Phytopathology® • 2025 • 115:573-586 • https://doi.org/10.1094/PHYTO-11-24-0372-LE

Letter to the Editor

Preserving the Biologically Coherent Generic Concept of *Phytophthora*, "Plant Destroyer"

"We can see no reason why a Darwinian should adopt the concept of paraphyly" **(Ernst Mayr and Walter Bock 2002)**

Clive M. Brasier,[1,†] Niklaus J. Grünwald,[2,†] Tyler B. Bourret,[3] Francine Govers,[4] Bruno Scanu,[5]
David E. L. Cooke,[6] Tanay Bose,[7] David L. Hawksworth,[8] Z. Gloria Abad,[9] M. Victoria Albarracin,[10]
Wael Alsultan,[11] Astrid E. Altamirano-Junqueira,[12] Arild R. Arifin,[13] Matthew J. Arnet,[14]
Herbert Dustin R. Aumentado,[15] József Bakonyi,[16] Wei H. Belisle,[17] Alessandra Benigno,[18] John C. Bienapfl,[19]
Guillaume J. Bilodeau,[20] Jaime E. Blair,[21] Leticia Botella,[22] Andrea Brandano,[5] Santa Olga Cacciola,[23] Ignazio Carbone,[24]
Vanina L. Castroagudin,[19] Narayanan Chaendaekattu,[25] Jonathan D. Consford,[26] Tamara Corcobado,[27]
Paul A. Covey,[28] Hazel A. Daniels,[29] Antonio Deidda,[5] Anne E. Dorrance,[30] Erika N. Dort,[31] André Drenth,[32]
Fryni Drizou,[33] Edouard Evangelisti,[34] Sebastian N. Fajardo,[35] Yufeng Fang,[36] Christopher M. Ference,[37]
Susan J. Frankel,[38] Erica M. Goss,[39] David I. Guest,[40] Giles E. S. J. Hardy,[41] Anna R. H. Harris,[1]
Mehari Desta Hawku,[42] Kurt Heungens,[43] Chuanxue Hong,[44] Ian J. Horner,[14] Marília Horta Jung,[22]
Olumayowa J. Iyanda,[45] Brittney-Aidan Jamieson,[7] Steven N. Jeffers,[46] Howard S. Judelson,[47] Muhammad Junaid,[48]
Eleni Kalogeropoulou,[49] Sophien Kamoun,[50] Seogchan Kang,[51] Takao Kasuga,[52] Tomáš Kudláček,[22,53]
Jared LeBoldus,[54,55] Christopher A. Lee,[56] DeWei Li,[57] Alejandro K. Llanos,[58] Horacio D. Lopez-Nicora,[59]
Helena Machado,[60] Gaetano Magnano di San Lio,[61] Cristiana Maia,[62] Kajal Mandal,[63,64] Patricia Manosalva,[47]
Frank N. Martin,[65] Michael E. H. Matson,[66] Rebecca L. McDougal,[29] John M. McDowell,[67] Richard W. Michelmore,[68]
Ivan Milenković,[22,69] Salvatore Moricca,[18] Reza Mostowfizadeh-Ghalamfarsa,[70] Zoltán Á. Nagy,[22]
Ekaterina V. Nikolaeva,[71] Paula Ortega-López,[72] Trudy Paap,[7] Camilo H. Parada-Rojas,[54] Francesca Peduto Hand,[58]
Ana Pérez-Sierra,[73] Martin Pettersson,[74] Pramod Prasad,[75] Alina S. Puig,[76] Milica Raco,[54] Nasir A. Rajput,[77]
Jean B. Ristaino,[24] Suzanne Rooney-Latham,[17] Michael F. Seidl,[78] Simon F. Shamoun,[79] Alejandro Solla,[80]
Christoffel F. J. Spies,[81] Martha A. Sudermann,[54] Tedmund J. Swiecki,[82] Miaoying Tian,[83] Sucheta Tripathy,[63,64]
Seiji Uematsu,[84] Kris Van Poucke,[43] Aikaterini E. Vichou,[49] Monika Walter,[14] Joan F. Webber,[1] Nari M. Williams,[14]
Michael J. Wingfield,[7] Dhananjay Yadav,[85] Xiao Yang,[86] and Thomas Jung[22,†]

[1] Forest Research, Alice Holt Lodge, Farnham, GU10 4LH, Surrey, U.K.
[2] Horticultural Crops Disease and Pest Management Research Unit, U.S. Department of Agriculture-Agricultural Research Service, Corvallis, OR 97330, U.S.A.
[3] Mycology and Nematology Genetic Diversity and Biology Laboratory, U.S. Department of Agriculture-Agricultural Research Service, Beltsville, MD 20705, U.S.A.
[4] Laboratory of Phytopathology, Wageningen University and Research, 6708 PB Wageningen, the Netherlands
[5] Department of Agricultural Sciences, University of Sassari, 07100 Sassari, Italy
[6] The James Hutton Institute, Invergowrie, Dundee, DD2 5DA, U.K.
[7] Department of Biochemistry, Genetics, and Microbiology, Forestry and Agricultural Biotechnology Institute (FABI), University of Pretoria, Hatfield, Pretoria 0082, South Africa
[8] Royal Botanic Gardens, Kew, Richmond, TW9 3AB, U.K.
[9] U.S. Department of Agriculture-PPQ Science & Technology, McDonough, GA 30252, U.S.A.
[10] U.S. Department of Agriculture-APHIS, Plant Protection and Quarantine. Permitting and Compliance Coordination, Riverdale, MD 20737, U.S.A.
[11] MK Agronomy B.V., Roelofarendsveen, the Netherlands
[12] University of São Paulo, Luiz de Queiroz College of Agriculture. Av. Pádua Dias, 11-Agronomia, Piracicaba-SP, 13418-900, Brazil
[13] Washington State University, Tree Fruit Research and Extension Center, Wenatchee, WA 98801, U.S.A.
[14] The New Zealand Institute for Plant and Food Research Limited, Havelock North 4157, New Zealand
[15] Center of Excellence in Fungal Research, Mae Fah Luang University, Chiang Rai 57100, Thailand
[16] Plant Protection Institute, HUN-REN Centre for Agricultural Research, Fehérvári út 132-144, H-1116 Budapest, Hungary
[17] California Department of Food and Agriculture, Plant Pest Diagnostics Center, Sacramento, CA 95832, U.S.A.
[18] Department of Agricultural, Food, Environmental and Forest Sciences and Technologies (DAGRI), Plant Pathology and Entomology Division, University of Florence, Firenze 50144, Italy
[19] U.S. Department of Agriculture-APHIS-PPQ Science and Technology, Plant Pathogen Confirmatory Diagnostics Laboratory, Laurel, MD 20708, U.S.A.

[†] Corresponding authors: C. M. Brasier; clive.brasier@forestresearch.gov.uk, N. J. Grünwald; nik.grunwald@usda.gov, and T. Jung; thomas.jung@mendelu.cz

C. M. Brasier and N. J. Grünwald are co-first authors.

The author(s) declare no conflict of interest.

---

[20] Canadian Food Inspection Agency, Ottawa Laboratory Fallowfield, Ottawa Plant Laboratory, Ottawa K2J 4S1, Canada
[21] Franklin & Marshall College, Department of Biology, Lancaster, PA 17603, U.S.A.
[22] Department of Forest Protection and Wildlife Management, Phytophthora Research Centre, Mendel University in Brno, 613 00 Brno, Czech Republic
[23] Department of Agriculture, Food and Environment (Di3A), University of Catania, 100-95123 Catania, Italy
[24] Department of Entomology and Plant Pathology, North Carolina State University, Raleigh, NC 27695, U.S.A.
[25] Rubber Research Institute of India, Kottayam 686009, India
[26] Department of Plant and Environmental Sciences, New Mexico State University, Las Cruces, NM 88003, U.S.A.
[27] Austrian Research Centre for Forests (BFW), Department of Forest Protection, Unit of Phytopathology, 1130 Vienna, Austria
[28] Cargill, Fort Collins, CO 80525, U.S.A.
[29] Scion Research (New Zealand Forest Research Institute Limited), Rotorua 3010, New Zealand
[30] Department of Plant Pathology, The Ohio State University, Wooster, OH 43210, U.S.A.
[31] Department of Forest & Conservation Sciences, Faculty of Forestry, University of British Columbia, Vancouver, BC V6T 1Z4, Canada
[32] The University of Queensland, Centre for Horticultural Science, Brisbane, Australia
[33] Institute of Mediterranean Forest Ecosystems, Hellenic Agricultural Organisation-Dimitra, Terma Alkmanos, 11528 Athens, Greece
[34] Institut Sophia Agrobiotech, UMR INRAE 1355, CNRS 7254, Université Côte d'Azur Sophia Antipolis, France
[35] Department of Plant Pathology, University of California, Davis, CA 95616, U.S.A.
[36] GreenLight Biosciences Inc., Durham, NC 27709, U.S.A.
[37] U.S. Department of Agriculture-Agricultural Research Service, U.S. Pacific Basin Agricultural Research Center, Hilo, HI 96720, U.S.A.
[38] U.S. Forest Service, Pacific Southwest Research Station, Vallejo, CA 94592, U.S.A.
[39] Department of Plant Pathology and Emerging Pathogens Institute, University of Florida, Gainesville, FL 32611, U.S.A.
[40] Sydney Institute of Agriculture, School of Life and Environmental Sciences, The University of Sydney, Sydney, NSW 2006, Australia
[41] Harry Butler Institute, Murdoch University, Murdoch, WA 6150, Australia
[42] Department of Crop Sciences, College of Agriculture, Animal Sciences and Veterinary Medicine, University of Rwanda, Musanze, Rwanda
[43] Flanders Research Institute for Agriculture, Fisheries, and Food (ILVO), Merelbeke 9820, Belgium
[44] Virginia Polytechnic Institute and State University, Virginia Beach, VA 23455, U.S.A.
[45] Afe Babalola University, Ado-Ekiti Department of Agricultural Sciences, College of Sciences, Ado-Ekiti 5454, Nigeria
[46] Department of Plant and Environmental Sciences, Clemson University, Clemson, SC 29634, U.S.A.
[47] Department of Microbiology and Plant Pathology, University of California, Riverside, CA 92521, U.S.A.
[48] Cocoa Research Group, Faculty of Agriculture, Hasanuddin University, Kampus Unhas Tamalanrea, 90245 Makassar, Indonesia
[49] Benaki Phytopathological Institute, Scientific Directorate of Phytopathology, Laboratory of Mycology, Athens 14561, Greece
[50] The Sainsbury Laboratory, University of East Anglia, Norwich Research Park, Norwich, NR4 7UH, U.K.
[51] Department of Plant Pathology and Environmental Microbiology, Pennsylvania State University, University Park, PA 16802, U.S.A.
[52] U.S. Department of Agriculture-Agricultural Research Service, University of California, Davis, CA 95616, U.S.A.
[53] University of Greifswald, Institute for Mathematics and Computer Science & Center for Functional Genomics of Microbes, 17489 Greifswald, Germany
[54] The Department of Botany and Plant Pathology, The Oregon State University, Corvallis, OR 97331, U.S.A.
[55] The Forest Engineering, Resources and Management Department, The Oregon State University, Corvallis, OR 97331, U.S.A.
[56] California Department of Forestry and Fire Protection, Trinidad, CA 95570, U.S.A.
[57] The Connecticut Agricultural Experiment Station Valley Laboratory, Windsor, CT 06095, U.S.A.
[58] Universidad Nacional Agraria La Molina, Lima 12, Peru
[59] Department of Plant Pathology, The Ohio State University, Columbus, OH 43210, U.S.A.
[60] Instituto Nacional de Investigação Agrária e Veterinária I.P. Av. da República, Quinta do Marquês, 2780-159 Oeiras, Portugal
[61] University Mediterranea of Reggio Calabria, Department of Agriculture, 89124 Reggio Calabria, Italy
[62] Centre of Marine Sciences (CCMAR), Universidade do Algarve, Campus de Gambelas, 8005-139 Faro, Portugal
[63] CSIR-Indian Institute of Chemical Biology, Academy of Scientific and Innovative Research (AcSIR), Kolkata 700032, India
[64] CSIR-Human Resource Development Centre, Ghaziabad 201002, India
[65] U.S. Department of Agriculture-Agricultural Research Service, Crop Improvement and Protection Research Unit, Salinas, CA 93905, U.S.A.
[66] Mars Incorporated, Davis, CA 95616, U.S.A.
[67] School of Plant and Environmental Sciences, Virginia Polytechnic Institute and State University, Blacksburg, VA 24061, U.S.A.
[68] The Genome Center, University of California, Davis, CA 95616, U.S.A.
[69] University of Belgrade, Faculty of Forestry, 11030 Belgrade, Serbia
[70] Department of Plant Protection, School of Agriculture, Shiraz University, Shiraz 7144113131, Iran
[71] Pennsylvania Department of Agriculture, Harrisburg, PA 17110, U.S.A.
[72] Real Jardín Botánico (RJB-CSIC), 28014 Madrid, Spain
[73] Instituto Valenciano de Investigaciones Agrarias Carretera, 46113 Moncada, Valencia, Spain
[74] Division of Biotechnology and Plant Health, Norwegian Institute of Bioeconomy Research (NIBIO), Ås 1431, Norway
[75] ICAR-Indian Institute of Wheat & Barley Research, Regional Station, Flowerdale, Shimla 171002, India
[76] U.S. Department of Agriculture-Agricultural Research Service Foreign Disease-Weed Science Research Unit, Frederick, MD 21702, U.S.A.
[77] Department of Plant Pathology, University of Agriculture, Faisalabad 38000, Pakistan
[78] Theoretical Biology & Bioinformatics, Utrecht University, 3584CH Utrecht, Netherlands
[79] Natural Resources Canada, Canadian Forest Service Pacific Forestry Centre, Victoria, BC V8Z 1M5, Canada
[80] Universidad de Extremadura, Faculty of Forestry, 10600 Plasencia, Spain
[81] Agricultural Research Council - Plant Health and Protection, Stellenbosch 7599, South Africa
[82] Phytosphere Research, Vacaville, CA 95687, U.S.A.
[83] Department of Plant Pathology, University of Georgia, Tifton, GA 31794, U.S.A.
[84] Laboratory of Molecular and Cellular Biology, Department of Bioregulation and Bio-interaction, Tokyo University of Agriculture and Technology, Tokyo 183-8509, Japan
[85] East West Seed International, Village Rambha, Indri, Nilokheri 132117, India
[86] Plant and Pest Diagnostic Clinic, Department of Plant Industry, Clemson University, Pendleton, SC 29670, U.S.A.

Accepted for publication 4 March 2025.

Abstract

Phytophthora is a long-established, well-known, and globally important genus of plant pathogens. Phylogenetic evidence has shown that the biologically distinct, obligate biotrophic downy mildews evolved from *Phytophthora* at least twice. Because, cladistically, this renders *Phytophthora* "paraphyletic," it has been proposed that *Phytophthora* evolutionary clades be split into multiple genera (Crous et al. 2021; Runge et al. 2011; Thines 2023, 2024). In this letter, we review arguments for the retention of the generic name *Phytophthora* with a broad circumscription made by Brasier et al. (2022) and by many delegates at an open workshop organized by The American Phytopathological Society. We present our well-considered responses to the genus splitting proposals, both in general terms and in terms of the specific proposals for new genera, alongside new information regarding the biological properties and mode of origin of the *Phytophthora* clades. We consider that the proposals are mostly non-rigorous and not supported by the scientific evidence. Further, given (i) the apparent lack of any distinguishing biological characteristics (synapomorphies) between the *Phytophthora* clades; (ii) the fundamental monophyly of *Phytophthora* in the original Haeckelian sense (Haeckel 1877); (iii) the fact that paraphyly is not a justification for taxonomic splitting; and (iv) the considerable likely damage to effective scientific communication and disease management from an unnecessary breakup of the genus, we report that workshop delegates voted unanimously in favor of preserving the current generic concept and for seeking endorsement of this view by a working group of the International Commission on the Taxonomy of Fungi.

Keywords: clades, cladistics, disease management, downy mildews, oomycetes, Pangea, paraphyly, phylogeny, plant biosecurity, scientific communication, taxonomy

In modern taxonomy, species circumscriptions are often relatively well defined. However, genera are still often loosely described as groups of species with similar characters or biological properties derived from a common ancestor. In consequence, their circumscription can be more open to debate, especially in the context of different macroevolutionary theories. This has recently become the case for the genus *Phytophthora*, a globally significant group of destructive plant pathogens affecting plants in forests, horticulture, agriculture, natural ecosystems, and urban landscapes (Brasier et al. 2022).

The genus *Phytophthora* was first described almost 150 years ago (de Bary 1876), and for nearly a century, a broad generic concept, promulgated in the 1930s to 1960s mainly by C. M. Tucker and G. M. Waterhouse (Abad et al. 2023; Brasier 1991; Brasier et al. 2022; Erwin and Ribeiro 1996; Waterhouse et al. 1983), was almost unanimously accepted by *Phytophthora* researchers and plant health practitioners worldwide. Throughout this period, systematic interest was largely focused on the morphology-based groups proposed by Waterhouse (1963). By the early 1990s, however, more holistic, population-based taxonomic concepts for *Phytophthora* were advocated, including molecular profiling and consideration of the adaptive evolutionary processes underlying the emergence of taxonomic units (Brasier 1991; Hansen 1991).

The first hard evidence for evolutionary substructure within the genus stemmed from the resolution of 10 molecular phylogenetic clades, which was presented alongside evidence that the biologically distinct downy mildews (DMs) had evolved from Phytophthoras (Cooke et al. 2000). Although the authors speculated on evolutionary trends in *Phytophthora*, no evidence of significant biological differences between the clades was found. Since then, surveys in natural ecosystems have greatly enhanced our knowledge of *Phytophthora* diversity (Brasier 2009; Burgess et al. 2018; Jung et al. 2024). Nonetheless, nearly all subsequent molecular phylogenies involving representative *Phytophthora* species and DMs have produced a similar topology, with DMs emerging on long branches from a paraphyletic *Phytophthora* genus (Abad et al. 2023; Bourret et al. 2018; Coomber et al. 2023; McCarthy and Fitzpatrick 2017; Runge et al. 2011; Scanu et al. 2021; Thines et al. 2023).

To date, all DMs and *Phytophthora* species have been consistently shown to share one common ancestor. However, Runge et al. (2011) argued that the paraphyly of *Phytophthora* with respect to DMs necessitated the splitting of *Phytophthora* into multiple new genera on cladistic grounds (also Crous et al. 2021). In response, Brasier et al. (2022) undertook a comprehensive assessment of the history, biological characteristics, evolutionary structure, and social impact of the *Phytophthora* genus and its relationship to the DMs. It was concluded that splitting the genus into several genera is unwarranted, emphasizing that *Phytophthora* is an ancient, historic, biologically cohesive, and evolutionarily successful genus and that a single name has very high value for clear scientific communication and disease management. Further, strongly advocating for the preservation of the current generic concept to avoid unnecessary taxonomic confusion or unintended consequences for global plant and food biosecurity, a proposal was made to secure a consensus on maintenance of the current broad usage of the generic name and to make a request to the International Commission on the Taxonomy of Fungi to review the evidence for maintaining the concept.

Most recently, coming from a perspective of redefining DM taxonomy and pursuing the theme of recognizing multiple new genera within the current concept of *Phytophthora*, Thines et al. (2023) and Thines (2023, 2024) proposed assigning the described taxa in *Phytophthora* Clade 4 to what is generally considered a synonymous generic name, *Peronophythora.* That genus was established by Chen (1961) to accommodate a single, morphologically unique species, *Peronophythora litchii*, and later transferred to *Phytophthora* (Göker et al. 2007). However, neither a clear statement as to why Clade 4 species should be reclassified in the resurrected *Peronophythora* nor a taxonomic redescription with synapomorphies for *Peronophythora* in their new interpretation was provided (Thines et al. 2023; Box 1). Introducing a new or unfamiliar scientific name carries an important responsibility: Such names remain in databases in perpetuity, even if the name is not validly published or recognized as a synonym of an already known genus or species (Aime et al. 2021). This development therefore added greater urgency to the process of preserving the long-established concept of *Phytophthora*.

An open registration virtual workshop entitled "The Genus *Phytophthora* – Don't Change a Winning Concept?," kindly hosted by The American Phytopathological Society (hereafter, APS Workshop), was convened from 22 to 25 April 2024 to gauge the scientific consensus for retaining the name *Phytophthora* for all major clades within the genus. With over 265 participants from 45 countries, the workshop explored the broad ramifications of the case and proceeded to a vote on a motion, for or against, maintaining the present broad generic circumscription.

In this letter, we build on the case for preserving the current generic concept made by Brasier et al. (2022) and during the APS Workshop, present new evidence regarding the biological properties and origins of some of the clades, and critically evaluate the recent proposals of Thines et al. (2023) and Thines (2023, 2024). We also present the results of the community vote, which unanimously recommended the preservation of the present circumscription. All oral presentations were recorded during the APS Workshop and are available open access (American Phytopathological Society 2024).

Phytophthora Is a Biologically Cohesive Genus Across All of Its Clades

In the decades following the introduction of the generic name *Phytophthora* (Greek for "plant destroyer"), with *P. infestans* as the "type" species (de Bary 1876), there was a tendency to assign newly discovered, biologically similar species to novel genera based on small morphological or behavioral differences (examples include *Blepharospora cambivora*, *Kawakamia cyperi*, *Mycelophagus castaneae*, *Phloeophthora syringae*, *Pythiacistis citrophthora*, and *Pythiomorpha gonapodyides*; Waterhouse 1970). These generic names were later treated as synonymous with and transferred into *Phytophthora* as the wider properties of the genus (beyond *P. infestans*) were resolved (Blackwell et al. 1941; Buisman 1927; Drechsler 1931; Leonian 1925; Tucker 1931; Waterhouse 1956). By the 1960s, it was universally accepted that, structurally and behaviorally, *Phytophthora* was a highly variable yet easily diagnosable and biologically meaningful genus. This is in striking contrast to the view of Thines (2024) that "the genus *Phytophthora* has been a catch-all for plant-pathogenic oomycetes infecting a variety of land plants."

Following the initial resolution of the *Phytophthora* phylogenetic clades (Cooke et al. 2000), now considered to comprise 11 major and at least 5 minor clades (Abad et al. 2023; Bourret et al. 2018; Chen et al. 2022; Coomber et al. 2023) (Fig. 1), the evidence for biological cohesion has been strengthened by the demonstration of considerable diversity in morphological structures, breeding systems, and lifestyles not only across the clades but even within single clades (Brasier et al. 2022; Burgess et al. 2018; Jung et al. 2011, 2017b, c, 2022, 2024). Clade 2, for example, exhibits almost all the morphological and behavioral features of the genus at large (Jung 2024; Jung et al. 2024; Fig. 2). Furthermore, no clade shows a unique combination of major characters and special morphological adaptations (=synapomorphies) that could reasonably be expected of a distinct genus (Brasier et al. 2022; Jung 2024).

Origins of the clades

Understanding the origins of the *Phytophthora* clades is also important for determining their taxonomic status: Clade diversity and the mode of clade emergence are complementary issues. Therefore, taxonomic choices need to be based not only on phenotypic differences and phylogenetic monophyly but also, where possible, on an understanding of the evolutionary processes, whether largely neutral or adaptive, that gave rise to the phylogenetic nodes (Brasier 2009; Brasier et al. 2022; Jung et al. 2024). Collectively, the clades, though phylogenetically divergent, tend to have clear and often overlapping geographical associations yet strong conformity in biological and behavioral characteristics. It is suggested that they originated through the migration of a group of early Phytophthoras on the emerging continents following the breakup of Pangea around 175 Mya. As a result, a degree of genotypic divergence via genetic drift, and local adaptation to different climates, hosts, and host tissues occurred but without marked phenotypic divergence (Brasier et al. 2022; Jung et al. 2022, 2024). Supporting evidence for such a pattern of events can be seen in individual clades, including substantial new information regarding subclade distribution and synapomorphies in Clades 2 and 10 (Figs. 2 and 3; Jung et al. 2022, 2024), and in the apparent local radiation of taxa from a common progenitor, for example, radiation of Clade 1c (which includes *P. infestans*) in Central America through host specialization (Brasier and Hansen 1992; Grünwald and Flier 2005; Grünwald and Goss 2011; Goss et al. 2014).

Overall, the remarkable diversity of form and behavior in *Phytophthora*, coupled with the plasticity of its genetic system, makes it extremely flexible, facilitating high potential adaptability to new environments and hosts (Brasier et al. 2022). A consequence of this flexibility is that *Phytophthora* species from phylogenetically divergent clades occurring on different continents can exhibit remarkably similar characters and character combinations. Examples, among many, include *P. infestans* in Clade 1c, *P. meadii* in Clade 2a, and *P. ramorum* in Clade 8c, geographically associated with the Americas, the Indian subcontinent, and East Asia, respectively (Brasier et al. 2022; Goss et al. 2014; Jung et al. 2021, 2024), and *P. tropicalis* in Clade 2b from Central and South America and *P. heterospora* and *P. palmivora* in Clade 4 from Southeast Asia (Jung 2024; Jung et al. 2024; Scanu et al. 2021).

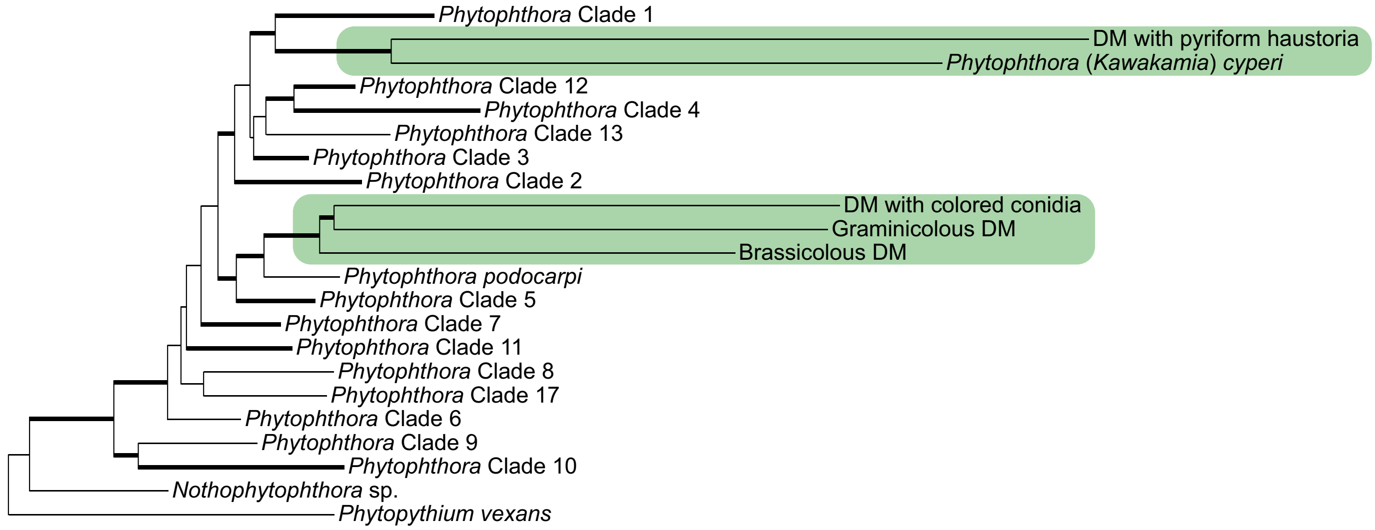

Fig. 1. Condensed phylogenetic tree inferred from a 134-taxon, six-locus nuclear alignment (LSU, *btub*, *tef1a*, *hsp90*, *rpl10*, and *enl*) showing the relationships between the *Phytophthora* clades and downy mildew (DM) groups (redrawn from Bourret et al. 2018). Groups or taxa with an obligate biotrophic lifestyle are highlighted in green. Thicker branches received bootstrap support of 95% or greater. DMs with pyriform haustoria comprise the genera *Basidiophora*, *Benua*, ***Bremia***, *Novotelnova*, *Paraperonospora*, ***Plasmopara***, *Plasmoverna*, and *Protobremia*. DMs with colored conidia comprise the genera ***Peronospora*** and ***Pseudoperonospora***. Graminicolous DMs comprise the genera *Baobabopsis*, *Eraphthora*, *Graminivora*, ***Peronosclerospora***, *Poakatesthia*, *Sclerophthora*, ***Sclerospora***, and *Viennotia*. Brassicolous DMs comprise the genera ***Hyaloperonospora*** and *Perofascia.* Genera shown in bold were included in the analysis. The obligate biotroph *Phytophthora cyperi* (originally *Peronospora cyperi*), while often referred to as *Phytophthora cyperi*, was considered a DM (as *Kawakamia cyperi*) by Thines et al. (2023) and Brasier et al. (2022).

The Relationship of *Phytophthora* to the DMs Is Accepted

The DMs have a substantially different “lifestyle” from Phytophthoras (Table 1), probably evolving from their *Phytophthora* ancestors via one or more rapid “evolutionary jumps” (Brasier et al. 2022), that is, by a macro-evolutionary event, which justifies the erection of new genera (Mayr and Bock 2002). Most notably, DMs are obligate biotrophs with narrow host ranges, often infecting *Asteraceae*, *Brassicaceae*, and *Poaceae*, producing determinate sporangiophores and, in many genera, directly germinating conidia-like sporangia. Key *Phytophthora* characteristics such as saprotrophy, necrotrophy, culturability, and the ability to infect woody tissues are absent, and many DM genera cannot form zoospores. Whereas Phytophthoras exhibit high ecological flexibility, DMs have apparently sacrificed ecological flexibility for more sophisticated and intimate host and host tissue specialization (Brasier et al. 2022; Dick 2001, 2002; Fletcher and Michelmore 2023; Shaw 1981). Of course, among such a wide array of characters, there are variants, including individual *Phytophthora* species that have developed unique sporangial characteristics, in rare cases strongly resembling sporangia of DMs (Table 1; Brasier et al. 2022; Jung 2024; Scanu et al. 2021). There are also several unculturable and seemingly host-specific species that nevertheless strongly resemble *Phytophthora* and not the DMs (Bourret et al. 2025; Ho et al. 2004; Zheng and Ho 2000).

Although the earliest molecular phylogeny revealed that the DMs arose directly from Phytophthoras (Cooke et al. 2000), more recently, it has been shown (Fig. 1) that they may have done so at least twice (Bourret 2024; Bourret et al. 2018, 2025; Dussert et al. 2019; Fletcher et al. 2019, 2023; McCarthy and Fitzpatrick 2017; Scanu et al. 2021; Winkworth et al. 2022). These studies have also typically revealed *Phytophthora* clades as a tight, fundamentally monophyletic, “bush-like” evolutionary cluster; that is, Phytophthoras as a group are closely related and have arisen from a common ancestor (Fig. 1). Further, in contrast to the relatively

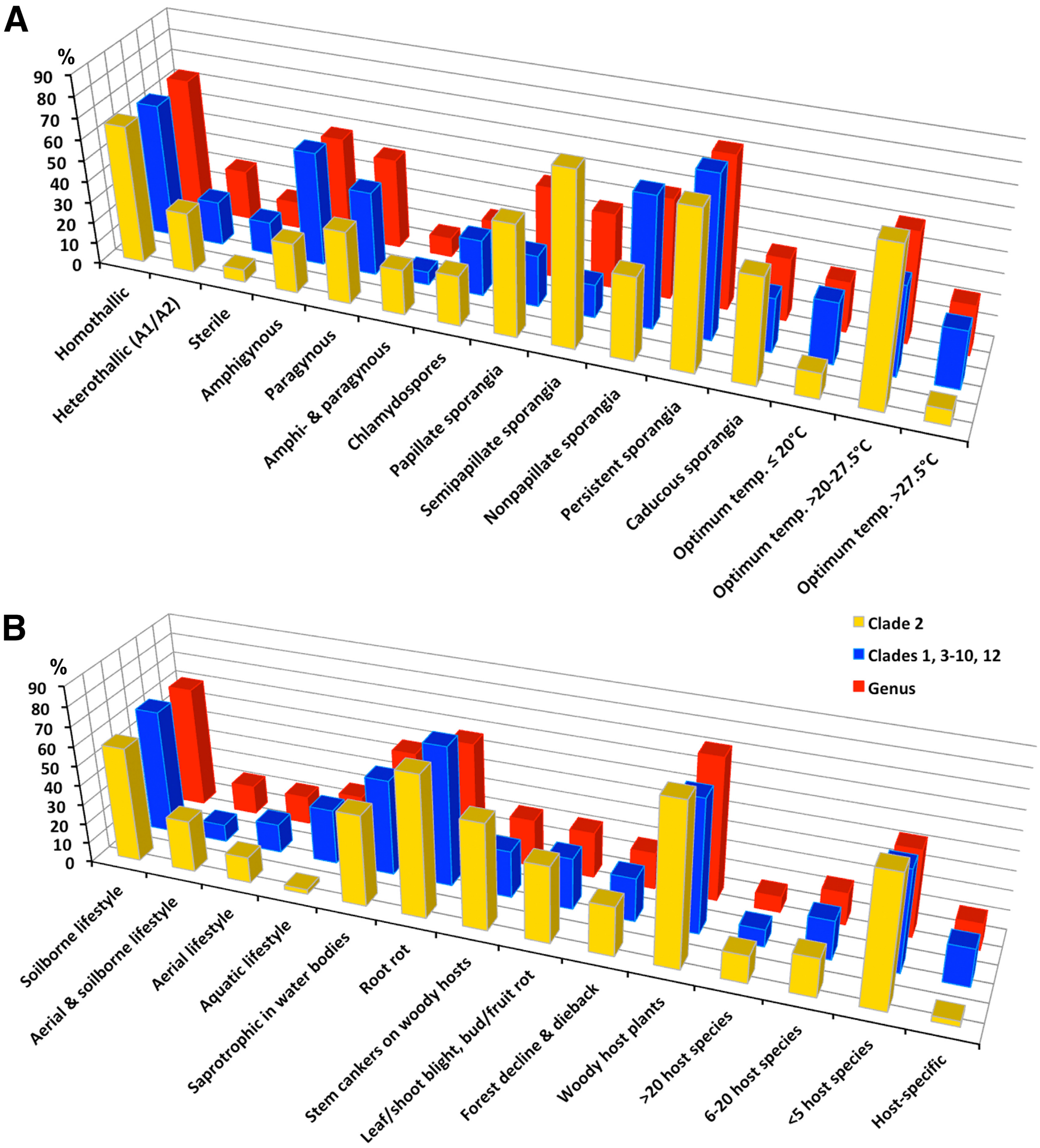

Fig. 2. Comparison of the properties of the 84 species and informally designated taxa in *Phytophthora* major Clade 2 with those of 173 species in 10 other major clades (Clades 1, 3 to 10, and 12) and with the genus as a whole (all 11 major clades, 257 species/taxa), showing that Clade 2 is highly representative of the genus. Bars reflect the percentages (*y* axis) of species in each group showing the indicated characteristics. **A,** Morphological and physiological characteristics and breeding systems. **B,** Lifestyles, diseases, and host ranges.

neutral evolutionary processes postulated for the emergence of the *Phytophthora* clades, the DM lineages, from their longer branch lengths, appear to have emerged relatively recently from *Phytophthora* through host jumps and radiative, adaptive macroevolution. Also, because they are often adapted to and therefore physically and spatially restricted to a single host, DMs are probably more reproductively isolated compared with most Phytophthoras.

The now substantial evidence that the DMs have evolved from *Phytophthora* renders *Phytophthora* "paraphyletic" (a group of organisms that share a common ancestor but do not contain all of its descendants), which has led to a proposal to distribute the main phylogenetic clades of *Phytophthora* among five or more "resurrected" old, or new, generic names (Runge et al. 2011; Thines 2023, 2024; Thines et al. 2023). However, we consider that whether *Phytophthora* is or is not paraphyletic in terms of taxonomic cladism is not relevant to its taxonomic status. Thus, we contend (i) that the tendency of taxonomic cladists to focus the definition of monophyly on biologically distinct descendants (in this case the DMs) and not on the progenitor (*Phytophthora*) as in the original 1877 Haeckelian sense (Haeckel 1877) is non-Darwinian and (ii) that cladism overemphasizes lineages without taking into account the evolutionary processes (at the nodes) that gave rise to their emergence or the evidence gaps represented by past reticulations (e.g., hybridization events, horizontal gene transfer) and extinctions (Bourret 2024; Brasier et al. 2022; Hörandl 2006, 2007; Lachance 2016; Mayr and Bock 2002; Zander 2013) or lack of sampling of evolutionarily in-

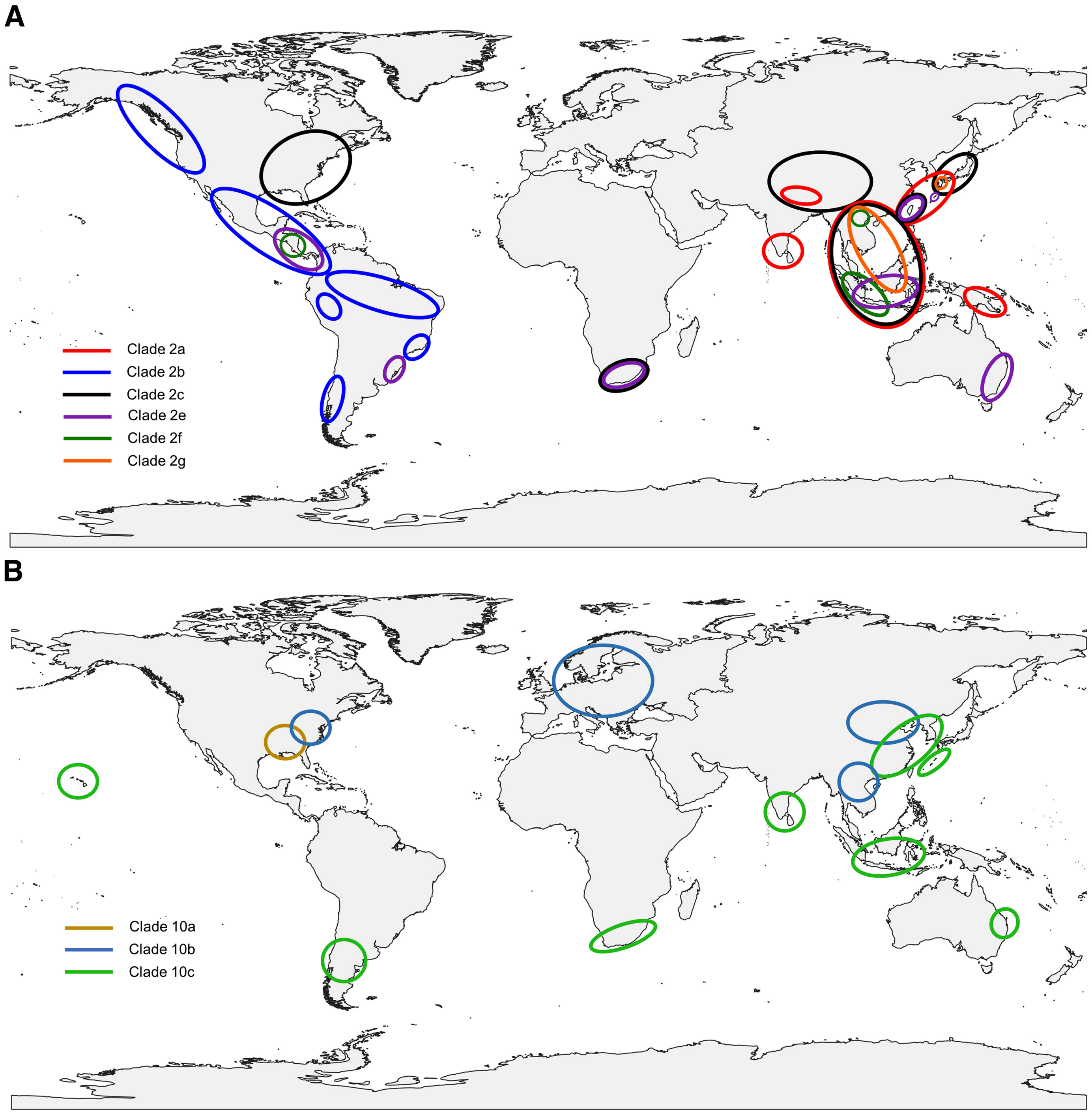

Fig. 3. Natural global biogeography (omitting probable anthropogenic introductions) of **A,** *Phytophthora* Clade 2 and its six subclades (redrawn from Jung et al. 2024) and **B,** *Phytophthora* Clade 10 and its three subclades (based on data from Jung et al. 2022).

termediate taxa. The apparently rapid emergence of the DMs in their obligate biotrophy niche appears to be a consequence of at least two independent events that have not influenced the parental taxon, *Phytophthora*. Accordingly, in agreement with Mayr and Bock (2002) and others, the emergence of the DM progenitors should not have taxonomic consequences for the ancient parental genus *Phytophthora*. Paraphyly is a normal and inevitable event in the ultimate taxonomy system: the Tree of Life (Crisp and Chandler 1996; Ross 2014).

Moreover, despite a rapid increase in the number of described *Phytophthora* species (Brasier 2009; Brasier et al. 2022; Jung et al. 2022, 2024) and much new information from well over a century of detailed taxonomic description and experimentation with Phytophthoras, meaningful sets of biological differences ("synapomorphies"), that is, differences sufficient to justify recognizing them as different genera, have not, so far, been demonstrated between the *Phytophthora* clades or groups of clades. The biological cohesiveness of the *Phytophthora* clades and their essential distinctiveness from the DMs are generally well understood and accepted by the international *Phytophthora* and plant pathology communities (Brasier et al. 2022, 2024; Jung 2024; Jung et al. 2024).

Actions and Reactions

The evidence of the taxonomic status of *Phytophthora* relative to the DMs, in particular the evidence of *Phytophthora* paraphyly (Cooke et al. 2000), DM polyphyly (Bourret et al. 2018), and the case for retention of the broad *Phytophthora* circumscription

BOX 1

Responses to recent proposals by Thines et al. (2023) and Thines (2023, 2024) to name new genera within *Phytophthora*

Thines (2023) proposed the transfer of all known Clade 4 *Phytophthora* species into the resurrected genus *Peronophythora* (originally erected by Chen [1961] for *P. litchii*). This proposal was based primarily on cladistic criteria, a "first step in the process of relieving *Phytophthora* of its paraphyly," and on the occurrence of a few "downy mildew-like" characters in the otherwise culturable, zoosporic *P. litchii* (Thines et al. 2023). However, the fact that none of the other nine currently described species in Clade 4 fits the original description of *Peronophythora* invalidates this argument. Further, Thines et al. (2023) also state that Clade 4 species produce great amounts of aerial and papillate sporangia borne on somewhat differentiated sporangiophores and usually produce aplerotic oospores. However, these traits, or a combination of them, are not generally considered common features of Clade 4: 6 of the 10 species in the clade have persistent sporangia, associated with a soilborne lifestyle, and 4 of them (*P. alticola*, *P. arenaria*, *P. cathayensis*, and *P. panamensis*) and all four Clade 4 species with caducous sporangia (*P. heterospora*, *P. litchii*, *P. megakarya*, and *P. palmivora*) tend to have both aplerotic and plerotic oospores (Brasier and Griffin 1979; Chen et al. 2022; Jung et al. 1999, 2017b; Kao and Leu 1980; Morales-Rodríguez et al. 2021; Paap et al. 2017; Rea et al. 2011; Scanu et al. 2021; Simamora et al. 2015). The proposal to reactivate the genus *Peronophythora* without a consistent clade-wide description, and without presenting a proper scientific justification, is taxonomically imprudent.

Thines (2024) proposed the transfer of *Phytophthora* Clade 12 taxa into *Peronophythora*, despite its members being exclusively soilborne fine root pathogens lacking the synapomorphies listed in the original description of *Peronophythora* or in the statements claimed to distinguish the resurrected genus from *Phytophthora* (Thines et al. 2023). Further, there are no consistent phylogenetic data supporting Clades 4 and 12 as sibling clades (Bourret et al. 2018; Chen et al. 2022; Scanu et al. 2021; Seidl and Bourret 2024; Van Poucke et al. 2021; Winkworth et al. 2022). Therefore, this Clade 12 proposal is not supported by the evidence.

Thines et al. (2023) and Thines (2024) also proposed transferring other *Phytophthora* clades to currently unused or new genera. This is based, in our view, on oversimplified or flawed conceptions of their biological properties:

a) Proposal to transfer Clade 2 taxa to the synonymized genus *Pythiacystis*, erected by Smith and Smith (1906), to accommodate the sterile papillate Clade 2 species *P. citrophthora*: In practice, the generic name *Pythiacystis* was soon declared redundant by Leonian (1925), who in transferring *P. citrophthora* to *Phytophthora*, stated, "This organism is so obviously a *Phytophthora* species that the genus *Pythiacystis* is no longer tenable." The main justification by Thines (2024) for transferring Clade 2 species to *Pythiacystis* (besides a desire to render *Phytophthora* holophyletic) appears to be based on the misconception that all Clade 2 species are terrestrial with semipapillate sporangia. This ignores evidence that the currently 84 Clade 2 taxa with available data are very diverse and include species with (i) a mainly or partially aerial lifestyle (32%); (ii) mainly or partially papillate sporangia (59.5%); (iii) mainly nonpapillate sporangia (5%); and (iv) partially nonpapillate sporangia (31%) (Jung 2024; Jung et al. 2024) (Fig. 2). Hence, based on these characteristics, the transfer of *Phytophthora* Clade 2 taxa to the genus *Pythiacystis* is taxonomically inappropriate.

b) Proposal to transfer Clade 6 taxa to the genus *Pythiomorpha* introduced by Petersen (1909) for *P. gonapodyides*: Blackwell et al. (1941) and Waterhouse (1958) demonstrated that the characteristics listed by Petersen and others for differentiating *Pythiomorpha* from *Phytophthora* (i.e., proliferating sporangia, irregular undulating hyphal growth, diplanetic zoospores, absence of true conidia, and the aquatic habitat) were in fact common features of known *Phytophthora* species and concluded that *Pythiomorpha* was an invalid genus. In addition, features listed by Thines (2024) as the characteristics of a potentially resurrected genus *Pythiomorpha*, such as nonpapillate sporangia, simple nondifferentiated sporangiophores, frequent internal proliferation, and an aquatic lifestyle, are common across many *Phytophthora* clades, including Clades 2, 6, 7, 8, 9, 10, and 11 (Abad et al. 2023; Brasier et al. 2022; Burgess et al. 2018; Chen et al. 2022; Hong et al. 2010; Jung et al. 2002, 2011, 2017a, 2022, 2024; Rahman et al. 2015; Safaiefarahani et al. 2015; Yang and Hong 2013). Consequently, the proposed resurrection of *Pythiomorpha* for Clade 6 is not justified.

c) Proposal to transfer *Phytophthora* Clade 8 species to the genus *Phloeophthora*: The latter genus was erected by Klebahn (1905) to accommodate the self-fertile semipapillate Clade 8 species *P. syringae* but was soon declared redundant by Klebahn (1909) himself, who transferred it into *Phytophthora*. Further, the implication by Thines (2024) that Clade 8 is terrestrial (soil inhabiting) with mostly nonpapillate sporangia is unsound, as this ignores the predominantly semipapillate species from subclades 8b, 8c, and 8d, including *P. syringae* and the predominantly or partly aerial subclade 8c pathogens *P. foliorum*, *P. hibernalis*, *P. lateralis*, and *P. ramorum* (Donahoo et al. 2006; Webber et al. 2012; Werres et al. 2001). Moreover, the species from Clade 8a with predominantly nonpapillate, internally proliferating sporangia and an A1 × A2 breeding system, such as *P. cryptogea*, *P. drechsleri*, and *P. pseudocryptogea*, do not conform to the original description of *Phloeophthora* (Grünwald et al. 2012; Jung et al. 2003; Klebahn 1905; Safaiefarahani et al. 2015).

d) Proposal to transfer *Phytophthora* Clades 9 and 10 to a new genus, *Phytophthoropsis*, characterized by nonpapillate sporangia on simple sporangiophores and an aquatic saprotrophic lifestyle: This is a considerable oversimplification that ignores the soilborne and partially airborne pathogenic lifestyle of the Clade 9 species *P. constricta* in dry heathlands of southwestern Australia (Rea et al. 2011); the eucalypt canopy-dwelling Clade 9 species *P. captiosa* and *P. fallax* in Australasia (Dick et al. 2006); and the fact that Clade 10c comprises exclusively aerial pathogens, such as the four species of the *P. kernoviae* complex and *P. boehmeriae*, *P. celebensis*, *P. gondwanensis*, *P. javanensis*, *P. morindae*, and *P. multiglobulosa*, which form papillate caducous sporangia in composite sympodia (Brasier et al. 2005; Jung et al. 2022; Nelson and Abad 2010).

(Brasier et al. 2022), is inevitably resulting in publication chain-reactions. Highly relevant to our case for *Phytophthora* retention are recent publications by Thines et al. (2023) and Thines (2023, 2024). These put forward broad taxonomic proposals for new genera and generic names for existing clades of *Phytophthora*, and make specific comments about statements within Brasier et al. (2022) and Bourret et al. (2018).

We present our detailed responses to these comments or proposals in Boxes 1 and 2, together with some related observations. Broadly, we view most of the taxonomic proposals in Thines et al. (2023) and Thines (2023, 2024) as non-rigorous, unsupported by the evidence, or scientifically inappropriate. Further, if one accepts that on current evidence, the proposals to split *Phytophthora* into separate genera are biologically and phylogenetically inappropriate, then we consider as largely irrelevant the particulars of any genus name that might be assigned during such a process, whether they include new names or resurrected names (Thines 2023, 2024; Thines et al. 2023).

Lack of Suitable Nomenclatural Alternatives

In the context of the rather narrow cladistic notion that the evolution of the DMs renders *Phytophthora* “paraphyletic” (and in those terms, a “problem to be rectified”), various nomenclatural options have been presented (Bourret et al. 2018; Brasier et al. 2022; Runge et al. 2011; Voglmayr 2008). Each one of these “solutions” would probably be unsatisfactory to one scientific circle or another (Voglmayr 2008). They include (i) placing all DMs and *Phytophthora* species in a single genus under the oldest generic name, *Peronospora*, which is evolutionarily unsound, as it puts biologically distinct derived taxa (i.e., the DMs) before their ancestral progenitor (*Phytophthora*); (ii) reclassifying all DMs under the parental group *Phytophthora*, which is at first sight more logical but conflicts with the International Code of Nomenclature for algae, fungi, and plants (ICNafp) because *Peronospora* is the earlier generic name, originally published in 1837 (Corda 1837; the code could also consider a proposal for the conservation of the name *Phytophthora* over *Peronospora*, but taxonomic chaos could ensue during the anticipated lengthy period of deliberation required before such a decision could be reached and confirmed); and (iii) describing at least six new genera within *Phytophthora* to conserve the DM genera. However, as already indicated, this is biologically unsound given the lack of meaningful biological differences between the *Phytophthora* clades or groups of clades and the likelihood that the clades are probably more a product of genetic drift than of adaptation.

Although there is an option to apply names to the various *Phytophthora* clades by recognizing them as subgenera or sections within the genus, Brasier et al. (2022) considered that, given the absence of significant biological differences between clades, this would probably add little to communication or our understanding and could be even more confusing to end users. The informal clade labeling system is now universally applied, usefully reflects the present evolutionary understanding, and can be adapted flexibly as more phylogenetic information, such as additional subclades or minor clades, accumulates.

Therefore, in the absence of strong evidence to the contrary, and also taking into consideration the critical importance of effective scientific communication (see below), preservation of the status quo would appear to be the most scientifically rational, pragmatic, and sensible choice.

Critical Value of Preserving the Broad Generic Concept of *Phytophthora* for Scientific, Regulatory, and Social Communication

As scientists, we attempt to erect and amend genera using scientific data, but genera are still human constructs. Generic names are, therefore, part of our “human ecosystem,” where biological science

BOX 2

Responses to other statements by Thines et al. (2023) and Thines (2023, 2024)

Thines et al. (2023) quote a phrase from a paper by Jung et al. (2017c) that describes the *Nothophytophthora* genus as a new sister genus of *Phytophthora*. However, they use the quote out of context, and their interpretation implying that *Phytophthora* and *Nothophytophthora* resemble each other in many morphological characters is misleading. In fact, Jung et al. (2017c) described multiple morphological and behavioral characteristics that distinguish the two genera. Distinguishing characteristics of *Nothophytophthora* include the exclusive formation of nonpapillate, often caducous sporangia with a conspicuous opaque basal plug, typically above the shedding point; the absence of sporangial pedicels; the absence of an A1 × A2 breeding system; generally low cardinal temperatures for growth; and very slow growth rates in culture. Furthermore, in multigene phylogenies, *Nothophytophthora* resides in a sister position to *Phytophthora* rather than within the *Phytophthora* clades (Fig. 1), with genetic distances to Clades 6, 7, and 10 of 8 to 9.2% (LSU-*btub-cox1-nadh1* alignment) and 31.9 to 43.2% (ITS), respectively (Jung et al. 2017c).

Whether the DMs have emerged from *Phytophthora* once or twice (Bourret 2024; Bourret et al. 2018; Cooke et al. 2000) (Fig. 1), that is, whether they are mono- or polyphyletic, is not pivotal to the case for preserving the broad *Phytophthora* concept. By some definitions, paraphyletic clades can only be paraphyletic once—a clade that is multiply paraphyletic would be considered polyphyletic and thus not supported under any definition of monophyly. However, these strict Hennigian clade terms are merely a set of definitions favored by some systematists and are not binding.

How the DMs evolved within *Phytophthora* remains a methodologically difficult question (Bourret 2024; Bourret et al. 2018; Seidl and Bourret 2024), and debates about phylogenetic methods are beyond the scope of this letter. Nonetheless, it is notable that, despite coming to a different conclusion regarding DM polyphyly and claiming to have produced a tree with an authoritative topology, Thines et al. (2023) applied none of the standard measures used by Bourret et al. (2018) to specifically evaluate potential long-branch effects in their inferences and substitution saturation in their datasets. Further, a more thorough investigation indicates that the DM monophyly indicated in Thines et al. (2023) is probably an artifact of nucleotide substitution saturation: Filtering the fast-evolving third-codon sites from their dataset resulted in trees with two DM clades, as did trees inferred from translated amino acid alignments (Bourret 2024).

Thines et al. (2023) commented twice that the statement of Brasier et al. (2022) that the DM genera are more closely related to each other than are some closely related *Phytophthora* species is incorrect, suggesting that genetic distances between DM genera are, in fact, considerable and often greater. However, Brasier et al. (2022) were referring to synapomorphies, not to genetic distances, pointing out that generic differences between some DMs are even more limited in critical synapomorphies than those between some phylogenetically very closely related *Phytophthora* species, for example, *P. ramorum* and *P. hibernalis* in Clade 8c. Indeed, Brasier et al. (2022) noted that in phylogenies, “the much longer average branch lengths in the DMs largely distinguish them from the more tightly clustered ‘bush-like’ *Phytophthora* clades” and supported the conclusion of Bourret et al. (2018) that this probably reflects a rapid evolution towards enhanced host specialization and obligate biotrophy.

The statement by Thines (2009) and Thines et al. (2023) that the traditional divide between *Phytophthora* and DMs is artificial, with obligate biotrophy probably being the only distinguishing synapomorphy, is not borne out by the evidence (Table 1) (Brasier et al. 2022).

meets social science. Consequently, they have an important social dimension, especially in the realm of scientific communication and, with pathogens, in the regulation and management of global plant and animal health and biosecurity (Brasier et al. 2022; Crous et al. 2021). The importance of this aspect is increasingly being highlighted where "unnecessary" generic changes are promulgated, the latter sometimes by those unfamiliar with front-line disease management (Brasier et al. 2022; de Hoog et al. 2023; Denning 2024; Geiser et al. 2013, 2021; Summerell 2019). Typically, the application or retention of a broad generic concept is recommended to maintain stability in names.

The genus *Phytophthora* is foundational to plant pathology. Indeed, to both plant pathology and mycology stakeholders worldwide, the impact of *Phytophthora* needs little introduction: The very meaning of the genus name, "plant destroyer," reflects this. Current impacts range from threats to food and crop biosecurity with significant economic consequences (for example, potato late blight, cocoa black pod, and sudden larch death), to damage to natural environments and ethnic cultures (for example, cork oak decline, jarrah dieback, kauri dieback, and sudden oak death), which are often financially incalculable (Brasier et al. 2022). In addition, there is the enormous global biosecurity challenge of protecting crops and natural ecosystems from previously "unknown" *Phytophthora* threats, reflected, for example, in the steady escalation in recorded *Phytophthora*-associated diebacks and declines (Brasier et al. 2022, 2024; Jung et al. 2018, 2024; Scanu et al. 2015, 2024).

These problems all require effective scientific discourse in research, disease management, regulation, and public awareness. As a biologically cohesive genus, for well over a century the current *Phytophthora* concept has had and continues to have a very high scientific communication and plant and food biosecurity value. It has long been fundamental to accurate knowledge and information transfer for scientists across disciplines ranging from mycology and plant pathology to social history. This value is indicated in a crude numerical sense by the many conference proceedings and five or more books dedicated to the genus since 1978, the >16,000 scientific papers on *Phytophthora* in Scopus, or the >180,000 citations on Google Scholar and by the numerous legally constituted quarantine statutes worldwide specifying measures against *Phytophthora* introduction or spread.

TABLE 1. Main characteristics differentiating *Phytophthora* from the downy mildews

	Taxonomic group	
Characteristics	*Phytophthora*	Downy mildews
Nutrition		
Saprotrophy	×	
Necrotrophy	×	
Hemibiotrophy	×	
Biotrophy	×	×[a]
Culturability	×[b]	
Lifestyle		
Water inhabiting	×	
Soil inhabiting	×	
Aerial inhabiting	×	×
Roots	×	
Stems	×	×
Foliar tissues	×	×
Woody tissues	×	
High ecological flexibility	×	
Asexual dispersal		
Zoospore formation	×	×[c]
Non-caducous zoosporangia	×	
Caducous zoosporangia	×	×[c]
Conidia	×[d]	×
Indeterminate sporangiophores	×	
Determinate sporangiophores	×[e]	×

[a] All downy mildews are obligate biotrophs.

[b] For some *Phytophthora* species, attempts to grow them in vitro have failed (e.g., *P. cyperi* = *Kawakamia cyperi*, *P. cyperi-bulbosi*, *P. lepironiae*, and *P. polygoni*).

[c] Ten of the twenty known downy mildew genera form sporangia and zoospores.

[d] *P. heterospora* from Clade 4 is the only *Phytophthora* species known to form conidia (in addition to sporangia) (Scanu et al. 2021).

[e] *P. litchii* from Clade 4 is the only *Phytophthora* species known to form determinate sporangiophores (Chen 1961).

Aspects of the potential "social harm" that could occur in the event of scientifically unjustified taxonomic changes to the *Phytophthora* genus have been described previously (Brasier et al. 2022; Jung et al. 2024) and across the APS Workshop (Brasier et al. 2024; Frankel 2024; Scanu et al. 2024; Webber 2024). However, it is worth reemphasizing a couple of these.

First, many damaging *Phytophthora* disease syndromes, from cocoa black pod disease to diebacks of entire Mediterranean-climate ecosystems, involve not only multiple (usually introduced) *Phytophthora* species but multiple *Phytophthora* clades. For example, in the current oak decline syndromes in Europe, at least 26 different *Phytophthora* species from 9 different clades are involved (Brasier et al. 2022; Jung et al. 2018). One vegetation dieback syndrome in western North America involves 51 *Phytophthora* taxa from 7 different clades (Frankel et al. 2020). In such examples, the symptoms caused by the different Phytophthoras on the same host are often indistinguishable (Jung et al. 2018; Scanu et al. 2024). The scientific confusion, potential legal confusion in the context of quarantine legislation and litigation, confusion in fungicide registration and labeling, and even disruption to global biosecurity that could result if the *Phytophthora* clades were unnecessarily split into multiple genera is self-evident. As Frankel (2024) has pointed out, lawyers can "make hay" with legal attempts to control introduced pathogens if the very name of the pathogen is "in dispute." At the very least, thousands of government and industry legal and management documents worldwide would need to be revised.

Second, the current excellent understanding among plant health regulators and scientists about what is meant by *Phytophthora* is a valuable asset in food crop and habitat protection. In some parts of the world, the impact of the genus on the wider environment is now so frequent and devastating that terms such as "Phytophthora root rot" and "Phytophthora dieback" are in common usage by amateur conservation groups, horticultural magazines, and the popular media (Brasier et al. 2022). Unnecessary or inappropriate designation of multiple new genera would seriously damage this public understanding.

In this context, in addition to *Peronophythora* (Box 1), Thines et al. (2023) and Thines (2024) propose new generic names such as *Pseudophytophthora* (literally "false plant destroyer"), *Paraphytophthora* ("somewhat a plant destroyer"), and *Phytophthoropsis* ("appears like a *Phytophthora*"), claiming that this would meet the low communications barrier recommended by Brasier et al. (2022). Clearly, having five or six such generic names for Phytophthoras in scientific publications, biosecurity documents, and at the public interface would be confusing and create a significant barrier to clear communication, rapid risk assessment, and timely responses. Further, phylogenies presented by Bourret et al. (2018) and Bourret (2024) suggest that the number of new generic names needed to render *Phytophthora* strictly "holophyletic" has been underestimated due to undersampling of the higher-numbered clades; hence, yet more minor clades are likely to be discovered.

Indeed, considering the principle that "taxonomy's purpose is to foster clear scientific communication … and weigh the costs of altering long-standing, effective communication" (Booth 1978; Wingfield et al. 2012, as paraphrased by Geiser et al. 2021), the statements of Thines et al. (2023) and Thines (2024) suggest insufficient appreciation of the damage to scientific and popular communication and global plant biosecurity that could result from an unnecessary breakup of the *Phytophthora* genus.

Canvas of Global Scientific Opinion on Preserving the Current *Phytophthora* Generic Concept

An option of trying to secure a consensus on the generic circumscription of *Phytophthora* among researchers actively involved with *Phytophthora* and other oomycetes via a working group of the International Commission on the Taxonomy of Fungi was advocated by Brasier et al. (2022). This same route was used by the International Commission of *Penicillium* and *Aspergillus* (recognized by both the International Commission on the Taxonomy of Fungi and the International Union of Microbiological Societies) to retain the use of *Aspergillus* in the broad circumscription and not to accept various segregate generic names (Samson et al. 2017). That decision was supported by 10 of the 11 members of the Commission and has been adopted almost universally. A similar approach has been advocated by Hyde et al. (2023) for other cases dealing with major differences in opinion regarding taxonomic concepts.

To assess the scientific consensus, a motion proposing the retention of the name *Phytophthora* for all major clades of the genus *Phytophthora* was voted on by delegates following the 22 to 25 April 2024 online APS Workshop "The Genus *Phytophthora* – Don't Change a Winning Concept?" The workshop was inclusive and open to all participants and all speakers. The participants were invited to vote on the following motion:

"We now recommend that the current concept of the genus *Phytophthora* be retained with its current circumscription and not divided into a number of separate genera on the basis that:

- With the exception of the emergent DMs, *Phytophthora* is a fundamentally monophyletic genus exhibiting strong biological cohesion. Its multiple phylogenetic clades exhibit numerous overlapping morphological and behavioral properties (synapomorphies) but no distinguishing combinations of synapomorphies, such that, overall, no clade or group of clades stands out as a unique biological entity.
- The DM genera that evolved from among the *Phytophthora* clades are clearly distinguished from *Phytophthora* by many striking morphological and behavioral character differences.
- The genus is of considerable historical importance to mycology and plant pathology.
- The genus has enormous, global economic and ecological impact due to the diseases it causes to crops and natural ecosystems.
- Both well-known disease syndromes and many other disease symptoms with very similar etiology are often caused by species from multiple *Phytophthora* clades.
- To break up or rename the clades of the genus without sound scientific justification (evidence of multiple distinguishing synapomorphies) could be seriously damaging to global scientific communication, biosecurity and disease regulation."

Of the 265 people registered for the APS Workshop, 166 voted on the motion over a 14-day post-workshop voting period. Of the 166 responders, 164 (98.8%) voted for the motion and 2 (1.2%) abstained. There were no votes against the motion.

All workshop participants and speakers were invited to coauthor this "Letter to the Editor" addressing the need for *Phytophthora* preservation. Of the 166 responders, 120 (72.3%) expressed a wish to be a co-author and 46 (27.7%) declined.

Review by the International Commission on the Taxonomy of Fungi

As APS Workshop participants who voted for the above motion, many of us are closely engaged with the science around the taxonomy, biology, evolution, and environmental management of *Phytophthora*, or in parallel fields of research. We tend not to consider the *Phytophthora* genus (or the DMs) largely as an assemblage of lineages on a cladogram. Dealing with *Phytophthora* on a day-to-day basis, many of us have developed a more holistic view and a professional understanding of what the name *Phytophthora* represents. The result of the workshop vote is evidence of our overwhelming support for the view that, given the absence of strong scientific evidence to the contrary, the current concept of the genus *Phytophthora* should be retained and protected to avoid unnecessary damage to effective scientific and regulatory communication.

We further recommend that the retention of the broad concept of *Phytophthora* should be supervised by a consensus of the scientific community, including especially any proposals to change the taxonomic structure of the genus. Any such proposals should, as far as practicable, take proper account of whether the changes are justified in terms of the phenotypic properties of the taxonomic units concerned, the likely evolutionary patterns and processes (e.g., adaptive or neutral variation and shared common ancestors) underlying their origins, and the social, economic, and regulatory impact of the changes.

On this basis, we request the International Commission on the Taxonomy of Fungi to form a representative Working Group to review the evidence and make its views known regarding maintaining the current circumscription of the genus *Phytophthora*.

Acknowledgments

We thank the U.S. Department of Agriculture-Agricultural Research Service for supporting the workshop and The American Phytopathological Society (APS) for hosting the workshop. We are particularly grateful to Melissa Schultea and Katie Hamel for their dedicated and highly professional management and organization of the APS Workshop "The Genus *Phytophthora* – Don't Change a Winning Concept?" (22 to 25 April 2024).

Literature Cited

Abad, Z. G., Burgess, T. I., Bourret, T., Bensch, K., Cacciola, S. O., Scanu, B., Mathew, R., Kasiborski, B., Srivastava, S., Kageyama, K., Bienapfl, J. C., Verkleij, G., Broders, K., Schena, L., and Redford, A. J. 2023. *Phytophthora*: Taxonomic and phylogenetic revision of the genus. Stud. Mycol. 106:259-348.

Aime, M. C., Miller, A. N., Aoki, T., Bensch, K., Cai, L., Crous, P. W., Hawksworth, D. L., Hyde, K. D., Kirk, P. M., Lücking, R., May, T. W., Malosso, E., Redhead, S. A., Rossman, A. Y., Stadler, M., Thines, M., Yurkov, A. M., Zhang, N., and Schoch, C. L. 2021. How to publish a new fungal species, or name, version 3.0. IMA Fungus 12:11.

American Phytopathological Society. 2024. The Genus *Phytophthora* – Don't Change a Winning Concept? Three-day open workshop, 22–25 April 2024. American Phytopathological Society Workshop.

Blackwell, E. M., Waterhouse, G. M., and Thompson, M. V. 1941. The invalidity of the genus *Pythiomorpha*. Trans. Br. Mycol. Soc. 25:148-165.

Booth, C. 1978. Do you believe in genera? Trans. Br. Mycol. Soc. 71:1-9.

Bourret, T. B. 2024. Common ground and shifting paradigms: How to reconcile *Phytophthora* evolution, cladistics, taxonomy, and biosecurity. Webinar presentation in: The Genus *Phytophthora* – Don't Change a Winning Concept? American Phytopathological Society Workshop, 22–25 April 2024, Session 3 - Part 1. Starting time 1:06:17.

Bourret, T. B., Blomquist, C. L., Mohan, S. K., Sampangi, R., Ho, H. H., and Mohammed, I. A. 2025. First detection of the obligate biotroph *Phytophthora cyperi* causing disease on yellow nutsedge in the United States, and establishment of molecular barcoding sequences for the species. PhytoFrontiers 5:60-66.

Bourret, T. B., Choudhury, R. A., Mehl, H. K., Blomquist, C. L., McRoberts, N., and Rizzo, D. M. 2018. Multiple origins of downy mildews and mito-nuclear discordance within the paraphyletic genus *Phytophthora*. PLoS One 13:e0192502.

Brasier, C., Scanu, B., Cooke, D., and Jung, T. 2022. *Phytophthora*: An ancient, historic, biologically and structurally cohesive and evolutionarily successful generic concept in need of preservation. IMA Fungus 13:12.

Brasier, C. M. 1991. Current questions in *Phytophthora* systematics: The role of the population approach. Pages 104-128 in: *Phytophthora*. J. A. Lucas, R. C. Shattock, D. S. Shaw, and L. R. Cooke, eds. Cambridge University Press, Cambridge, U.K.

Brasier, C. M. 2009. *Phytophthora* biodiversity: How many *Phytophthora* species are there? Pages 101-115 in: Phytophthoras in Forests and Natural Ecosystems: Proceedings of the Fourth Meeting of the International Union of Forest Research Organizations (IUFRO) Working Party S07.02.09, General Technical Report PSW-GTR-221. E. M. Goheen and S. J. Frankel, eds. USDA Forest Service, Pacific Southwest Research Station, Albany, CA.

Brasier, C. M., Beales, P. A., Kirk, S. A., Denman, S., and Rose, J. 2005. *Phytophthora kernoviae* sp. nov., an invasive pathogen causing bleeding stem lesions on forest trees and foliar necrosis of ornamentals in the UK. Mycol. Res. 109:853-859.

Brasier, C. M., and Griffin, M. J. 1979. Taxonomy of '*Phytophthora palmivora*' on cocoa. Trans. Br. Mycol. Soc. 72:111-143.

Brasier, C. M., Grunwald, N., Bourret, T., Govers, F., Cooke, D., Scanu, B., and Jung, T. 2024. *The Phytophthora* genus – History, characteristics and the case for retaining the concept. Webinar presentation in: The Genus *Phytophthora* – Don't Change a Winning Concept? American Phytopathological Society Workshop, 22–25 April 2024, Session 1. Starting time 0:05:00.

Brasier, C. M., and Hansen, E. M. 1992. Evolutionary biology of *Phytophthora*. Part II: Phylogeny, speciation, and population structure. Annu. Rev. Phytopathol. 30:173-200.

Buisman, C. J. 1927. Root rots caused by Phycomycetes. Ph.D. thesis. University of Utrecht, Utrecht, the Netherlands.

Burgess, T. I., Simamora, A. V., White, D., Williams, B., Schwager, M., Stukely, M. J. C., and Hardy, G. E. S. J. 2018. New species from *Phytophthora* Clade 6a: Evidence for recent radiation. Persoonia 41:1-17.

Chen, C. C. 1961. A species of *Peronophythora* gen. nov. parasitic on litchi fruit in Taiwan. National Taiwan University, Chinese Taipei, Special Publication of College of Agriculture 10.

Chen, Q., Bakhshi, M., Balci, Y., Broders, K. D., Cheewangkoon, R., Chen, S. F., Fan, X. L., Gramaje, D., Halleen, F., Horta Jung, M., Jiang, N., Jung, T., Májek, T., Marincowitz, S., Milenković, I., Mostert, L., Nakashima, C., Nurul Faziha, I., Pan, M., Raza, M., Scanu, B., Spies, C. F. J., Suhaizan, L., Suzuki, H., Tian, C. M., Tomšovský, M., Úrbez-Torres, J. R., Wang, W., Wingfield, B. D., Wingfield, M. J., Yang, Q., Yang, X., Zare, R., Zhao, P., Groenewald, J. Z., Cai, L., and Crous, P. W. 2022. Genera of phytopathogenic fungi: GOPHY 4. Stud. Mycol. 101:417-564.

Cooke, D. E. L., Drenth, A., Duncan, J. M., Wagels, G., and Brasier, C. M. 2000. A molecular phylogeny of *Phytophthora* and related oomycetes. Fungal Genet. Biol. 30:17-32.

Coomber, A., Saville, A., Carbone, I., and Ristaino, J. B. 2023. An open T-BAS phylogeny for emerging *Phytophthora* species. PLoS One 18:e0283540.

Corda, A. C. J. 1837. Icones Fungorum Hucusque Cognitorum, J. G. Calve, ed. Ann. Mag. Nat. Hist. 1:1-32.

Crisp, M. D., and Chandler, G. T. 1996. Paraphyletic species. Telopea 6:813-844.

Crous, P. W., Rossman, A. Y., Aime, M. C., Allen, W. C., Burgess, T., Groenewald, J. Z., and Castlebury, L. A. 2021. Names of phytopathogenic fungi: A practical guide. Phytopathology 111:1500-1508.

de Bary, A. 1876. Researches into the nature of the potato-fungus *Phytophthora infestans*. J. Roy. Agric. Soc. Engl. 12:239-269.

de Hoog, S., Walsh, T. J., Ahmed, S. A., Alastruey-Izquierdo, A., Alexander, B. D., Arendrup, M. C., Babady, E., Bai, F.-Y., Balada-Llasat, J.-M., Borman, A., Chowdhary, A., Clark, A., Colgrove, R. C., Cornely, O. A., Dingle, T. C., Dufresne, P. J., Fuller, J., Gangneux, J.-P., Gibas, C., Glasgow, H., Gräser, Y., Guillot, J., Groll, A. H., Haase, G., Hanson, K., Harrington, A., Hawksworth, D. L., Hayden, R. T., Hoenigl, M., Hubka, V., Johnson, K., Kus, J. V., Li, R., Meis, J. F., Lackner, M., Lanternier, F., Leal, S. M., Jr., Lee, F., Lockhart, S. R., Luethy, P., Martin, I., Kwon-Chung, K. J., Meyer, W., Nguyen, M. H., Ostrosky-Zeichner, L., Palavecino, E., Pancholi, P., Pappas, P. G., Procop, G. W., Redhead, S. A., Rhoads, D. D., Riedel, S., Stevens, B., Sullivan, K. O., Vergidis, P., Roilides, E., Seyedmousavi, A., Tao, L., Vicente, V. A., Vitale, R. G., Wang, Q.-M., Wengenack, N. L., Westblade, L., Wiederhold, N., White, L., Wojewoda, C. M., and Zhang, S. X. 2023. A conceptual framework for nomenclatural stability and validity of medically important fungi: A proposed global consensus guideline for fungal name changes supported by ABP, ASM, CLSI, ECMM, ESCMID-EFISG, EUCAST-AFST, FDLC, IDSA, ISHAM, MMSA, and MSGERC. J. Clin. Microbiol. 61:e00873-23.

Denning, D. W. 2024. Renaming *Candida glabrata*—A case of taxonomic purity over clinical and public health pragmatism. PLoS Pathog. 20:e1012055.

Dick, M. A., Dobbie, K., Cooke, D. E. L., and Brasier, C. M. 2006. *Phytophthora captiosa* sp. nov. and *P. fallax* sp. nov. causing crown dieback of *Eucalyptus* in New Zealand. Mycol. Res. 110:393-404.

Dick, M. W. 2001. Straminipilous Fungi: Systematics of the Peronosporomycetes Including Accounts of the Marine Straminipilous Protists, the Plasmodiophorids and Similar Organisms. Kluwer Academic Press, Dordrecht, the Netherlands.

Dick, M. W. 2002. Towards an understanding of the evolution of the downy mildews. Pages 1-57 in: Advances in Downy Mildew Research. P. T. N. Spencer-Phillips, U. Gisi, and A. Lebeda, eds. Kluwer Academic Press, Dordrecht, the Netherlands.

Donahoo, R., Blomquist, C. L., Thomas, S. L., Moulton, J. K., Cooke, D. E. L., and Lamour, K. H. 2006. *Phytophthora foliorum* sp. nov., a new species causing leaf blight of azalea. Mycol. Res. 110:1309-1322.

Drechsler, C. 1931. A crown-rot of hollyhocks caused by *Phytophthora megasperma* n. sp. J. Wash. Acad. Sci. 21:513-526.

Dussert, Y., Mazet, I. D., Couture, C., Gouzy, J., Piron, M.-C., Kuchly, C., Bouchez, O., Rispe, C., Mestre, P., and Delmotte, F. 2019. A high-quality grapevine downy mildew genome assembly reveals rapidly evolving and lineage-specific putative host adaptation genes. Genome Biol. Evol. 11:954-969.

Erwin, D. C., and Ribeiro, O. K. 1996. *Phytophthora* Diseases Worldwide. American Phytopathological Society, St. Paul, MN.

Fletcher, K., Gil, J., Bertier, L. D., Kenefick, A., Wood, K. J., Zhang, L., Reyes-Chin-Wo, S., Cavanaugh, K., Tsuchida, C., Wong, J., and Michelmore, R. 2019. Genomic signatures of heterokaryosis in the oomycete pathogen *Bremia lactucae*. Nat. Commun. 10:2645.

Fletcher, K., Martin, F., Isakeit, T., Cavanaugh, K., Magill, C., and Michelmore, R. 2023. The genome of the oomycete *Peronosclerospora sorghi*, a cosmopolitan pathogen of maize and sorghum, is inflated with dispersed pseudogenes. G3 13:jkac340.

Fletcher, K., and Michelmore, R. 2023. Genome-enabled insights into downy mildew biology and evolution. Annu. Rev. Phytopathol. 61:165-183.

Frankel, S. J. 2024. Importance of 'genus stability' in the management and regulation of Phytophthoras on native plants in Western North America. Webinar presentation in: The Genus *Phytophthora* – Don't Change a Winning Concept? American Phytopathological Society Workshop, 22–25 April 2024, Session 2. Starting time 1:34:35.

Frankel, S. J., Conforti, C., Hillman, J., Ingolia, M., Shor, A., Benner, D., Alexander, J. M., Bernhardt, E., and Swiecki, T. J. 2020. *Phytophthora* introductions in restoration areas: Responding to protect California native flora from human-assisted pathogen spread. Forests 11:1291.

Geiser, D. M., Al-Hatmi, A. M. S., Aoki, T., Arie, T., Balmas, V., Barnes, I., Bergstrom, G. C., Bhattacharyya, M. K., Blomquist, C. L., Bowden, R. L., Brankovics, B., Brown, D. W., Burgess, L. W., Bushley, K., Busman, M., Cano-Lira, J. F., Carrillo, J. D., Chang, H.-X., Chen, C.-Y., Chen, W., Chilvers, M., Chulze, S., Coleman, J. J., Cuomo, C. A., de Beer, Z. W., de Hoog, G. S., Del Castillo-Múnera, J., Del Ponte, E. M., Diéguez-Uribeondo, J., Di Pietro, A., Edel-Hermann, V., Elmer, W. H., Epstein, L., Eskalen, A., Esposto, M. C., Everts, K. L., Fernández-Pavía, S. P., da Silva, G. F., Foroud, N. A., Fourie, G., Frandsen, R. J. N., Freeman, S., Freitag, M., Frenkel, O., Fuller, K. K., Gagkaeva, T., Gardiner, D. M., Glenn, A. E., Gold, S. E., Gordon, T. R., Gregory, N. F., Gryzenhout, M., Guarro, J., Gugino, B. K., Gutierrez, S., Hammond-Kosack, K. E., Harris, L. J., Homa, M., Hong, C.-F., Hornok, L., Huang, J.-W., Ilkit, M., Jacobs, A., Jacobs, K., Jiang, C., Jiménez-Gasco, M. D. M., Kang, S., Kasson, M. T., Kazan, K., Kennell, J. C., Kim, H.-S., Kistler, H. C., Kuldau, G. A., Kulik, T., Kurzai, O., Laraba, I., Laurence, M. H., Lee, T., Lee, Y.-W., Lee, Y.-H., Leslie, J. F., Liew, E. C. Y., Lofton, L. W., Logrieco, A. F., López-Berges, M. S., Luque, A. G., Lysøe, E., Ma, L.-J., Marra, R. E., Martin, F. N., May, S. R., McCormick, S. P., McGee, C., Meis, J. F., Migheli, Q., Mohamed Nor, N. M. I., Monod, M., Moretti, A., Mostert, D., Mulè, G., Munaut, F., Munkvold, G. P., Nicholson, P., Nucci, M., O'Donnell, K., Pasquali, M., Pfenning, L. H., Prigitano, A., Proctor, R. H., Ranque, S., Rehner, S. A., Rep, M., Rodríguez-Alvarado, G., Rose, L. J., Roth, M. G., Ruiz-Roldán, C., Saleh, A. A., Salleh, B., Sang, H., Scandiani, M. M., Scauflaire, J., Schmale, D. G., III, Short, D. P. G., Šišić, A., Smith, J. A., Smyth, C. W., Son, H., Spahr, E., Stajich, J. E., Steenkamp, E., Steinberg, C., Subramaniam, R., Suga, H., Summerell, B. A., Susca, A., Swett, C. L., Toomajian, C., Torres-Cruz, T. J., Tortorano, A. M., Urban, M., Vaillancourt, L. J., Vallad, G. E., van der Lee, T. A. J., Vanderpool, D., van Diepeningen, A. D., Vaughan, M. M., Venter, E., Vermeulen, M., Verweij, P. E., Viljoen, A., Waalwijk, C., Wallace, E. C., Walther, G., Wang, J., Ward, T. J., Wickes, B. L., Wiederhold, N. P., Wingfield, M. J., Wood, A. K. M., Xu, J.-R., Yang, X.-B., Yli-Mattila, T., Yun, S.-H., Zakaria, L., Zhang, H., Zhang, N., Zhang, S. X., and Zhang, X. 2021. Phylogenomic analysis of a 55.1-kb 19-gene dataset resolves a monophyletic *Fusarium* that includes the *Fusarium solani* species complex. Phytopathology 111:1064-1079.

Geiser, D. M., Aoki, T., Bacon, C. W., Baker, S. E., Bhattacharyya, M. K., Brandt, M. E., Brown, D. W., Burgess, L. W., Chulze, S., Coleman, J. J., Correll, J. C., Covert, S. F., Crous, P. W., Cuomo, C. A., De Hoog, G. S., Di Pietro, A., Elmer, W. H., Epstein, L., Frandsen, R. J. N., Freeman, S., Gagkaeva, T., Glenn, A. E., Gordon, T. R., Gregory, N. F., Hammond-Kosack, K. E., Hanson, L. E., Jímenez-Gasco, M. D. M., Kang, S., Kistler, H. C., Kuldau, G. A., Leslie, J. F., Logrieco, A., Lu, G., Lysøe, E., Ma, L.-J., McCormick, S. P., Migheli, Q., Moretti, A., Munaut, F., O'Donnell, K., Pfenning, L., Ploetz, R. C., Proctor, R. H., Rehner, S. A., Robert, V. A. R. G., Rooney, A. P., bin Salleh, B., Scandiani, M. M., Scauflaire, J., Short, D. P. G., Steenkamp, E., Suga, H., Summerell, B. A., Sutton, D. A., Thrane, U., Trail, F., Van Diepeningen, A., VanEtten, H. D., Viljoen, A., Waalwijk, C., Ward, T. J., Wingfield, M. J., Xu, J.-R., Yang, X.-B., Yli-Mattila, T., and Zhang, N. 2013. One fungus, one name: Defining the genus *Fusarium* in a scientifically robust way that preserves longstanding use. Phytopathology 103:400-408.

Göker, M., Voglmayr, H., Riethmüller, A., and Oberwinkler, F. 2007. How do obligate parasites evolve? A multi-gene phylogenetic analysis of downy mildews. Fungal Genet. Biol. 44:105-122.

Goss, E. M., Tabima, J. F., Cooke, D. E. L., Restrepo, S., Fry, W. E., Forbes, G. A., Fieland, V. J., Cardenas, M., and Grünwald, N. J. 2014. The Irish potato famine pathogen *Phytophthora infestans* originated in central Mexico rather than the Andes. Proc. Natl. Acad. Sci. U.S.A. 111:8791-8796.

Grünwald, N. J., and Flier, W. G. 2005. The biology of *Phytophthora infestans* at its center of origin. Annu. Rev. Phytopathol. 43:171-190.

Grünwald, N. J., and Goss, E. M. 2011. Evolution and population genetics of exotic and re-emerging pathogens: Novel tools and approaches. Annu. Rev. Phytopathol. 49:249-267.

Grünwald, N. J., Werres, S., Goss, E. M., Taylor, C. R., and Fieland, V. J. 2012. *Phytophthora obscura* sp. nov., a new species of the novel *Phytophthora* subclade 8d. Plant Pathol. 61:610-622.

Haeckel, E. 1877. Anthropogenie oder Entwickelungsgeschichte des Menschen: Gemeinverständlich wissenschaftliche Vorträge über die Grundzüge der menschlichen Keimes-und Stammes-Geschichte, 3rd ed. W. Engelmann, Leipzig, Germany.

Hansen, E. M. 1991. Variation in the species of the *Phytophthora megasperma* complex. Pages 148-163 in: *Phytophthora*. J. A. Lucas, R. C. Shattock, D. S. Shaw, and L. R. Cooke, eds. Cambridge University Press, Cambridge, U.K.

Ho, H. H., Zheng, F. C., and Zheng, H. C. 2004. *Phytophthora cyperi* on *Digitaria ciliaris* in Hainan Province of China. Mycotaxon 90:431-435.

Hong, C. X., Gallegly, M. E., Richardson, P. A., Kong, P., Moorman, G. W., Lea-Cox, J. D., and Ross, D. S. 2010. *Phytophthora hydropathica*, a new pathogen identified from irrigation water, *Rhododendron catawbiense* and *Kalmia latifolia*. Plant Pathol. 59:913-921.

Hörandl, E. 2006. Paraphyletic versus monophyletic taxa—evolutionary versus cladistic classifications. Taxon 55:564-570.

Hörandl, E. 2007. Neglecting evolution is bad taxonomy. Taxon 56:1-5.

Hyde, K. D., Abdel-Wahab, M. A., Abdollahzadeh, J., Abeywickrama, P. D., Absalan, S., Afshari, N., Ainsworth, A. M., Akulov, O. Y., Aleoshin, V. V., Al-Sadi, A. M., Alvarado, P., Alves, A., Alves-Silva, G., Amalfi, M., Amira, Y., Amuhenage, T. B., Anderson, J. L., Antonín, V., Aouali, S., Aptroot, A., Apurillo, C. C. S., Araújo, J. P. M., Ariyawansa, H. A., Armand, A., Arumugam, E., Asghari, R., Assis, D. M. A., Atienza, V., Avasthi, S., Azevedo, E., Bahkali, A. H., Bakhshi, M., Banihashemi, Z., Bao, D. F., Baral, H. O., Barata, M., Barbosa, F. R., Barbosa, R. N., Barreto, R. W., Baschien, C., Belamesiatseva, D. B., Bennett Reuel, M., Bera, I., Bezerra, J. D. P., Bezerra, J. L., Bhat, D. J., Bhunjun, C. S., Bianchinotti, M. V., Błaszkowski, J., Blondelle, A., Boekhout, T., Bonito, G., Boonmee, S., Boonyuen, N., Bregant, C., Buchanan, P., Bundhun, D., Burgaud, G., Burgess, T., Buyck, B., Cabarroi-Hernández, M., Cáceres, M. E. S., Caeiro, M. F., Cai, L., Cai, M. F., Calabon, M. S., Calaça, F. J. S., Callalli, M., Camara, M. P. S., Cano-Lira, J. F., Cantillo, T., Cao, B., Carlavilla, J. R., Carvalho, A., Castañeda-Ruiz, R. F., Castlebury, L., Castro-Jauregui, O., Catania, M. D. V., Cavalcanti, L. H., Cazabonne, J., Cedeño-Sanchez, M. L., Chaharmiri-Dokhaharani, S., Chaiwan, N., Chakraborty, N., Chaverri, P., Cheewangkoon, R., Chen, C., Chen, C. Y., Chen, K. H., Chen, J., Chen, Q., Chen, W. H., Chen, Y. P., Chethana, K. W. T., Coleine, C., Condé, T. O., Corazon-Guivin, M. A., Cortés-Pérez, A., Costa-Rezende, D. H., Courtecuisse, R., Crouch, J. A., Crous, P. W., Cui, B. K., Cui, Y. Y., da Silva, D. K. A., da Silva, G. A., da Silva, I. R., da Silva, R. M. F., da Silva Santos, A. C., Dai, D. Q., Dai, Y. C., Damm, U., Darmostuk, V., Daroodi, Z., Das, K., Davoodian, N., Davydov, E. A., Dayarathne, M. C., Decock, C., de Groot, M. D., De Kesel, A., dela Cruz, T. E. E., De Lange, R., Delgado, G., Denchev, C. M., Denchev, T. T., de Oliveira, N. T., de Silva, N. I., de Souza, F. A., Dentinger, B., Devadatha, B., Dianese, J. C., Dima, B., Diniz, A. G., Dissanayake, A. J., Dissanayake, L. S., Doğan, H. H., Doilom, M., Dolatabadi, S., Dong, W., Dong, Z. Y., Dos Santos, L. A., Drechsler-Santos, E. R., Du, T. Y., Dubey, M. K., Dutta, A. K., Egidi, E., Elliott, T. F., Elshahed, M. S., Erdoğdu, M., Ertz, D., Etayo, J., Evans, H. C., Fan, X. L., Fan, Y. G., Fedosova, A. G., Fell, J., Fernandes, I., Firmino, A. L., Fiuza, P. O., Flakus, A., Fragoso de Souza, C. A., Frisvad, J. C., Fryar, S. C., Gabaldón, T., Gajanayake, A. J., Galindo, L. J., Gannibal, P. B., García, D., García-Sandoval, S. R., Garrido-Benavent, I., Garzoli, L., Gautam, A. K., Ge, Z.-W., Gené, D. J., Gentekaki, E., Ghobad-Nejhad, M., Giachini, A. J., Gibertoni, T. B., Góes-Neto, A., Gomdola, D., Gomes de Farias, A. R., Gorjón, S. P., Goto, B. T., Granados-Montero, M. M., Griffith, G. W., Groenewald, J. Z., Groenewald, M., Grossart, H. P., Gueidan, C., Gunarathne, A., Gunaseelan, S., Gusmão, L. F. P., Gutierrez, A. C., Guzmán-Dávalos, L., Haelewaters, D., Halling, R., Han, Y. F., Hapuarachchi, K. K., Harder, C. B., Harrington, T. C., Hattori, T., He, M. Q., He, S., He, S. H., Healy, R., Herández-Restrepo, M., Heredia, G., Hodge, K. T., Holgado-Rojas, M., Hongsanan, S., Horak, E., Hosoya, T., Houbraken, J., Huang, S. K., Huanraluek, N., Hur, J. S., Hurdeal, V. G., Hustad, V. P., Iotti, M., Iturriaga, T., Jafar, E., Janik, P., Jany, J. L., Jayalal, R. G. U., Jayasiri, S. C., Jayawardena, R. S., Jeewon, R., Jerônimo, G. H., Jesus, A. L., Jin, J., Johnston, P. R., Jones, E. B. G., Joshi, Y., Justo, A., Kaishian, P., Kakishima, M., Kaliyaperumal, M., Kang, G. P., Kang, J. C., Karakehian, J. M., Karimi, O., Karpov, S. A., Karunarathna, S. C., Kaufmann, M., Kemler, M., Kezo, K., Khyaju, S., Kirchmair, M., Kirk, P. M., Kitaura, M. J., Klawonn, I., Kolarik, M., Kong, A., Kuhar, F., Kukwa, M., Kumar, S., Kušan, I., Lado, C., Larsson, K. H., Latha, K. P. D., Lee, H. B., Leonardi, M., Leontyev, D. L., Lestari, A. S., Li, C. J. Y., Li, D. W., Li, H., Li, H. Y., Li, L., Li, Q. R., Li, W. L., Li, Y., Li, Y. C., Li, Y. X., Liao, C. F., Liimatainen, K., Lim, Y. W., Lin, C. G., Linaldeddu, B. T., Linde, C. C., Linn, M. M., Liu, F., Liu, J. K., Liu, N. G., Liu, S., Liu, S. L., Liu, X. F., Liu, X. Y., Liu, X. Z., Liu, Z. B., Lu, L., Lu, Y. Z., Luangharn, T., Luangsa-ard, J. J., Lumbsch, H. T., Lumyong, S., Luo, L., Luo, M., Luo, Z. L., Ma, J., Machado, A. R., Madagammana, A. D., Madrid, H., Magurno, F., Magyar, D., Mahadevan, N., Maharachchikumbura, S. S. N., Maimaiti, Y., Malosso, E., Manamgoda, D. S., Manawasinghe, I. S., Mapook, A., Marasinghe, D. S., Mardones, M., Marin-Felix, Y., Márquez, R., Masigol, H., Matočec, N., May, T. W., McKenzie, E. H. C., Meiras-Ottoni, A., Melo, R. F. R., Mendes-Alvarenga, R. L., Mendieta, S., Meng, Q. F., Menkis, A., Menolli, N., Jr., Mešić, A., Meza Calvo, J. G., Mikhailov, K. V., Miller, S. L., Moncada, B., Moncalvo, J. M., Monteiro, J. S., Monteiro, M., Mora-Montes, H. M., Moreau, P. A., Mueller, G. M., Mukhopadyay, S., Murugadoss, R., Nagy, L. G., Najafiniya, M., Nanayakkara, C. M., Nascimento, C. C., Nei, Y., Neves, M. A., Neuhauser, S., Niego, A. G. T., Nilsson, R. H., Niskanen, T., Niveiro, N., Noorabadi, M. T., Noordeloos, M. E., Norphanphoun, C., Nuñez Otaño, N. B., O'Donnell, R. P., Oehl, F., Olariaga, I., Orlando, O. P., Pang, K. L., Papp, V., Pawłowska, J., Peintner, U., Pem, D., Pereira, O. L., Perera, R. H., Perez-Moreno, J., Perez-Ortega, S., Péter, G., Phillips, A. J. L., Phonemany, M., Phukhamsakda, C., Phutthacharoen, K., Piepenbring, M., Pires-Zottarelli, C. L. A., Poinar, G., Pošta, A., Prieto, M., Promputtha, I., Quandt, C. A., Radek, R., Rahnama, K., Raj, K. N. A., Rajeshkumar, K. C., Rämä, T., Rambold, G., Ramírez-Cruz, V., Rasconi, S., Rathnayaka, A. R., Raza, M., Ren, G. C., Robledo, G. L., Rodriguez-Flakus, P., Ronikier, A., Rossi, W., Ryberg, M., Ryvarden, L. R., Salvador–Montoya, C. A., Samant, B., Samarakoon, B. C., Samarakoon, M. C., Sánchez-Castro, I., Sánchez-García, M., Sandoval-Denis, M., Santamaria, B., Santiago, A. L. C. M. A., Sarma, V. V., Savchenko, A., Savchenko, K., Saxena, R. K., Scholler, M., Schoutteten, N., Seifollahi, E., Selbmann, L., Selcuk, F., Senanayake, I. C., Shabashova, T. G., Shen, H. W., Shen, Y. M., Silva-Filho, A. G. S., Simmons, D. R., Singh, R., Sir, E. B., Song, C. G., Souza-Motta, C. M., Sruthi, O. P., Stadler, M., Stchigel, A. M., Stemler, J., Stephenson, S. L., Strassert, J. F. H., Su, H. L., Su, L., Suetrong, S., Sulistyo, B., Sun, Y. F., Sun, Y. R., Svantesson, S., Sysouphanthong, P., Takamatsu, S., Tan, T. H., Tanaka, K., Tang, A. M. C., Tang, X., Tanney, J. B., Tavakol, N. M., Taylor, J. E., Taylor, P. W. J., Tedersoo, L., Tennakoon, D. S., Thamodini, G. K., Thines, M., Thiyagaraja, V., Thongklang, N., Tiago, P. V., Tian, Q., Tian, W. H., Tibell, L., Tibell, S., Tibpromma, S., Tkalčec, Z., Tomšovský, M., Toome-Heller, M., Torruella, G., Tsurykau, A., Udayanga, D., Ulukapi, M., Untereiner, W. A., Uzunov, B. A., Valle, L. G., Van Caenegem, W., Van Den Wyngaert, S., Van Vooren, N., Velez, P., Verma, R. K., Vieira, L. C., Vieira, W. A. S., Vizzini, A., Walker, A., Walker, A. K., Wanasinghe, D. N., Wang, C. G., Wang, K., Wang, S. X., Wang, X. Y., Wang, Y., Wannasawang, N., Wartchow, F., Wei, D. P., Wei, X. L., White, J. F., Wijayawardene, N. N., Wijesinghe, S. N., Wijesundara, D. S. A., Wisitrassameewong, K., Worthy, F. R., Wu, F., Wu, G., Wu, H. X., Wu, N., Wu, W. P., Wurzbacher, C., Xiao, Y. P., Xiong, Y. R., Xu, B., Xu, L. J., Xu, R., Xu, R. F., Xu, R. J., Xu, T. M., Yakovchenko, L., Yan, J. Y., Yang, H. D., Yang, J., Yang, Z. L., Yang, Y. H., Yapa, N., Yasanthika, E., Youssef, N. H., Yu, F. M., Yu, Q., Yu, X. B., Yu, Y. X., Yu, Z. F., Yuan, H. S., Yuan, Y., Yurkov, A., Zafari, D., Zamora, J. C., Zare, R., Zeng, M., Zeng, N. K., Zeng, X. Y., Zhang, F., Zhang, H., Zhang, J. F., Zhang, J. Y., Zhang, Q. Y., Zhang, S. N., Zhang, W., Zhang, Y., Zhang, Y. X., Zhao, C. L., Zhao, H., Zhao, Q., Zhao, R. L., Zhou, L. W., Zhou, M., Zhurbenko, M. P., Zin, H. H., and Zucconi, L. 2023. Global consortium for the classification of fungi and fungus-like taxa. Mycosphere 14:1960-2012.

Jung, T. 2024. Biological cohesion and synapomorphy within *Phytophthora* -- and its contrast to *Pythium*. Webinar presentation in: The Genus *Phytophthora* – Don't Change a Winning Concept? American Phytopathological Society Workshop, 22–25 April 2024, Session 1. Starting time 1:34:50.

Jung, T., Cooke, D. E. L., Blaschke, H., Duncan, J. M., and Oßwald, W. 1999. *Phytophthora quercina* sp. nov., causing root rot of European oaks. Mycol. Res. 103:785-798.

Jung, T., Hansen, E. M., Winton, L., Oßwald, W., and Delatour, C. 2002. Three new species of *Phytophthora* from European oak forests. Mycol. Res. 106:397-411.

Jung, T., Jung, M. H., Cacciola, S. O., Cech, T., Bakonyi, J., Seress, D., Mosca, S., Schena, L., Seddaiu, S., Pane, A., di San Lio, G. M., Maia, C., Cravador, A., Franceschini, A., and Scanu, B. 2017b. Multiple new cryptic pathogenic *Phytophthora* species from *Fagaceae* forests in Austria, Italy and Portugal. IMA Fungus 8:219-244.

Jung, T., Jung, M. H., Scanu, B., Seress, D., Kovács, G. M., Maia, C., Pérez-Sierra, A., Chang, T.-T., Chandelier, A., Heungens, K., Van Poucke, K., Abad-Campos, P., Léon, M., Cacciola, S. O., and Bakonyi, J. 2017a. Six new *Phytophthora* species from ITS Clade 7a including two sexually functional heterothallic hybrid species detected in natural ecosystems in Taiwan. Persoonia 38:100-135.

Jung, T., Horta Jung, M., Webber, J. F., Kageyama, K., Hieno, A., Masuya, H., Uematsu, S., Pérez-Sierra, A., Harris, A. R., Forster, J., Rees, H., Scanu, B., Patra, S., Kudláček, T., Janoušek, J., Corcobado, T., Milenković, I., Nagy, Z., Csorba, I., Bakonyi, J., and Brasier, C. M. 2021. The destructive tree pathogen *Phytophthora ramorum* originates from the Laurosilva forests of East Asia. J. Fungi 7:226.

Jung, T., Milenković, I., Balci, Y., Janoušek, J., Kudláček, T., Nagy, Z. Á., Baharuddin, B., Bakonyi, J., Broders, K. D., Cacciola, S. O., Chang, T.-T., Chi, N. M., Corcobado, T., Cravador, A., Đorđević, B., Durán, A., Ferreira, M., Fu, C.-H., Garcia, L., Hieno, A., Ho, H.-H., Hong, C., Junaid, M., Kageyama, K., Kuswinanti, T., Maia, C., Májek, T., Masuya, H., Magnano di San Lio G., Mendieta-Araica, B., Nasri, N., Oliveira, L. S. S., Pane, A., Pérez-Sierra, A., Rosmana, A., Von Stowasser, E. S., Scanu, B., Singh, R., Stanivuković, Z., Tarigan, M., Thu, P. Q., Tomić, Z., Tomšovský, M., Uematsu, S., Webber, J. F., Zeng, H.-C., Zheng, F.-C., Brasier, C. M., and Jung, M. H. 2024. Worldwide forest surveys reveal forty-three new species in *Phytophthora* major Clade 2 with fundamental implications for the evolution and biogeography of the genus and global plant biosecurity. Stud. Mycol. 107:251-388.

Jung, T., Milenković, I., Corcobado, T., Májek, T., Janoušek, J., Kudláček, T., Tomšovský, M., Nagy, Z. Á., Durán, A., Tarigan, M., Sanfuentes von Stowasser, E., Singh, R., Ferreira, M., Webber, J. F., Scanu, B., Chi, N. M., Thu, P. Q., Junaid, M., Rosmana, A., Baharuddin, B., Kuswinanti, T., Nasri, N., Kageyama, K., Hieno, A., Masuya, H., Uematsu, S., Oliva, J., Redondo, M., Maia, C., Matsiakh, I., Kramarets, V., O'Hanlon, R., Tomić, Ž., Brasier, C. M., and Horta Jung, M. 2022. Extensive morphological and behavioural diversity among fourteen new and seven described species in *Phytophthora* Clade 10 and its evolutionary implications. Persoonia 49: 1-57.

Jung, T., Nechwatal, J., Cooke, D. E. L., Hartmann, G., Blaschke, M., Oßwald, W. F., Duncan, J. M., and Delatour, C. 2003. *Phytophthora pseudosyringae* sp. nov., a new species causing root and collar rot of deciduous tree species in Europe. Mycol. Res. 107:772-789.

Jung, T., Pérez-Sierra, A., Durán, A., Horta Jung, M., Balci, Y., and Scanu, B. 2018. Canker and decline diseases caused by soil- and airborne *Phytophthora* species in forests and woodlands. Persoonia 40:182-220.

Jung, T., Scanu, B., Bakonyi, J., Seress, D., Kovács, G. M., Durán, A., Sanfuentes von Stowasser, E., Schena, L., Mosca, S., Thu, P. Q., Nguyen, C. M., Fajardo, S., González, M., Pérez-Sierra, A., Rees, H., Cravador, A., Maia, C., and Horta Jung, M. 2017c. *Nothophytophthora* gen. nov., a new sister genus of *Phytophthora* from natural and semi-natural ecosystems. Persoonia 39:143-174.

Jung, T., Stukely, M. J. C., Hardy, G. E. S. J., White, D., Paap, T., Dunstan, W. A., and Burgess, T. I. 2011. Multiple new *Phytophthora* species from ITS Clade 6 associated with natural ecosystems in Australia: Evolutionary and ecological implications. Persoonia 26:13-39.

Kao, C. W., and Leu, L. S. 1980. Sporangium germination of *Peronophythora litchii*, the causal organism of litchi downy blight. Mycologia 72:737-748.

Klebahn, H. 1905. Eine neue Pilzkrankheit der *Syringen* (A new fungal disease of Syringae). Zentralbl. Bakt. 15:335-336.

Klebahn, H. 1909. Die neue Zweig- und Knospenkrankheit. Pages 18-75 in: Krankheiten des Flieders. Gebrüder Borntraeger Verlag, Berlin.

Lachance, M.-A. 2016. Paraphyly and (yeast) classification. Int. J. Syst. Evol. Microbiol. 66:4924-4929.

Leonian, L. H. 1925. Physiological studies on the genus *Phytophthora*. Am. J. Bot. 12:444-498.

Mayr, E., and Bock, W. J. 2002. Classifications and other ordering systems. J. Zool. Syst. Evol. Res. 40:169-194.

McCarthy, C. G. P., and Fitzpatrick, D. A. 2017. Phylogenomic reconstruction of the oomycete phylogeny derived from 37 genomes. mSphere 2:e00095-17.

Morales-Rodríguez, C., Wang, Y., Martignoni, D., and Vannini, A. 2021. *Phytophthora cathayensis* sp. nov., a new species pathogenic to Chinese Hickory (*Carya cathayensis*) in southeast China. Fungal Syst. Evol. 7: 99-111.

Nelson, S. C., and Abad, Z. G. 2010. *Phytophthora morindae*, a new species causing black flag disease on noni (*Morinda citrifolia* L.) in Hawaii. Mycologia 102:122-134.

Paap, T., Croeser, L., White, D., Aghighi, S., Barber, P., Hardy, G. E. S. J., and Burgess, T. I. 2017. *Phytophthora versiformis* sp. nov., a new species from Australia related to *P. quercina*. Australas. Plant Pathol. 46:369-378.

Petersen, H. E. 1909. Studier over Ferskvands-Phycomyceter. Bot. Tidsskrift 29:345-440.

Rahman, M. Z., Uematsu, S., Suga, H., and Kageyama, K. 2015. Diversity of *Phytophthora* species newly reported from Japanese horticultural production. Mycoscience 56:443-459.

Rea, A. J., Burgess, T. I., Hardy, G. E. S. J., Stukely, M. J. C., and Jung, T. 2011. Two novel and potentially endemic species of *Phytophthora* associated with episodic dieback of Kwongan vegetation in the south-west of Western Australia. Plant Pathol. 60:1055-1068.

Ross, H. A. 2014. The incidence of species-level paraphyly in animals: A reassessment. Mol. Phylogenet. Evol. 76:10-17.

Runge, F., Telle, S., Ploch, S., Savory, E., Day, B., Sharma, R., and Thines, M. 2011. The inclusion of downy mildews in a multi-locus-dataset and its reanalysis reveals a high degree of paraphyly in *Phytophthora*. IMA Fungus 2:163-171.

Safaiefarahani, B., Mostowfizadeh-Ghalamfarsa, R., Hardy, G. E. S. J., and Burgess, T. I. 2015. Re-evaluation of the *Phytophthora cryptogea* species complex and the description of a new species, *Phytophthora pseudocryptogea* sp. nov. Mycol. Prog. 14:108.

Samson, R. A., Hubka, V., Varga, J., Houbraken, J., Hong, S.-B., Klaassen, C. H. W., Perrone, G., Seifert, K. A., Magistà, D., Visagie, C. M., Kocsubé, S., Szigeti, G., Yaguchi, T., Peterson, S. W., and Frisvad, J. C. 2017. Response to Pitt & Taylor 2016: Conservation of *Aspergillus* with *A. niger* as the conserved type is unnecessary and potentially disruptive. Taxon 66:1439-1446.

Scanu, B., Jung, T., Masigol, H., Linaldeddu, B. T., Jung, M. H., Brandano, A., Mostowfizadeh-Ghalamfarsa, R., Janoušek, J., Riolo, M., and Cacciola, S. O. 2021. *Phytophthora heterospora* sp. nov., a new pseudoconidia-producing sister species of *P. palmivora*. J. Fungi 7:870.

Scanu, B., Linaldeddu, B. T., Deidda, A., and Jung, T. 2015. Diversity of *Phytophthora* species from declining Mediterranean maquis vegetation, including two new species, *Phytophthora crassamura* and *P. ornamentata* sp. nov. PLoS One 10:e0143234.

Scanu, B., Webber, J., and Jung, T. 2024. European forest disease syndromes involving multiple *Phytophthora* species and clades. Webinar presentation in: The Genus *Phytophthora* – Don't Change a Winning Concept? American Phytopathological Society Workshop, 22–25 April 2024, Session 1. Starting time 2:06:15.

Seidl, M. F., and Bourret, T. B. 2024. Peronosporaceae Phylogenetics. Webinar presentation in: The Genus *Phytophthora* – Don't Change a Winning Concept? American Phytopathological Society Workshop, 22–25 April 2024, Session 1. Starting time 0:38:50.

Shaw, C. G. 1981. Taxonomy and evolution. Pages 17-29 in: The Downy Mildews. D. M. Spencer, ed. Academic Press, New York.

Simamora, A. V., Stukely, M. J. C., Hardy, G. E. S. J., and Burgess, T. I. 2015. *Phytophthora boodjera* sp. nov., a damping-off pathogen in production nurseries and from urban and natural landscapes, with an update on the status of *P. alticola*. IMA Fungus 6:319-335.

Smith, R. E., and Smith, E. H. 1906. A new fungus of economic importance. Bot. Gaz. 42:215-221.

Summerell, B. A. 2019. Resolving *Fusarium*: Current status of the genus. Annu. Rev. Phytopathol. 57:323-339.

Thines, M. 2009. Bridging the gulf: *Phytophthora* and downy mildews are connected by rare grass parasites. PLoS One 4:e4790.

Thines, M. 2023. Nomenclatural novelties. Index Fungorum 548.

Thines, M. 2024. Phylogenomics of Phytophthora and suggestions to deal with its taxonomic implications. Webinar presentation in: The Genus *Phytophthora* – Don't Change a Winning Concept? American Phytopathological Society Workshop, 22–25 April 2024, Session 4.

Thines, M., Mishra, B., and Ploch, S. 2023. Multigene analyses with a broad sampling in *Phytophthora* and related genera provide evidence for the monophyly of downy mildews. Mycol. Prog. 22:82.

Tucker, C. M. 1931. Taxonomy of the genus *Phytophthora* de Bary. Univ. Mo. Agric. Exp. Stn. Res. Bull. 153:1-208.

Van Poucke, K., Haegeman, A., Goedefroit, T., Focquet, F., Leus, L., Jung, M. H., Nave, C., Redondo, M. A., Husson, C., Kostov, K., Lyubenova, A., Christova, P., Chandelier, A., Slavov, S., de Cock, A., Bonants, P., Werres, S., Palau, J. O., Marçais, B., Jung, T., Stenlid, J., Ruttink, T., and Heungens, K. 2021. Unravelling hybridization in *Phytophthora* using phylogenomics and genome size estimation. IMA Fungus 12:16.

Voglmayr, H. 2008. Progress and challenges in systematics of downy mildews and white blister rusts: New insights from genes and morphology. Eur. J. Plant Pathol. 122:3-18.

Waterhouse, G. M. 1956. The genus *Phytophthora*. Diagnoses (or descriptions) and figures from the original papers. Commonw. Mycol. Inst. Misc. Publ. 12.

Waterhouse, G. M. 1958. The invalidity of the genus *Pythiomorpha*. II. Trans. Br. Mycol. Soc. 41:196-202.

Waterhouse, G. M. 1963. Key to the species of *Phytophthora* de Bary. Mycol. Pap. 92:1-22.

Waterhouse, G. M. 1970. The genus *Phytophthora* de Bary. Mycol. Pap. 122:1-59.

Waterhouse, G. M., Newhook, F. J., and Stamps, D. J. 1983. Present criteria for classification of *Phytophthora*. Pages 139-147 in: *Phytophthora*: Its Biology, Taxonomy, Ecology, and Pathology. D. C. Erwin, S.

Bartnicki-Garcia, and P. H. Tsao, eds. American Phytopathological Society, St. Paul, MN.

Webber, J. F. 2024. Protection of the genus *Phytophthora* for international scientific research and communication. Webinar presentation in: The Genus *Phytophthora* – Don't Change a Winning Concept? American Phytopathological Society Workshop, 22–25 April 2024, Session 1. Starting time 2:31:05.

Webber, J. F., Vettraino, A. M., Chang, T. T., Bellgard, S. E., Brasier, C. M., and Vannini, A. 2012. Isolation of *Phytophthora lateralis* from *Chamaecyparis* foliage in Taiwan. For. Pathol. 42:136-143.

Werres, S., Marwitz, R., Man In't veld, W. A., De Cock, A. W. A. M., Bonants, P. J. M., De Weerdt, M., Themann, K., Ilieva, E., and Baayen, R. P. 2001. *Phytophthora ramorum* sp. nov., a new pathogen on *Rhododendron* and *Viburnum*. Mycol. Res. 105:1155-1165.

Wingfield, M. J., de Beer, W., Slippers, B., Wingfield, B. D., Groenewald, J. Z., Lombard, L., and Crous, P. W. 2012. One fungus, one name promotes progressive plant pathology. Mol. Plant Pathol. 13:604-613.

Winkworth, R. C., Neal, G., Ogas, R. A., Nelson, B. C. W., McLenachan, P. A., Bellgard, S. E., and Lockhart, P. J. 2022. Comparative analyses of complete Peronosporaceae (Oomycota) mitogenome sequences — Insights Into structural evolution and phylogeny. Genome Biol. Evol. 14:evac049.

Yang, X., and Hong, C. 2013. *Phytophthora virginiana* sp. nov., a high-temperature tolerant species from irrigation water in Virginia. Mycotaxon 126:167-176.

Zander, R. H. 2013. A Framework for Post-Phylogenetic Systematics. Zetetic Publications, St. Louis, MO.

Zheng, X. B., and Ho, H. H. 2000. The sexual stage of *Phytophthora polygoni* Saw. Bot. Bull. Acad. Sin. 41:57-60.