient reason to separate the genus from *Phytophthora* which also proliferate their sporangia. She further noted that the occurrence of *Pythiomorpha* on organic matter in water is no reason for excluding it from *Phytophthora*. FITZPATRICK concurred in this disposition. Further evidence for combining the two genera is given in an exhaustive study by BLACKWELL, WATERHOUSE, and THOMPSON (1941).

BUISMAN was also alert to the similarity of *Blepharospora* to *Phytophthora*. The chestnut fungus, *B. cambivora* Petri (1918) was characterized by the infrequent production of inconspicuously papillate, proliferous sporangia which were borne on long, unbranched sporangiophores. Zoospores were produced within the sporangium and escaped through rupture of the apical papilla. BUISMAN demonstrated that these characters are not unique to *Blepharospora*, but occur also in *Phytophthora*, and recommended the merger of the two genera. TUCKER concurred in the transfer of *Blepharospora* to *Phytophthora.*

SIDERIS and PAXTON (1930) mentioned the association of *Pseudopythium phytophthoron* with pineapple fruits. In the absence of a published description by the authors the name becomes a *nomen nudum.* MEHRLICH (1932) presented conclusive evidence that this fungus is actually *Phytophthora cinnamomi* Rands. This instance is a good example of the difficulties encountered in attempting to describe members of the Pythiaceae solely on the basis of vegetative characteristics.

The formation of zoospores in *Phytophthora* has been reported by many mycologists and has been ably summarized by TUCKER and discussed and illustrated by BLACKWELL. The zoospores are typically delineated within the sporangium, escape through the apical aperature by dissolution of the papilla, and are occasionally briefly contained within the sessile evanescent vesicle. This process is not unique to *Phytophthora* as a similar process occurs in *Araiospora, Rhipidium,* and *Sapromyces,* of the Rhipidiaceae, and in *Basidiophora, Plasmopara, Peronoplasmopara,* some species of *Sclerospora,* and in some other members of the Peronosporaceae.

Zoospores are formed in the sporangium in *Sapromyces* and escape either directly into the surrounding medium or into the evanescent vesicle which ruptures and effects their release. *Sapromyces* sporangia also germinate by emitting their undifferentiated contents and forming zoospores exogenously. *Araiospora* and *Rhipidium* usually form their zoospores in the sporangia and release them through the ruptured papilla; the zoospores may or may not be temporarily confined by a vesicle. The fashioning of zoospores occasionally takes place in the vesicle. Sporangia sometimes germinate by germ tubes.

The germination of sporangia of *Plasmopara* is similar to that described for *Sapromyces* and *Pythiogeton,* while in the other mentioned genera of Peronosporaceae germination is more typically similar to *Phytophthora.*

DASTUR (1913), ROSENBAUM (1917), and BLACKWELL described and illustrated the formation of zoospores within the sporangium of *Phytophthora* and their movement into the vesicle prior to their release upon the disappearance of the vesicle. Sporangia of *P. cryptogea* Pethy. and Laff., *P. palmivora* Butler, and *P. parasitica* Dastur sometimes show protoplasmic cleavage within the sporangium and final zoospore fashioning in the sessile apical vesicle. At other times, notably in *P. palmivora,* the vesicle may be borne on a short stalk. Zoospores are occasionally formed in a stalked evanescent vesicle from apparently undifferentiated sporangial protoplasm.

The generic distinctions offered by BLACKWELL for the segregation of *Phytophthora, Pythiogeton,* and *Pythium* are clearly and convincingly presented. The application of the principle of place of sporulation is precluded by the gradation and overlapping of time of maturation, and multiplicity of form of germination known to occur. The inherent variability of biological material does not readily allow application of static descriptive taxonomic criteria.

Species of *Phytophthora,* like *Pythium,* are usually recognized without observations of zoospore formation. The morphology of the vegetative structures, sporangia, and organs of fusion provide the features necessary for identification. *Phytophthora* differs from *Pythium* in the production of compound sympodial sporangiophores, formation of nodal swellings on the sporangiophores, absence of filamentous sporangia, and the development of amphigynous antheridia. *Phytophthora* is usually considered to be somewhat more parasitic and less saprophytic than *Pythium* but the research of DE BRUYN (1922) convincingly demonstrates the saprophytic ability of *Phytophthora*. CANTINO (1950) suggests a phylogenetic difference between *Phytophthora* and other members of the Pythiaceae based on their nutritional requirements.

Despite variability in type of germination of vegetative reproductive structures and in the site of spore formation, these characters can still be considered indicative of generic distinction; however their usefulness should not be overemphasized. There are several features which may serve to distinguish *Phytophthora* from *Pythium*. Branched sporangiophores are not uncommon in *Phytophthora* but are uncommon in *Pythium*. Sporangia of *Phytophthora* are usually ovoid or obpyriform and often bear a conspicuous papilla while those of *Pythium* are generally filamentous, spheroidal, not often ovoid, and rarely bear a conspicuous papilla.

Perhaps the basic difference between *Pythium* and *Phytophthora* is the presence of amphigyny in *Phytophthora* and its absence in *Pythium*. This feature is unique to the Pythiaceae and not only provides an easily recognized structure, but exhibits an unusual developmental process. Additional support for this concept comes from the presence of amphigyny in the type species of *Phytophthora*.

PYTHIOGETON

Pythiogeton was erected by v. MINDEN (1916) to contain fungi that produce asymmetrical, proliferous or nonproliferous sporangia oriented with their long axes at right angles to the sporangiophore and that germinate by zoospores. A thin-walled, usually greatly elongated vesicle is formed at the narrowed end of the sporangium. The vesicle ruptures subsequent to the flow of sporangial contents into it and the zoospores are formed from the naked protoplast. The organs of fusion are not wel known and their production has been observed largely in mass water cultures. A single oospore is formed in each oogonium fertilized by paragynous antheridia. The antheridial stalk often coils about the oogonial stalk, or the stalks of both may become entwined. Further information on the organs of fusion and their association with vegetative reproductive structures is required before the status of the genus can adequately be appraised. *Pythiogeton* is usually distinguished from *Pythium* by its asymmetrical sporangia and the production of zoospores from the naked sporangial contents left upon collapse of the evanescent vesicle. Asymmetrical sporangia occur in several species of *Pythium*, particularly *P. marsipium* Drechs. Zoospores in this species are usually formed within the vesicle before it deliquesces. Zoospores in *P. volutum* Vanterpool, *P. irregulare*, and *P. vexans* sometimes arise from a naked protoplast resulting from the destruction of the vesicle. Though these occurrences may be irregular and atypical, they nonetheless demonstrate that sporangia have the propensity to produce zoospores from an extruded naked bit of protoplasm outside the sporangium and in the absence of a vesicle.

Retention of the genus *Pythiogeton* is suggested pending additional information pertinent to taxonomic criteria allowing its distinction from congeners of the Pythiaceae.

ZOOPHAGUS

SPARROW (1943) considered *Zoophagus* Sommerstorff to be a member of the Pythiaceae. *Zoophagus* possesses filamentous sporangia which produce zoospores in a terminal evanescent vesicle. A single oospore is formed within the oogonia following fertilization by paragynous antheridia. FITZPATRICK (1930) contended that the reproductive structures exemplified by *Zoophagus* are too similar to *Pythium* to justify recognition of *Zoophagus* as a separate genus. Observations of *Zoophagus* by the writer have shown that zoospores may be produced either in an acrogenous vesicle arising from a filamentous sporangium or from what appeared to be a naked protoplast at the apex of a short discharge tube in the absence of an organized vesicle. Fusion organs agreed with those described for the genus. Attempts to grow the fungus in pure culture on synthetic substrates were unsuccessful. A curious feature of the genus is the production of short, lateral, branched or unbranched hyphal extensions which serve to capture rotifers and other small aquatic animals. Although KARLING (1936) reported production of filamentous, unicellular, lateral vegetative structures which act as reproductive bodies in *Z. tentaclum* Karling, it seems unlikely that the fungus is a conidial Phycomycete. Until *Zoophagus* can be further studied, preferably in pure culture, it is proposed that it be retained as a genus closely related to *Pythium* but differing from it in possessing specialized vegetative structures used for the capture of small, water inhabiting animals.

DIASPORANGIUM

The genus *Diasporangium* was created by HÖHNK (1936) and *D. jonesianum* designated as the type species. The fungus was found in soil in association with *Pythium* and *Dictyuchus* and is only known from the original report. Sporangia are borne on short lateral branches arranged in whorls about the supporting hypha. They are at first spherical, but at maturity are more or less limoniform and oriented with the long axis at right angles to the sporangiophore. The sporangia germinate by the production of laterally biflagellate zoospores within the sporangium and without formation of a vesicle, by the emission of the naked protoplasm of the sporangium and its subsequent division into spherical masses representing zoospores, or by germ tubes. HÖNHK considered *Diasporangium* distinct from *Pythiogeton* by virtue of the symmetrical sporangia and the passive rather than forceful emission of the sporangial protoplasm. *Diasporangium* obviously differs from *Pythiogeton* by producing sporangia in whorls, which may possibly be a close monochasial sympodium; whether generic distinction on this basis is tenable will depend upon further study of the fungus and related species.

TRACHYSPHAERA

Trachysphaera fructigena Tabor and Bunting (1923) was described as a new genus and species for the fungus inciting the mealy pod disease of cocoa. With the possible exception of the oogonial protuberances, the fusion organs are identical to those of amphigynous *Phytophthora*. The vegetative reproductive structures are spherical, strongly echinulate, and are borne on short, rather tenuous stalks which may arise either singly from a simple vegetative branch, or in whorls from a swollen node of the branch. TABOR and BUNTING refer to the spiny vegetative reproductive bodies as conidia since they germinate only by the production of germ tubes. This condition may be analagous to that in *Pythium ultimum*. The production of spiny vegetative spores in whorls is indeed a unique feature, though their origin from swollen nodes is reminiscent of some species of *Phytophthora*. These organs differ from those of *Phytophthora* in being supported by secondary sporangiophores. *Trachysphaera* is obviously closely allied to *Phytophthora* but is retained as a distinct genus because of the type and form of the vegetative reproductive structures.

STIGEOSPORIUM

WEST (1916) assigned the binomial *Stigeosporium marattiacearum* West to a fungus occurring in the roots of several ferns, attributing the absence of fusion organs and the modification of vegetative reproductive bodies to its peculiar habitat. He reported the similarity of the fungus to *Phytophthora* in producing thick-walled spores resembling chlamydospores and the presence of hyphal elements resembling haustoria. GWYNNE-VAUGHAN and BARNES agreed that it bears some resemblance to *Phytophthora* and may be a member of the Pythiaceae. FITZPATRICK (1930) believed the fungus to be completely dissimilar from *Phytophthora* and perhaps related to *Allomyces* or *Blastocladia*. BUTLER (1938) contented that in spite of the curious chlamydospores observed in *Stigeosporium* their presence did not warrant retention of the genus. He considered it to be synonymous with *Rhizophagus*, an imperfect genus of the Endogonaceae. *Stigeosporium* therefore can be considered neither a valid genus nor a member of the Pythiaceae.

DISCUSSION

The foregoing discussion has shown that sporangia of the Pythiaceae germinate by the production of germ tubes and laterally biflagellate zoospores. Neither form of germination is unique to the Pythiaceae and is found in at least the Rhipidiaceae, Lagenidiaceae, and Peronosporaceae. Germ tubes permit renewed growth of the organism from sporangia, zoospores, or naked sporangial contents. Zoospores are produced from sporangia and naked sporangial contents. The site of zoospore formation is as variable within genera as it is between genera and therefore is of doubtful taxonomic value and significance. The typically monosporic oogonia of the Pythiaceae are also found in other families of the Phycomycetes. The oospores of the Pythiaceae differ from those of related groups in having an extremely thin epispore which is very difficult to distinguish from the outer oospore wall formed from the ooplasm. The thickness of the oospore is largely due to the size of the endospore wall. The character of the eucarpic thallus separates the genera of the Pythiaceae from the Rhipidiaceae and the holocarpic Lagenidiaceae. The Pythiaceae differ from the Peronosporaceae in producing their sporangia successively.

The writer suggests generic segregation into two groups on the basis of antheridial characters. *Pythium* and *Zoophagus* would represent one group in which the antheridia are hypogynous, paragynous and morphologically unidentifiable but in which antheridial nuclei are produced. *Phytophthora* and *Trachysphaera* would represent another group in which the antheridia are amphigynous and paragynous. The genera *Pythiogeton* and *Diasporangium* may be maintained or merged with *Pythium* depending upon the outcome of future studies on the significance of their sporangial form, mode of germination, and nature of the fusion organs. *Zoophagus* may be separated from *Pythium* by its production of specialized vegetative processes serving to capture small aquatic animals. *Trachysphaera* may be distinguished from *Phytophthora* by its sporangia. This concept recognizes priority of description and provides a morphologic basis for generic distinction; use of the mode of sporangial germination, which may be regulated by environmental conditions, is thereby avoided as a taxonomic feature.

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