

The taxonomy and biology of *Phytophthora* and *Pythium*

Abstract

The genera *Phytophthora* and *Pythium* include many economically important species which have been placed in Kingdom Chromista or Kingdom Straminipila, distinct from Kingdom Fungi. Their taxonomic problems, basic biology and economic importance have been reviewed. Morphologically, both genera are very similar in having coenocytic, hyaline and freely branching mycelia, oogonia with usually single oospores but the definitive differentiation between them lies in the mode of zoospore differentiation and discharge. In *Phytophthora*, the zoospores are differentiated within the sporangium proper and when mature, released in an evanescent vesicle at the sporangial apex, whereas in *Pythium*, the protoplast of a sporangium is transferred usually through an exit tube to a thin vesicle outside the sporangium where zoospores are differentiated and released upon the rupture of the vesicle. Many species of *Phytophthora* are destructive pathogens of especially dicotyledonous woody trees, shrubs and herbaceous plants whereas *Pythium* species attacked primarily monocotyledonous herbaceous plants, whereas some cause diseases in fishes, red algae and mammals including humans. However, several mycoparasitic and entomopathogenic species of *Pythium* have been utilized respectively, to successfully control other plant pathogenic fungi and harmful insects including mosquitoes while the others utilized to produce valuable chemicals for pharmacy and food industry.

Keywords: oomycota, pythiaceae, peronosporaceae, straminipila, chromista

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Introduction

Members of the genera *Phytophthora* de Bary and *Pythium* Pringsheim are economically important “fungal-like-organisms” or “pseudofungi” which have been widely studied throughout the world but their taxonomic treatment has been highly controversial. The production of globose oogonia in the sexual reproduction has placed them in the phylum Oomycota. Although members of Oomycota are similar to all filamentous fungi they have been excluded from Kingdom Fungi and placed in the Kingdom Chromista¹ along with several photosynthetic algal groups: brown algae (*Phaeophyta*), yellow green algae (*Xanthophyta*), golden algae (*Chrysophyta*) and diatoms (*Bacillariophyta*), that produce heterokont zoospores with two laterally inserted flagella, the anterior being tinsel-like and the posterior being smooth and whiplash, inserted at the same point. In order to better distinguish the colorless oomycetes from the pigmented algal allies, the term “straminopile” was introduced by Patterson,² based on the tubular hairs (mastigonemes) on the anterior flagellum of a heterokont zoospore as “straw with hairs”. It was formalized as a new kingdom Straminipila by Dick.³ The diploid (2N), cellulosic mycelium of oomycetes differs from the true fungi in producing oospores in sexual production and heterokont zoospores in asexual reproduction, whereas true fungi have chitinase, haploid (N) or dikaryotic (N+N) mycelium producing zygote, zygospores, ascospores or basidiospores in sexual reproduction and no zoospore or zoospore with single posterior whiplash flagellum in asexual reproduction.

The exclusion of oomycetes from Kingdom Fungi has been supported by molecular biology studies which however presented new problems to the classification of *Phytophthora* and *Pythium*. Morphologically, members of both genera are very similar in having

coenocytic, hyaline and freely branching mycelium although the hyphae of *Phytophthora* species are usually wider in diameter (5–7µm) and slow growing with approximately right angle branching whereas the hyphae of *Pythium* species are fast growing in general, narrower (4–6µm) wide, with the hyphae more flexuous or meandering on the agar plate. However, the definitive differentiation between them lies in the mode of zoospore differentiation and discharge. In *Phytophthora* species, the zoospores are differentiated within the sporangium proper and when mature, released in an evanescent vesicle at the sporangial apex, whereas in *Pythium* species, the protoplast of a sporangium is transferred usually through an exit tube to a thin vesicle outside the sporangium where zoospores are differentiated and released upon the rupture of the vesicle. For many years, they have been classified in the same family and same order: *Pythiaceae* and *Peronosporales*^{4,5} and were commonly referred to as Pythiaceae fungi.

There were attempts to separate them so that *Pythium* would be placed in family *Pythiaceae* whereas *Phytophthora* would be assigned to a new family *Phytophthoraceae*.^{6,7} However, this proposal has not received much support from the research community. On the other hand, recent molecular phylogenetic studies suggested that *Phytophthora* might be more closely allied with downy mildews like *Plasmopara* Schröter and *Peronospora* Corda.^{8,9} Thus, Kirk et al.,¹⁰ placed *Phytophthora* in family *Peronosporaceae* of order *Peronosporales* while retaining *Pythium* in family *Pythiaceae* of order *Pythiales*. In view of the fact that insufficient number of *Phytophthora* and *Pythium* species and none of the “unculturable” species of *Phytophthora* have been subjected to molecular analysis it might be premature to separate them from family *Pythiaceae* that they normally belong to. Many species of these two genera are potentially important plant pathogens^{11,12} and thus of great economic importance.

Phytophthora

The genus *Phytophthora* (Gr. Phytón, a plant; phthorá, destroyer) with 313 described species (www.mycobank.org) was established by de Bary in 1876¹³ with *P. infestans* as the type species. He recognized that the fungus causing late blight of potato in Europe in the 1840s, previously identified as *Botrytis infestans* Mont.,¹⁴ later *Peronospora infestans* (Mont.) Casp.,¹⁵ had unique conidiophore characteristics, which he considered distinct enough to be assigned a new genus name.

Species of *Phytophthora* can be readily identified by the aseptate hyphae with slight constriction at the base of its initially right-angled branches; by the ovoid, obpyriform to limoniform sporangia produced in succession on a typically sympodially branched, undifferentiated sporangiophore of indeterminate growth; by the differentiation of mature, laterally biflagellate zoospores within the sporangium proper; by its globose oogonium with single spherical oospore with thin or no periplasm and by antheridial configuration being amphigynous and/or paragynous.¹⁶ Most species of *Phytophthora* are soil-borne plant pathogens causing diseases of both herbaceous and woody mostly dicotyledonous plants, e.g. root rot, basal stem rot, leaf spot or blight as well as fruit rot. They can infect both cultivated and natural plants world-wide causing serious loss in agriculture and upsetting natural forest ecosystem, some of which have attained the status of major epidemics.^{17–19} Numerous new species were recently isolated from forests, streams and irrigation water but their pathogenicity have not been determined. Although *Phytophthora* species are well known for causing diseases of terrestrial plants, Govers et al.,²⁰ reported recently the widespread infection of a common seagrass species, *Zostera marina* (eelgrass) across the northern Atlantic and Mediterranean by *P. gemini* Man in't Velf, K. Rosend, Brouwe & de Cock, *P. inundata* Brasier, Sánch, Hern & Kirk and an unidentified species of *Phytophthora* threatening the conservation and restoration of vegetated marine coastal systems. The taxonomy of *Phytophthora* species has been traditionally based on morphological characters, e.g. the papillation, size, length/breadth ratio and caducity of sporangia as well as the ability to produce oospores in single cultures, antheridial configuration and oogonial size^{21–23} with the six morphological groups of *Phytophthora* created by Waterhouse²² widely accepted by researchers.

Hyphal swellings are not cut off by septa and when present may be single or clustered, terminal, intercalary or branching to form a network; spherical, oval to irregular, and vary considerably in size. They may be formed on agar plates but more commonly in water. Chlamydospores are sometimes confused with spherical hyphal swellings but they can be distinguished by a secondary wall, the presence of delimiting septum, and usually the internal reorganization of cytoplasm. They are hyaline to yellowish or brownish, thin to thick-walled (mostly 1–2 µm), terminal or intercalary.

There are three basic types of sporangia, based on the characteristics of the apex: (a) conspicuously papillate with hemispherical apical thickening over 3.5 µm deep (b) inconspicuously papillate (semi-papillate) with shallow apical thickening under 3.5 µm deep, and (c) non-papillate, without noticeable apical thickening. A plug may be formed in the sporangiophore, at the base of a papillate or semi-papillate sporangium. Just prior to zoospore release or when the non-papillate sporangia are exposed to air a slight thickening might be detected in non-papillate sporangia which thus appear as “semi-papillate”. The papillate and semi-papillate sporangia may be formed on agar media or host tissues, non-deciduous or deciduous in water with pedicels of variable length, and have narrow exit pores (under

7 µm) after the dissolution of the apical thickening. The non-papillate sporangia are usually formed only in water, non-deciduous, have wide exit pores (often over 10 µm) and the base of sporangium is not plugged so that the sporangiophore is capable of internal proliferation by producing a new sporangium “nested” within or extended on a new sporangiophore beyond the exit pore of the empty sporangium which often collapses after zoospore dehiscence. The process of internal proliferation can be repeated several times. Laterally biflagellate zoospores are formed within the sporangium and released in an evanescent vesicle, with the dissolution of the apical thickening for papillate and semi-papillate sporangium or inflation of the apex for non-papillate sporangium. The two flagella are inserted in the middle of a longitudinal groove of the ovoid zoospore (10–17 × 7–12 µm), with the anterior end slightly tapering while the posterior end roundish. The zoospore shape varies depending on the angle of observation, appearing as reniform or kidney-shaped only when viewed from the posterior end of the zoospore. The shorter anterior flagellum propels the zoospore with the longer, posterior flagellum trailing behind, serving as the rudder, and it glides smoothly in a spiral fashion while rotating clockwise along its longitudinal axis. In water, after a period of motility which can last up to 24 hr or more, the naked zoospore rounds up to form a spherical cyst (7–14 µm diam) with a cell wall while the flagella coil up and are discarded. An encysted zoospore may germinate by a germ tube, with or without a germ sporangium or by another zoospore, a process called “repeated emergence”. Occasionally, the sporangium can also germinate directly by one or more than one germ tubes at or near the apex, or close to the sporangiophore. The sporangium has been described as limoniform, obpyriform, ovoid or ellipsoidal, usually terminal, single, basally attached on an undifferentiated, unbranched or sympodially (close or lax) to irregularly branched, narrow sporangiophore (1–3 µm) wide. Occasionally, intercalary sporangia may be produced.

Phytophthora species can be either homothallic producing abundant sex organs readily in single cultures or heterothallic, requiring pairing in dual cultures with appropriate A1 or A2 mating types. Those isolates forming oospores with the A2 tester were designated as A1; those forming oospores with A1 tester, A2; those forming oospores with both A1 and A2 testers, A1A2; those that failed to form oospores, A0 (sterile or neuter). The oogonium is mostly terminal, globose to pyriform, hyaline, yellowish to brown, smooth but sometimes uneven or verrucose. The oospore is single, spherical, smooth, hyaline but sometimes yellowish; aplerotic leaving a conspicuous or an inconspicuous space between the relative thick oospore wall (1–3 µm or more) and the thin oogonial wall. In the strictest sense, oospores of *Phytophthora* are rarely plerotic although the term has been used by some researchers to refer to the condition when the oospore nearly fills the oogonium. There is usually one antheridium per oogonium. The antheridium may be paragynous, applied at the side of the oogonium, often near the oogonial stalk or amphigynous, encircling the oogonial stalk. The amphigynous antheridium may be unicellular or bicellular. The amphigyny is the result of penetration of the antheridial initial by the oogonial initial during the early stage of sexual reproduction.²⁴ The amphigynous antheridium is a unique feature of *Phytophthora*, shared only with the monotypic genus *Trachysphaera* Tabor & Bunting.²⁵ However, with the advent of molecular biology and automation, the concept of taxonomy has quickly changed so that Gallegly & Hong²⁶ used a combination of morphology and DNA fingerprints in their new key to *Phytophthora* whereas Ristaino²⁷ introduced a lucid key to the common *Phytophthora* species based on a series of interactive computer matrixes of morphological and molecular data. Attempts were made to develop a cyberinfrastructure

to facilitate the identification of *Phytophthora* species based solely on molecular data. Thus, Park et al.,²⁸ used the *Phytophthora* sequence database to develop a website: (www.phytophthoradb.org), whereas Grünwald et al.,²⁹ introduced another website: (www.Phytophthora-ID.org). Furthermore, there was a movement to shift from the six artificial morphological groups of Waterhouse²² to the establishment of phylogenetic clades of *Phytophthora* based on the molecular data to reflect a natural classification of special note is the establishment of eight clades established by Kroon et al.,³⁰ to be followed by ten clades by Blair et al.,³¹ and the existence of 10 clades among *Phytophthora* species is now well recognized.^{32,33} The morphological characteristic of the genus *Phytophthora* are illustrated by Figure 1. Terms used were defined by Blackwell.³⁴

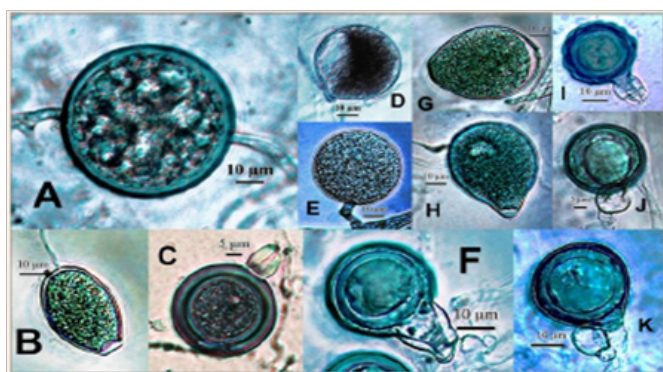


Figure 1 *Phytophthora*. A. Thick-walled chlamydospore. B. Semi-papillate sporangium. C, F. Amphigynous antheridia with smooth oogonia. D. Hyphal swelling. E. Thin-walled chlamydospore. G. Non-papillate sporangium. H. Papillate sporangium. I. Bicellular amphigynous antheridium with verrucose oogonium. J, K. Paragynous antheridia with smooth oogonia.

Pythium

The genus *Pythium* Pringsh., with 355 described species (www.mycobank.org), has been notoriously difficult for its taxonomy. Historically, there has also been great confusion regarding the validity of *Pythium* as a distinct genus. The genus was created by Pringsheim in 1858³⁵ and placed in the family *Saprolegniaceae*. However, *Pythium* Pringsh. was antedated by both *Pythium* Nees and *Artotrogus* Montagne.³⁶ Subsequently, proposals were made to conserve the genus *Pythium* Pringsh. against *Pythium* Nees³⁷ and *Astotrogus* Montagne³⁸ so that *Pythium* Pringsh became the de facto official genus name. However, there were attempts to split the genus *Pythium* into two genera to differentiate species with spherical sporangia from those with filamentous sporangia. Schröter³⁹ erected the family *Pythiaceae* in which he described *Pythium* having globose sporangia and *Nematosporangium* with filamentous sporangia. On the other hand, Sparrow⁴⁰ proposed species of *Pythium* with globose sporangia to be placed in a new genus, *Sphaerosporangium*.

Others tried to create various infrageneric taxa within *Pythium* but all these proposals have been rejected by Waterhouse,⁴¹ Plaats-Niterink,¹² and Dick.⁴² Nevertheless, recent phylogenetic studies based on molecular data have provided new evidence and rekindled interest to split the genus *Pythium*. Thus, Ko et al.,⁴³ erected a new genus *Aquaperonospora* Ko for species producing rigid, erect and branched sporangiophores forming sporangia synchronously on branchlet tips. Bala et al.,⁴⁴ proposed a new genus *Phytopythium* Abad for those species with globose to ovoid, often papillate and internally proliferating sporangia. Uzushashi et al.,⁴⁵ restricted the genus *Pythium* to those species with inflated or non-inflated filamentous sporangia

while creating four new genera to accommodate species with non-filamentous sporangia: *Ovatisporangium* Uzushashi, Tojo & Kakish for species with mainly ovoid to pyriform, sometimes irregular shaped-sporangia, *Elongiosporangium* Uzushashi, Tojo & Kakish for species with clavate to elongate sporangia, *Globisporangium* Uzushashi, Tojo & Hahish. for species with globose, sometimes proliferating sporangia and *Pilasporangium* Uzushashi, Tojo & Kakish. for species with globose, non-proliferating sporangia. Based on molecular phylogenetic analysis, de Cock et al.,⁴⁶ distinguished species of *Pythium* into 14 clades: A-K. All species in Clade K, including *Py. boreale* Duan, *Py. chamaehyphon* Sideris, *Py. cucurbitacearum* Takimoto, *Py. helicoides* Drechsler, *Py. indigofereae* Butler, *Py. oedochilum* Drechsler and *Py. vexans* de Bary were re-classified as species of *Phytopythium*⁴⁴ which is morphologically intermediate between *Phytophthora* and *Pythium*, with priority over and treated as synonymous with *Ovatisporangium*.⁴⁶ In distribution, the species of *Pythium* are cosmopolitan, widely distributed throughout the world ranging from tropical to temperate¹² and even arctic⁴⁷ and antarctic regions.⁴⁸

Economically, they are especially important as pathogens of monocotyledonous plants, causing serious damage to cereal crops and turf grasses, leading primarily to soft rot of fruit, rot of roots and stems, and pre- and post-emergence of seeds and seedlings by infecting mainly juvenile or succulent tissues.⁴⁹ Whereas *Pythium* diseases are common in tropical to temperate regions, cereal seedlings under snow could also be killed by *Pythium* spp.^{50,51} and an unidentified species of *Pythium* isolated from a colony of diseased leafy liverworts from Signy Island of Antarctic proved to be a potential plant pathogen to local vascular plants, based on artificial inoculation.⁵² Other species caused diseases in fish,⁵³ marine red algae^{54,55} and mammals including humans, causing pythiosis.^{56,57} On the other hand, some species of *Pythium* can produce valuable compounds for pharmaceutical and food industry, like polyunsaturated fatty acids, arachidonic acid and cicospentaenoic acid,⁵⁸ synthesize biotin, folic acid, pantothenic acid, riboflavin, thiamine and vitamin C, etc. and are capable of transforming sterols into cholesterol, ergosterol and sitosterol whereas the copious production of hydrolytic enzymes like pectinase, amylase and cellulase. might find uses in industry, for instance, in the breakdown of plant wastes for fermentation to produce biofuel.⁵⁹ There are some mycoparasitic species of *Pythium*, capable of controlling plant diseases due to other fungi.^{60,61} In fact, a pesticide has been developed from *Pythium* oligandrum and marketed for seed dressing, overhead spraying and soil drenches. In addition, other species of *Pythium* are entomopathogenic and can be used as biological control of mosquitoes and other harmful insects.^{62,63}

The identification and taxonomy of *Pythium* species has always been difficult due to the paucity of stable morphological characters despite the extensive studies in the early days by Mathews,⁶⁴ Sideris⁶⁵ and Middleton.⁶⁶ Waterhouse⁴¹ and Dick⁴² provided useful identification keys to the genus *Pythium*. Furthermore, Waterhouse⁶⁷ compiled the original descriptions of all *Pythium* species up to that time, but it was Plaats-Niterink¹² who wrote the most complete monograph on *Pythium* with a user-friendly identification key to 85 species which was well received by researchers. However, with the shape of sporangia and ornamentation of the oogonia serving as the primary diagnostic characters supplemented with other features including the size of oogonia and oospores, the extent of oogonial space occupied by the oospores, the origin, shape, number and method of attachment of antheridia to oogonia and the presence of hyphal swellings, the identification of *Pythium* species still

proves to be a challenging task due to the infraspecific variability and interspecific overlapping of these morphological data and the numerous new species reported since 1981. There is an urgent need for an updated identification key to include all species of *Pythium* described. Bouket et al.,⁶⁸ introduced a web-based identification program for 90 *Pythium* species based on morphological features. As in *Phytophthora*, molecular tools have become increasingly important in species differentiation of *Pythium*.⁶⁹ However, the large amount of molecular data obtained by many researchers have not yet been organized to provide a database website for species identification as in the case of *Phytophthora*. The phylogeny of *Pythium* based primarily on the sequencing of ITS region of the nuclear ribosomal DNA of 116 species and varieties revealed the existence of 11 major clades, designated as Clades A-K,⁷⁰ approaching a natural classification of the genus *Pythium*.

The sporangia of *Pythium* are usually produced in water and non-caducous. Some species have papillate sporangia but they lack the apical thickening characteristic of papillate sporangia in *Phytophthora*. The protoplasm of the sporangium is discharged through an exit tube to form a vesicle at the end where zoospores are differentiated and released upon the rupture of the vesicle. Morphologically similar to *Phytophthora*, zoospores of *Pythium* are laterally biflagellate and encyst after a period of motility to germinate into 1 or more than 1 germ tubes that will develop into mycelia. The sporangia can be filamentous, indistinguished from the rest of the mycelium, or slightly inflated to form dendroid structures or greatly inflated to form lobulate or toruloid complexes. In contrast, the sporangia can be globular, subglobular to ovoid, with or without internal proliferation; some may have apical papilla but lacks the apical thickening characteristic of those species of *Phytophthora* producing papillate or semi-papillate sporangia.

The sexual reproduction is by means of oogonia and antheridia. The oogonia can be globular to limoniform, terminal or intercalary on undifferentiated hyphae with the oogonial wall smooth or ornamented with projections of various length and evenly or unevenly distributed. The unicellular antheridia can be sessile or intercalary on the hyphae or terminal on a special stalk; monoclinal if they originate from the oogonial stalk, diclinous if they originate from a different hypha not closely connected with the one subtending the oogonium or hypogynous if the proximal portion of the oogonial stalk becomes an antheridium. The oogonium usually contains one or occasionally more than one spherical, smooth oospores which can be aplerotic or plerotic with the entire oogonial space fully occupied by the oospore. The oospore wall can be thin to thick. All species of *Pythium* with the exception of about seven species (*Py. catenulatum* Mathews, *Py. flevoense* Van der Plaats-Niterink, *Py. heterothallicum* Campbell & Hendrix, *Py. intermedium* de Bary, *Py. macrosporum* Vaartaja & Van der Plaats-Niterink, *Py. splendens* Braun and *Py. sylvaticum* Campbell & Hendrix) are homothallic, producing sex organs in single cultures.

Hyphal swellings can be present, often indistinguishable from young spherical oogonia or sporangia and are capable of germination to form a new mycelium; terminal, intercalary or catenulate, non-deciduous but can be deciduous in *Py. intermedium*. Thick-walled chlamydospores are rare, occurring only in *Py. dimorphum* Hendrix & Campbell and *Py. tracheiphilum* Matta. Appressoria are slight swellings formed by hyphae, especially when in contact with the walls of the Petri dishes, with various shapes and sizes, ranging from sickle-, club- or sausage-shaped to subglobose, single, terminal or intercalary forming chains or clusters.

The morphological characteristics of *Pythium* are summarized in Figure 2 & 3.

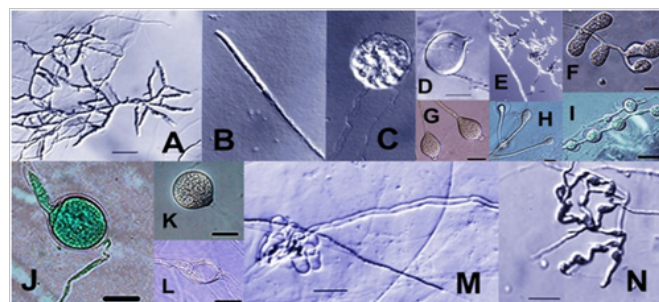


Figure 2 *Pythium*. A-C. Filamentous sporangia with single sporangium developed from hyphal tip (B) and zoospore formation in a vesicle at the end of an empty sporangium (C). D. Empty bursiform sporangium with short exit tube. F. Lobulate sporangium. G. Papillate globular sporangium. J. Globular sporangium with medium exit tube. H, L. Internally proliferating sporangia. M. Empty lobulated sporangium with long exit tube. E, N. Appressoria. I, K. Intercalary and terminal hyphal swellings. (All scale bars: 20µm; B,C at the same magnification as D).

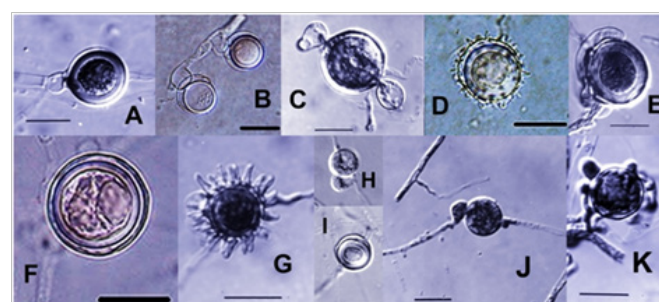


Figure 3 *Pythium*. A. Plerotic oospore with hypogynous antheridium. B. Aplerotic oospores with intercalary, basal antheridia. C. Oogonium with two crook-neck antheridia. D, G. Ornamented oogonia with conical projections in D and digital projections in G. E. Elongated, curved antheridium attached laterally on the oogonial surface. F, I. Smooth oogonium with aplerotic oospores. H. Oogonium with monoclinal antheridium. J. Oogonium with diclinous antheridium. K. Oogonium surrounded by several antheridia. (All scale bars at 20µm; H at the same magnification as I).

Conclusion

Although morphological characteristics will still serve as the basis for identification of *Phytophthora* and *Pythium* species^{12,27,29} it is clear that further studies using various molecular biology techniques are urgently needed to study the phylogeny of as many isolates as possible of all known species of these two economically highly important genera in order to develop a natural classification and rapid tools for identification of the unknown isolates especially when some key morphological characters are lacking. In *Phytophthora*, useful websites have been developed^{28,29} to allow species identification by BLAST against the collections in GenBank based primarily on similarity coefficient of the sequential analysis of the rDNA, especially the ITS region. However, the sequences housed in GenBank have not been carefully curated and mistakes could be made but this approach still seems to be the most promising as long as the isolates deposited could be checked for accuracy in identification and other molecular markers used more often by other researchers. In the future, species identification by automation should be the ultimate goal. Some species like *P. cyperi* and *P. polygoni* have been considered “unculturable” and attempts should be conducted to develop a

medium that can support their growth for studies. Meanwhile, at least they should be compared with other culturable species based on the nucleotide sequence and other molecular markers to determine their relationships. Tyler (personal communication) just completed an analysis of the nucleotide sequence of *P. polygoni* and found it to form a previously undescribed subgenera clade of *Phytophthora*. It is of interest to note recent isolations of *Phytophthora*-like organisms from natural and semi-natural ecosystems in Europe, Chile and Vietnam and based on morphological and phylogenetic studies they were treated a new sister genus of *Phytophthora*: *Nothophytophthora* gen. nov. Jung et al.⁷¹ As for *Pythium*, no data base has been developed to date to allow species identification based on molecular studies. It would be extremely useful if a contemporary, rigorous website can be constructed in the near future to allow more rapid identification of *Pythium* species based on molecular data because compared with *Phytophthora* species, the morphological characters of *Pythium* are even more complicated and variable.

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None.

Conflict of interest

The author declares no conflict of interest.

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