

Names of Phytopathogenic Fungi: A Practical Guide

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ABSTRACT

Using the correct name for phytopathogenic fungi and oomycetes is essential for communicating knowledge about species and their biology, control, and quarantine as well as for trade and research purposes. However, many plant pathogenic fungi are pleomorphic, meaning they produce different asexual (anamorph) and sexual (teleomorph) morphs in their life cycles. Therefore, more than one name has been applied to different morphs of the same species, which has confused users. The onset of DNA technologies makes it possible to connect different morphs of the same species, resulting in a move to a more natural classification system for fungi in which a single name for a genus and species can now be used. This move to a single nomenclature, coupled with the advent of molecular systematics and the introduction of polythetic taxonomic approaches, has been the main driving force for a reclassification of fungi, including pathogens. Nonetheless, finding the correct name for species remains challenging. In this article we outline a series of steps or considerations to greatly simplify this process and provide links to various online databases and resources to aid in determining the correct name. Additionally, a list of accurate names is provided for the most common genera and species of phytopathogenic fungi.

Keywords: DNA barcoding, dual nomenclature, fungal pathogens, International Code of Nomenclature, phylogeny, polyphasic identification, systematics

Global yield losses of $\leq 12\%$ of total crop production have been attributed to plant diseases (Reeleder 2003). In the past two decades, the severity of disease outbreaks caused by virulent oomycete and fungal plant pathogens has been steadily rising (Fisher et al. 2012; Santini et al. 2013), as has been the incidence of new emergent diseases (Almeida 2018). Because of the importance of accurate diagnosis of plant diseases and their disease-causing organisms, international collaboration and the development of several web-based databases to improve documenting

and naming of plant pathogenic fungi is also on the rise. All these efforts are crucial for the implementation of disease management strategies.

Scientific names of plant pathogenic fungi are key to our knowledge of these pathogens. Names convey information linked to the biology, distribution, and potential risk of pathogens and their diseases, and application of the correct name is essential for communicating about them. For instance, accurate knowledge of the genus of fungus responsible for any given plant disease immediately conveys information about its biology and potential importance. Conversely, inaccurate and outdated species names can lead to unnecessary control measures, restrictions, or accidental introductions of plant pathogens.

Fungal systematics, the field of science concerned with classification and evolutionary relationships between fungi, has changed exponentially since the first fungal DNA sequences were deposited in GenBank in 1991. Not only has our understanding of fungal interactions with plants changed dramatically since that time, but we have also gained the ability to recognize species irrespective of

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*The e-Xtra logo stands for “electronic extra” and indicates that one supplementary table is published online.

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the stage of life cycle encountered in the field, even in the absence of clear morphological features.

Nevertheless, mycologists face a daunting task, as only about 150,000 species have been described to date, whereas 2.2 to 3.8 million species have been estimated to exist (Hawksworth and Lücking 2017). Given the rate of about 2,000 species being described annually (Cheek et al. 2020), this means that it may take >1,800 years to describe those yet to be cataloged. Irrespective of the rate at which these unknown taxa are described, it is clear that many of them will be plant pathogens; even in 2019 many of the new species and genera described were pathogens of food crops (Cheek et al. 2020). The fact that so much fungal diversity remains to be added to our current knowledge of kingdoms *Fungi* and *Straminipila* (*Oomycetes*) means that changes in fungal taxonomy and nomenclature are inevitable and will remain an ever-present fact for practicing plant pathologists and mycologists dealing with fungal species, their names, and relationships.

MOLECULAR ERA

Beginning in the 1990s, the use of DNA sequence data has significantly improved fungal taxonomy and streamlined species identification. The first example of linking an asexual (*Sporothrix*) to a sexual (*Ophiostoma*) genus via molecular data was published by Berbee and Taylor (1992). Since that initial study, there has been a significant increase in DNA sequence data generated for fungi, leading to the discovery and description of many cryptic taxa across a range of plant pathogenic fungal genera and additional asexual and sexual morph linkages.

The application of DNA sequence technology to resolve links between sexual and asexual genera was first exploited in fungi of medical importance and in yeasts (Berbee and Taylor 1992; Bruns et al. 1991). Since then, identification and classification of plant pathogenic fungi have become increasingly reliant on DNA sequences of standardized genetic markers, a concept known as DNA barcoding (Hebert et al. 2003). DNA barcoding relies on public repositories such as the International Nucleotide Sequence Database Collaboration (<http://www.insdc.org/>) and UNITE (a database for molecular identification of fungi; <http://unite.ut.ee>), which accession hundreds of thousands of verified fungal sequence entries (meaning of good quality and applied to the correct name), and the NCBI type sequence project, which allows flagging and searching of data from type material (each fungal name has a unique type specimen with associated metadata) for accurate inference (Federhen 2015).

An important aspect of DNA barcoding is choosing the correct locus, or marker, for conducting comparisons. The Consortium for the Barcode of Life ratified the internal transcribed spacer region (ITS) of the nuclear ribosomal DNA repeat as the universal DNA barcode for the fungal kingdom (Schoch et al. 2012), and the ITS remains the most broadly used and powerful barcode marker for fungi. However, for many fungal genera the ITS locus resolves taxa only to the genus level. To address the low-resolution power of ITS in these groups, Stielow et al. (2015) tested 14 primer pairs targeting eight genetic markers for 1,500 important species across *Agaricomycotina*, *Pezizomycotina*, *Pucciniomycotina*, *Saccharomycotina*, and *Ustilaginomycotina* and recommended the *translation elongation factor 1-alpha* gene (*TEF1*) as secondary DNA barcode to supplement ITS for species identification. Secondary DNA barcodes have since been proposed for a range of different genera of plant pathogenic fungi (Marin-Felix et al. 2017, 2019a, b) (Supplementary Table S1).

For a few groups, such as rust fungi (Fig. 1), the ITS may contain indels that inhibit direct sequencing or include multiple disparate copies, even within individuals, that can vary enough to result in erroneous identifications (McTaggart and Aime 2018; Rush et al. 2019). For these fungi, other markers are used. For instance, the large subunit of the nuclear ribosomal DNA repeat operon is for

identifying rust fungi (Ullah et al. 2019). In Oomycota two mitochondrial *cytochrome oxidase c subunits* genes, *COX1* and *COX2*, are regularly used because they differentiate species across the *Peronosporales*, although *COX2* was more successful when amplifying from old herbaria specimens (Choi et al. 2015).

Although DNA barcode sequences, most commonly of the ITS, are used to identify species, there is no community consensus on the percentage identity (i.e., the percentage of base pairs that match each other between a reference and query sequence) that is necessary for confident identification. Vu et al. (2019) predicted the optimal identity threshold to discriminate filamentous fungal species to be as high as 99.6% for ITS; similar thresholds were determined for basidiomycete yeasts (Urbina and Aime 2018). However, in the phytopathogenic smut genus *Ceraceosorus* ITS percentage identity within species was found to be <90% (Kijpomyongpan and Aime 2016), and in a recent genomic study of *Hypoxylon fragiforme*, up to 19 ITS paralogs sharing <97% identity were found within a single genome (Stadler et al. 2020). Although clearly no single threshold will apply across all fungi, some guidelines for interpreting BLAST results have been detailed in Lücking et al. (2020). Finally, the use of BLAST results, and ITS sequence data in general, should be interpreted with care. Hofstetter et al. (2019) reported that up to 30% of the fungal sequences in NCBI were associated with the wrong taxon name.

Whereas DNA barcoding is a tool for identifying species, different methods are used to fully circumscribe the variation occurring within or between species. Currently the gold standard is to use multigene phylogenies to elucidate species relationships, often including ribosomal and protein coding genes, and analyzing these data via different algorithms, such as maximum parsimony, maximum likelihood, or Bayesian inference (Raja et al. 2017). Comparisons of whole or partial genomes are becoming increasingly feasible, and they generally support classifications based on a limited number of selected conserved genes (Haridas et al. 2020).

FINDING THE CORRECT SCIENTIFIC NAME FOR PLANT PATHOGENIC FUNGI

A number of recommended websites are available for finding the correct scientific name for fungi. In addition, we have provided a list of scientific names of the most common or important plant pathogenic fungi and their synonyms as supplementary material (Supplementary Table S1). However, the online databases listed here are more inclusive and should be consulted for up-to-date information.

U.S. National Fungus Collections Databases (<https://nt.ars-grin.gov/fungaldatabases/>). Provides scientific names of plant-associated fungi along with reports of their hosts and distribution. Allows search by host and geographic distribution.

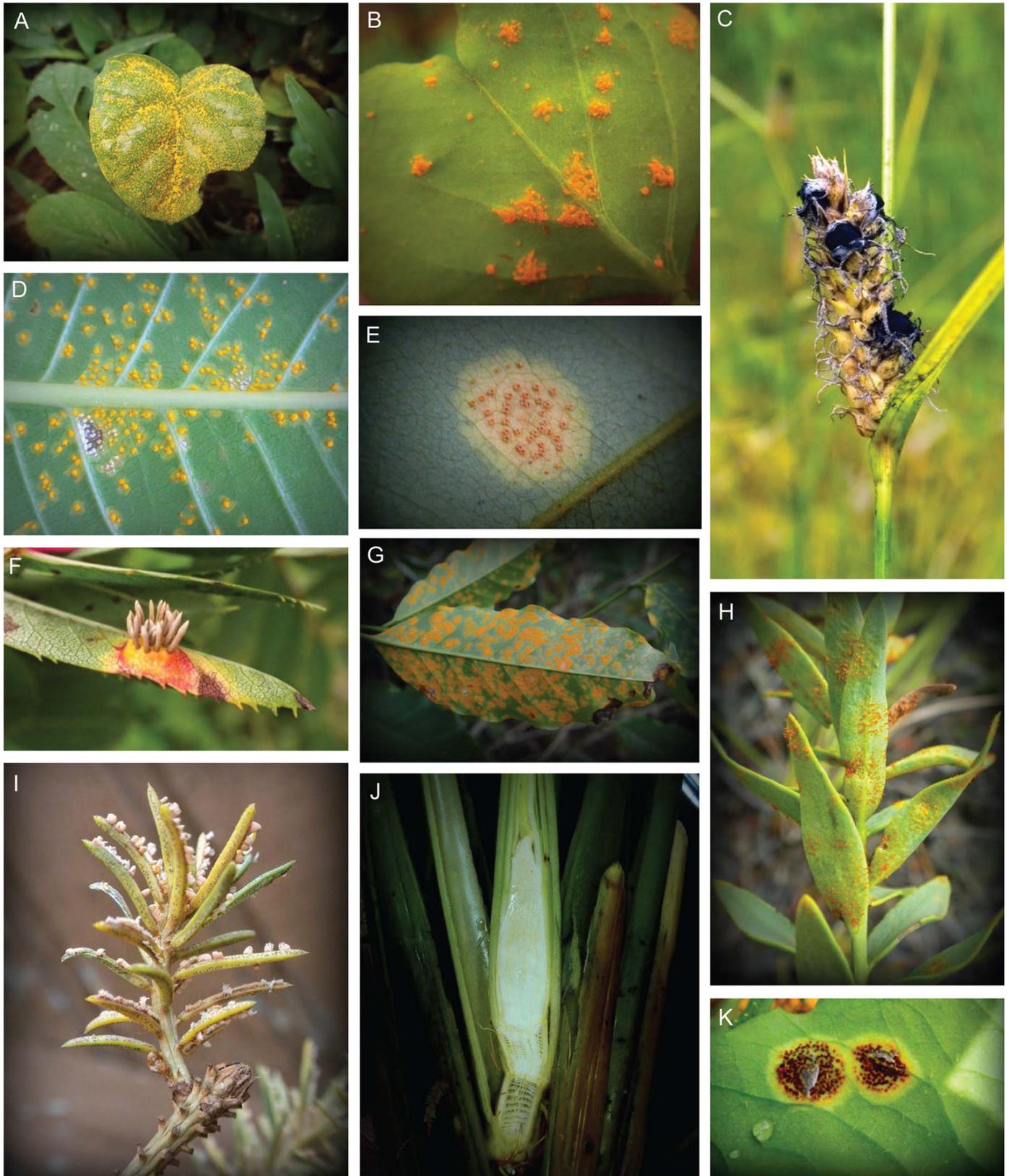
MycoBank (<https://www.mycobank.org/>). Includes all scientific names of fungi, with associated data, such as descriptions, illustrations, links to sequence data repositories, and updated names and higher classification.

Index Fungorum (www.indexfungorum.org/Names/Names.asp). Includes all scientific names of fungi with citations and links to the accepted name and links to protologues for select species.

Taxonomy at NCBI (<https://www.ncbi.nlm.nih.gov/taxonomy/>). Includes a hierarchical taxonomy for fungi and other organisms for which molecular data exist. Updates to NCBI taxonomy may lag behind those in MycoBank and Index Fungorum.

SCIENTIFIC NAMES OF PLANT PATHOGENIC FUNGI: HOW DOES IT HAPPEN?

Determining the scientific names of fungi is governed by a set of rules known as the International Code of Nomenclature for Algae, Fungi, and Plants (Turland et al. 2018), referred to as the Code.

**FIGURE 1**

Examples of phytopathogenic rust and smut fungi. **A**, Rust of *Lycianthes asarifolia* (*Caeoma*). **B**, Rust of *Oxalis* (*Puccinia oxalidis*). **C**, Smut of *Carex* (*Anthracoidea*). **D**, Rust of *Plumeria* (*Coleosporium plumeriae*). **E**, Rust of *Xylopia* (*Sphenorchidium*). **F**, Rust of *Sorbus* (*Gymnosporangium*). **G**, Rust of coffee (*Hemileia vastatrix*). **H**, Rust of willow (*Melampsora*). **I**, Rust of *Picea* (*Chrysomyxa*). **J**, Smut of water bamboo (*Ustilago esculenta*). **K**, Rust of hollyhock (*Leptopuccinia malvacearum*).

These rules are updated every 4 years for fungi at the International Mycological Congresses and every 6 years for all the organisms governed by the Code at the International Botanical Congresses. The basics of the Code for fungi are explained in Rossman and Palm-Hernandez (2008). The most consequential changes to the Code since that publication are explained below.

THE END OF DUAL NOMENCLATURE

Many important plant pathogenic fungi are pleomorphic ascomycetes and basidiomycetes, meaning that they can have more than one morph (Fig. 2). To deal with this complex situation, Article 59 of the old International Code of Botanical Nomenclature, until 2011, allowed different names to be applied to different morphs of the same fungus (Weresub and Pirozynski 1979). Furthermore, in an attempt to stabilize dual nomenclature, the International Code of Botanical Nomenclature dictated that where connections have been established, sexual morphs should have priority over asexual morph names (McNeill et al. 2006), which added an additional complication, because many such connections were later shown to be erroneous, again bringing the asexual name back into use. In 2011 the Code was revised to eliminate the use of two or more names for fungi, as explained in the section below.

ONE FUNGUS, ONE NAME

Transitioning to a single scientific name for fungi was strongly supported by plant pathologists who wanted stable names for genetic entities linked to important plant diseases. Although some fungi could have multiple different morphs with separate names, from 2011 onward, only one name, preferably linked to a DNA barcode (or genome), would be given preference. To pave the way for unitary nomenclature, the “One Fungus: One Name” symposium, held at the Royal Netherlands Academy of Arts and Sciences offices in Amsterdam, the Netherlands (20 to 21 April 2011), led to the Amsterdam Declaration on Fungal Nomenclature (Hawksworth et al. 2011), providing broad support among mycologists to move away from the system of dual nomenclature. This led to a momentous decision at the 18th International Botanical Congress in Melbourne, Australia, in which the Code abandoned dual nomenclature (McNeill et al. 2012). Since this decision, only one scientific name may be applied to one species of fungus (Fig. 2), consisting of a generic name and species epithet, occasionally with a lower rank such as variety, which is placed in a family, order, and higher ranks.

In theory the Code dictates that scientific names be determined by the principle of priority, that is, the first validly published name applied to a genus or species should be used regardless of morph. However, it is not always that simple. A major tenet of the Code is to contribute to the stability of scientific names; thus, provisions exist in the Code to conserve or protect names in common use that do not have priority over older, more obscure names. Hence, the principle of priority cannot be strictly applied in determining which names to use in all cases of dual nomenclature.

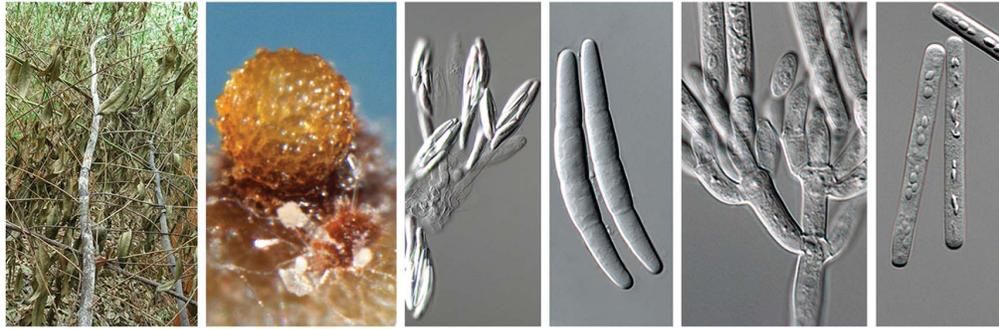
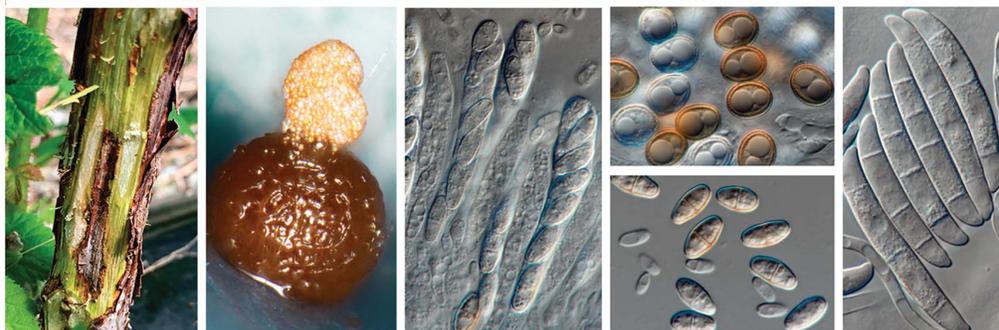
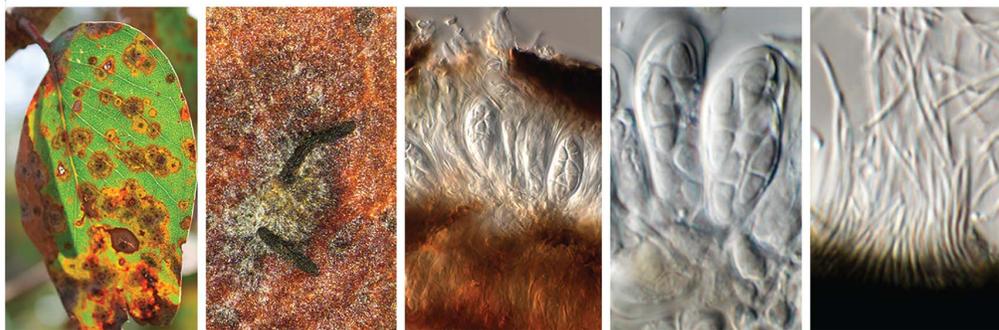
The merging of sexual and asexual generic and species names has been advanced by working groups established under the International Commission on the Taxonomy of Fungi (ICTF), which also included an International Subcommittee for the Taxonomy of Phytopathogenic Fungi. The ICTF coordinated the preparation and publication of lists of recommended generic names and important species names for protection of major groups of pleomorphic fungi and made them available for comment through its website (<https://www.fungaltaxonomy.org/>). Recommendations on lists of names to be accepted for protection against other competing names were then evaluated by the Nomenclature Committee for Fungi and recommended for approval by the General Committee on Nomenclature for action at the International Botanical Congress in Shenzhen, China, in 2017. Furthermore, the ICTF published

guidelines on requirements and best practices for describing new fungal species (Seifert and Rossman 2010), which has been updated version, incorporating recommendations of the revised Code (Aime et al. 2021).

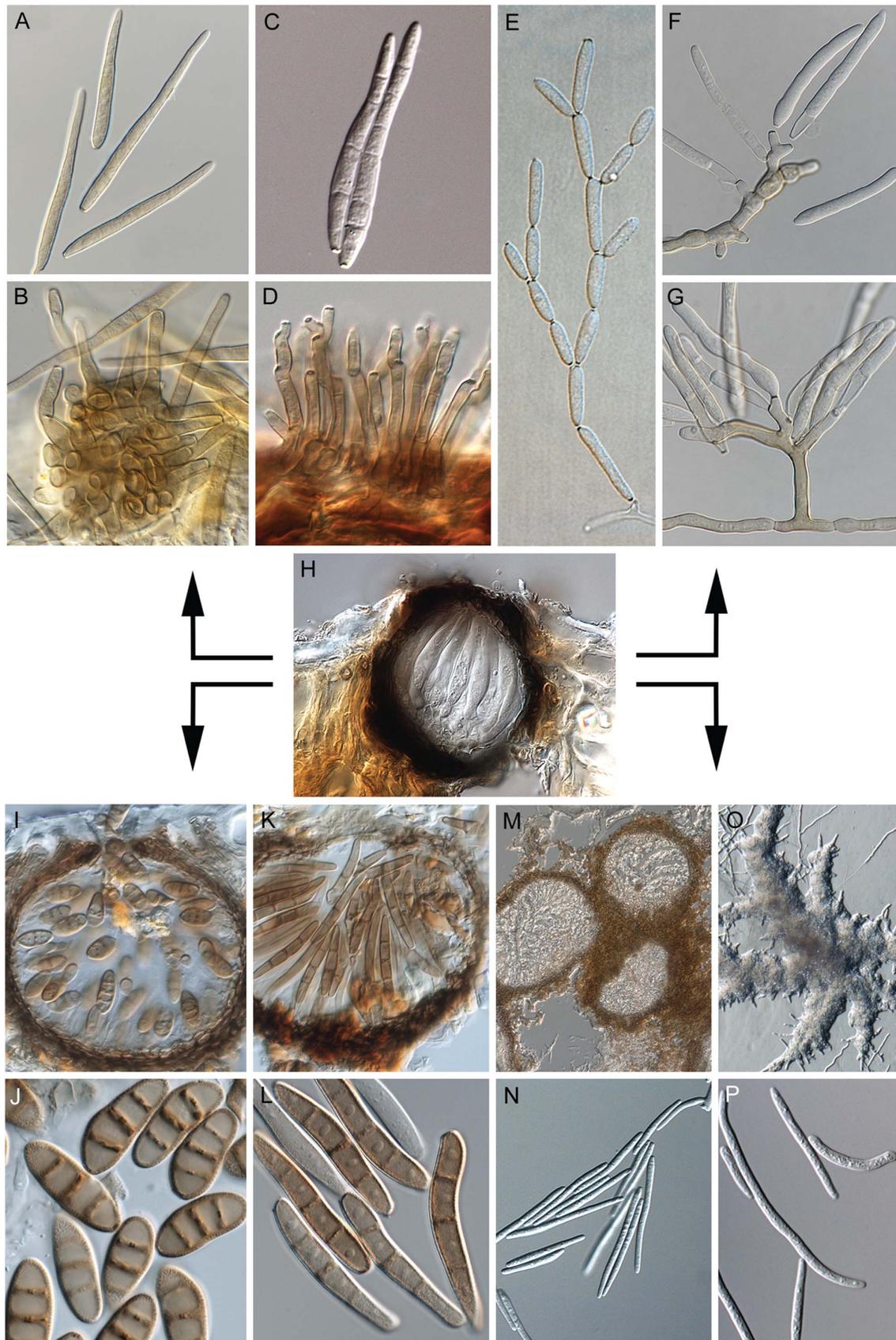
A single scientific name also adds clarity to quarantine regulations, disease management practices, and genome comparisons in research projects. However, it is important to bear in mind that relationships between asexual and sexual genera are not always one to one. For instance, some asexual rust fungal genera in the *Pucciniales* (e.g., *Uredo* and *Aecidium*) (Fig. 1) have species with sexual morphs belonging to >50 genera, and it may take years to resolve the correct names for rust fungi (Aime and McTaggart 2021). The reverse can also be true. For example, in older literature the genus *Mycosphaerella* was assumed to be the sexual morph of >30 asexual genera (Crous 2009). Recent treatment of the *Mycosphaerellaceae* revealed that these species were actually sexual morphs of many distinct genera (Fig. 3). Therefore, *Zymoseptoria graminicola* (syn. *Mycosphaerella graminicola*; see Quaedvlieg et al. 2011) is placed in a separate genus from *Pseudocercospora fijiensis* (syn. *Mycosphaerella fijiensis*; Crous et al. 2021), *Phloeospora ulmi* (syn. *Mycosphaerella ulmi*; Videira et al. 2017), *Neopseudocercospora brassicae* (syn. *Mycosphaerella brassicicola*; Videira et al. 2016), *Ramularia endophylla* (syn. *Mycosphaerella punctiformis*; Videira et al. 2016), or *Fulvia fulva* (syn. *Cladosporium fulvum*; Videira et al. 2017). Although all these genera are still members of the *Mycosphaerellaceae*, they are not included in the genus *Mycosphaerella*. Furthermore, the genus name *Mycosphaerella* is no longer used but is a synonym of the genus *Ramularia* (Videira et al. 2016). That “*Mycosphaerella*” with its numerous asexual morphs was shown to represent several distinct genera (Fig. 3) correlating to asexual morphs is not unique. This generic radiation observed in old morphologically conceived genera has been shown to be a common situation in several major pathogen complexes. Examples include *Botryosphaeriaceae*, which is now composed of 33 genera (Yang et al. 2017); *Cryphonectriaceae*, which now includes 21 genera (Jiang et al. 2020); *Ceratocystidaceae*, now with seven genera (de Beer et al. 2020); *Didymellaceae*, previously known as the *Phoma* complex, with 35 genera (Hou et al. 2020); *Teratosphaeriaceae*, now divided into 37 genera (Quaedvlieg et al. 2014); and *Fusarium* complex, now seven genera (Lombard et al. 2015), to name a few.

Although abandoning dual nomenclature in plant pathogenic fungi for the most part went smoothly, there were some instances of intense debate and even disagreement on which name to retain (Fig. 2). For instance, the causal organism of rice blast disease was commonly referred to as *Magnaporthe oryzae*. However, the genus *Magnaporthe* is polyphyletic, and the type, *M. salvinii* (*Magnaportheaceae*) is not congeneric with the causal organism of rice blast. The asexually typified generic name *Pyricularia* was shown to be the correct name for the rice blast fungus, resulting in the recommendation that the accurate scientific name for the fungus causing rice blast is *Pyricularia oryzae* (*Pyriculariaceae*), with the synonym *Magnaporthe oryzae* (Zhang et al. 2016).

Another example is blackleg of canola, where the causal organism has commonly been attributed to *Leptosphaeria maculans*, which is the sexual morph of *Plenodomus lingam* (Boerema and van Kesteren 1964). However, *Leptosphaeria doliolium*, type species of the genus *Leptosphaeria*, is genetically distinct from *Plenodomus* (Ariyawansa et al. 2015; de Gruyter et al. 2013), rendering *Plenodomus lingam* as the older, valid name for the pathogen causing blackleg of canola. However, in some cases generation of new data and the application of polythetic concepts have resulted in the resurrection of old names and the application of a more practical taxonomic concept. The recent article by Wittstein et al. (2020) concerns such an example in which most of the “harmless” saprobes are accommodated in *Rosellinia sensu stricto* and the more important pathogens in the resurrected genus *Dematophora*.

Calonectria*Fusarium**Hypsotheca**Neocosmospora**Thyridula***FIGURE 2**

Examples of disease symptoms and morphological structures of genera of phytopathogenic fungi with a single generic name (alternatives in parentheses). The examples portrayed here are *Calonectria* (syn. *Cylindrocladium*), *Fusarium* (syn. *Gibberella*), *Hypsotheca* (unnamed asexual morphs), *Neocosmospora* (fusarium-like morph unnamed), *Thyridula* (aulographina-like morph unnamed).

**FIGURE 3**

A selection of sporocarps and conidia of genera in *Mycosphaerellaceae* that share a mycosphaerella-like sexual morph. These genera are best distinguished based on the morphology of their asexual morphs. **A and B**, *Puniphilomyces circumscissa*. **C and D**, *Cercospora* sp. **E**, *Ramularia agastaches*. **F and G**, *Paracercosporidium microsorum*. **H**, Sexual morph of *Virosphaerella irregularis*, depicted as example of mycosphaerella-like sexual morph. **I and J**, *Sonderhenia eucalypticola*. **K and L**, *Sonderhenia eucalyptorum*. **M and N**, *Septoria agrimoniicola*. **O and P**, *Zymoseptoria tritici*.

The genus *Fusarium* includes a vast number of species, many of which are important plant pathogenic fungi. Historically the genus has been divided into groups with differing biology, some of which are now separated into one or more segregate genera. The type species of *Fusarium* is *F. sambucinum*, which is synonymous with *Gibberella pulvicaris*, the type species of *Gibberella*. With the change to one name, the generic name *Fusarium* has priority over *Gibberella*. All of the species related to *Fusarium sambucinum* are regarded as *Fusarium* in the strict or narrow sense, that is, *sensu stricto*. However, that leaves the question of what to do with hundreds of additional species that have been sequenced and regarded as groups of related species but are not closely related to *F. sambucinum*. For some of these groups a generic name exists. For example, the group of species in *Fusarium* known as the *F. solani* species complex has increased rapidly over the past 20 years to >80 species. For this group, the generic name *Neocosmospora* exists, and this genus has now been monographed (Sandoval-Denis et al. 2019), thus providing plant pathologists a rapid means of using DNA barcodes to identify these species. In another example, *Albonectria rigidiuscula* is a common tropical species for which the asexual name *Fusarium decemcellulare* has been applied. One could recognize this species as a *Fusarium* if one regards *Fusarium* in the broad sense, or *sensu lato*, and use the name *F. decemcellulare*; alternatively, one could recognize this subgroup within *Fusarium* as a distinct genus and apply the name *Albonectria* to the entire group. In this case the name *F. decemcellulare* could be placed in the genus *Albonectria*.

As one can imagine, controversy exists over whether to conceive of the genus *Fusarium* as a very large group with hundreds of species or to recognize the groups within *Fusarium* at the generic level by using existing and new generic names. On one hand, plant pathologists are familiar with the names in *Fusarium* and would like to retain them (Geiser et al. 2021), but how large and morphologically diverse should a genus be? Should a generic name reflect the biology of a group of species? Some of the *Fusarium* groups have a different morphology and biology, attack different hosts, or have diverse distribution patterns, and may be better recognized as distinct genera (P. W. Crous et al. 2021).

Even within the broadly conceived *Fusarium*, species complexes exist that are gradually being recognized with numerous distinct species. When that happens, scientific names must change to reflect the true genetic diversity of the complex and to define each species. For example, the *Fusarium oxysporum* complex was recently epitypified, and 15 cryptic species within that complex have been described and named to date (Lombard et al. 2019). As another example, Panama disease of banana (cultivar Cavendish) is caused by *Fusarium oxysporum* f. sp. *cubense* tropical race 4. Using a multigene phylogeny and morphology, several species associated with Panama disease were described from banana, with tropical race 4 being renamed as *F. odoratissimum* (Maryani et al. 2019).

The pathogenic Oomycota are predominantly in the order *Peronosporales* and include the downy mildews, which are obligate pathogens, >160 *Phytophthora* species causing numerous diseases (root and canker rots, leaf and seed diseases), and *Pythium* species best known as damping-off pathogens. The generic names have been stable for almost a century, and therefore there are few conflicted names in recent literature. However, numerous new species have been described since the advent of molecular systematics, several of which are closely related to well-known pathogens, indicating that many records before 2000 may be incorrect (Abad et al. 2019). Based on molecular systematics, *Pythium* was resolved into 11 well defined clades, labeled A to K (Lévesque and De Cock 2004). Clade K was closely related to *Phytophthora* and was described as a new genus *Phytopythium* (Bala et al. 2010). At a similar time Uzuhashi et al. (2010) segregated species from the 11 clades into five genera based on molecular systematics and morphological features (*Pythium sensu stricto*, *Elongisporangium*,

Globisporangium, *Ovatisporangium*, and *Pilasporangium*); however, there was no phylogenetic support for any particular arrangement of these clades, and this classification has not been widely accepted. *Ovatisporangium* included all the species in clade K but is a later synonym of *Phytopythium*, which has precedence. Paraphyly in *Pythium* has been supported in a phylogeny based on 277 core orthologous genes derived from whole-genome sequences (Ascunce et al. 2017), but these authors have not proposed new generic names for the clades. *Phytophthora* is paraphyletic with the downy mildews embedded within the phylogeny, as demonstrated with several genes (Bourret et al. 2018; Runge et al. 2011) and with >2,000 single-copy genes derived from whole genomes (McCarthy and Fitzpatrick 2017). It can therefore be expected that *Phytophthora* will resolve into several genera in future studies.

DETERMINING THE RIGHT SCIENTIFIC NAME FOR A PLANT PATHOGENIC FUNGUS: THINGS TO CONSIDER

- Since the abandonment of dual nomenclature, each fungal species may have only one scientific name. The choice of which name to apply depends on the organism and is not always straightforward. If you already think you know the scientific name of your plant pathogenic fungus, consult the list included here or one of the databases listed previously to determine whether the name has changed.
- To determine the identity of your pathogen, it is recommended that you first generate a barcode sequence of your taxon. An ITS sequence serves as the official DNA barcode locus for Fungi and is also the most common barcode in public repositories. However, this locus does not discriminate all taxa, some species can have multiple copies of ITS, and different loci need to be applied in some groups, such as rust fungi (28S) and *Fusarium* (*TEF1*) (see Supplementary Table S1 for secondary barcode loci).
- Consult databases such as the International Nucleotide Sequence Database Collaboration (<http://www.insdc.org/>) and UNITE (<http://unite.ut.ee>) to obtain an identification by using your DNA barcode. Ex-type sequences are authentic for the name and should be regarded as reference indicators. For a database of ex-type DNA barcodes, see NCBI (<https://www.ncbi.nlm.nih.gov/projects/RefSeq>). Bear in mind that results from public databases that are not annotated as types should be interpreted with caution because many sequences are labeled with outdated or incorrect names. In all cases, consult the original publication in which the sequence was published to confirm authenticity of the name, followed by a search of the name repositories to determine whether the name is still up to date.
- In many genera of plant pathogenic fungi, ITS or 28S will not be able to resolve the species or genus in question, and secondary barcodes (e.g., *TEF1*, *COX1*, *COX2*) will have to be used. Note that secondary barcodes often depend on the genus in question, and databases such as <https://www.plantpathogen.org> can provide current information on these (also see Supplementary Table S1 for secondary barcode loci).
- Once you are certain that you have the species in question, you need to decide which name to apply. There are several online databases, and these may have conflicting opinions. For plant pathogenic fungi, consult MycoBank (<http://www.MycoBank.org>), Index Fungorum (<http://www.indexfungorum.org/names/names.asp>), and the U.S. Department of Agriculture (<https://nt.ars-grin.gov/fungaldbases/>).
- To resolve potential generic and species conflicts (synonyms), consult the ICTF (<https://www.fungaltaxonomy.org>), genera of Plant Pathogenic Fungi (<https://www.plantpathogen.org>), or one of the authors of this article.
- If you know the host and geographic location, you can consult the U.S. National Fungus Collections Fungus–Host Database (<https://nt.ars-grin.gov/fungaldbases/fungushost/fungushost.cfm>)

to determine which species have been reported from a given host and region.

- Unfortunately, only a fraction of the fungal species estimated to occur have been described (an estimated 95% remain uncataloged), and of these an even smaller portion are known from DNA sequence data in repositories. Thus, a significant chance exists of finding a new species or genus. If this is the case, you would have to describe the novel species of plant pathogenic fungi.
- To describe a new species, consult Seifert and Rossman (2010) and Aime et al. (2021). Or save yourself a lot of time and contact a mycologist who specializes in describing plant pathogenic fungi (<https://ima-mycology.org/>).

Scientific names of fungi will continue to change as more is learned about the definition and phylogeny of each genus and species. Since the days of describing fungi purely from morphology, characteristics such as the color and septation of spores are often not definitive in placing species in genera or even in defining species. Genera that were once broadly defined have been split into several genera, often with species once placed there removed to other genera. Theoretically, each well-defined genus includes only closely related species. In addition, many species that were once thought to represent only one species have now been determined to be complexes, and therefore each species is defined more precisely to reflect their biology, and as a result the scientific name changes to reflect that increased knowledge (Lücking et al. 2021).

LITERATURE CITED

- Abad, Z. G., Burgess, T., Bienapfl, J. C., Redford, A. J., Coffey, M., and Knight, L. 2019. IDphy: Molecular and morphological identification of *Phytophthora* species based on the types and other well-authenticated specimens. USDA APHIS PPQ S&T Beltsville Lab, USDA APHIS PPQ S&T ITP, Centre for Phytophthora Science and Management, and World Phytophthora Collection. <https://idtools.org/id/phytophthora/index.php>
- Aime, M. C., and McTaggart, A. R. 2021. A higher-rank classification for rust fungi, with notes on genera. *Fungal Syst. Evol.* 7:21-47.
- Aime, M. C., Miller, A. N., Aoki, T., Bensch, K., Cai, L., et al. 2021. How to publish a new fungal species, or name, version 3.0. *IMA Fungus* 12:11.
- Almeida, R. P. P. 2018. Emerging plant disease epidemics: Biological research is key but not enough. *PLoS Biol.* 16:e2007020.
- Ariyawansa, H. A., Phukhamsakda, C., Thambugala, K. M., Bulgakov, T. S., Wanasinghe, D. N., Perera, R. H., Mapook, A., Camporesi, E., Kang, J. C., Jones, E. B. G., Bahkali, A. H., Jayasiri, S. C., and Hyde, K. D. 2015. Revision and phylogeny of Leptosphaeriaceae. *Fung. Div.* 74:19-51.
- Ascunce, M. S., Hugueta-Tapia, J. C., Ortiz-Urquiza, A., Keyhani, N. O., Braun, E. L., and Goss, E. M. 2017. Phylogenomic analysis supports multiple instances of polyphyly in the oomycete peronosporalean lineage. *Mol. Phylog. Evol.* 114:199-211.
- Bala, K., Robideau, G. P., Lévesque, C. A., de Cock, A. W. A. M., Abad, Z. G., Lodhi, A. M., Shahzad, S., Ghaffar, A., and Coffey, M. D. 2010. *Phytophthora* Abad, de Cock, Bala, Robideau, Lodhi & Lévesque, gen. nov. and *Phytophthora sindhum* Lodhi, Shahzad & Lévesque, sp. nov. *Fungal Planet* 49. *Persoonia* 24:136-137.
- Berberie, M. L., and Taylor, J. W. 1992. 18S ribosomal RNA gene sequence characters place the human pathogen *Sporothrix schenckii* in the genus *Ophiostoma*. *Exp. Mycol.* 16:87-91.
- Boerema, G. H., and van Kesteren, H. A. 1964. The nomenclature of two fungi parasitizing *Brassica*. *Persoonia* 3:17-28.
- Bouret, 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.
- Bruns, T. D., White, T. J., and Taylor, J. W. 1991. Fungal molecular systematics. *Annu. Rev. Ecol. Syst.* 22:525-564.
- Cheek, M., Lughadha, E. C., Kirk, P., Lindon, H., Carretero, J., Looney, B., Douglas, B., Haelewaters, D., Gaya, E., Llewellyn, T., Ainsworth, A. M., Gafforov, Y., Hyde, K. D., Crous, P. W., Hughes, M., Walker, B. E., Forzza, R. C., Wong, K. M., and Niskanen, T. 2020. New scientific discoveries: Plants and fungi. *Plants People Planet* 2:371-388.
- Choi, Y. J., Beakes, G., Glockling, S., Kruse, J., Nam, B., Nigrelli, L., Ploch, S., Shin, H. D., Shivas, R. G., Telle, S., Voglmayr, H., and Thines, M. 2015. Towards a universal barcode of oomycetes: A comparison of the *cox1* and *cox2* loci. *Mol. Ecol. Resour.* 15:1275-1288.
- Crous, P. W. 2009. Taxonomy and phylogeny of the genus *Mycosphaerella* and its anamorphs. *Fung. Div.* 38:1-24.
- Crous, P. W., Carlier, J., Roussel, V., and Groenewald, J. Z. 2021. *Pseudocercospora* and allied genera associated with leaf spots of banana (*Musa* spp.). *Fungal Syst. Evol.* 7:1-19.
- Crous, P. W., Lombard, L., Sandoval-Denis, M., Seifert, K. A., Schroers, H.-J., et al. 2021. *Fusarium*: More than a node or a foot-shaped basal cell. *Stud. Mycol.* (in press).
- de Beer, Z. W., Duong, T. A., Barnes, I., Wingfield, B. D., and Wingfield, M. J. 2014. Redefining *Ceratocystis* and allied genera. *Stud. Mycol.* 79:187-219.
- de Gruyter, J., Woudenberg, J. H. C., Aveskamp, M. M., Verkley, G. J. M., Groenewald, J. Z., and Crous, P. W. 2013. Redisposition of phoma-like anamorphs in *Pleosporales*. *Stud. Mycol.* 75:1-36.
- Federhen, S. 2015. Type material in the NCBI Taxonomy Database. *Nucleic Acids Res.*: D1086-D1098.
- Fisher, M. C., Henk, D. A., Briggs, C. J., Brownstein, J. S., Madoff, L. C., McCraw, S. L., and Gurr, S. J. 2012. Emerging fungal threats to animal, plant and ecosystem health. *Nature* 484:186-194.
- Geiser, D. M., Al-Hatmi, A., Aoki, T., Arie, T., Balmas, V., et al. 2021. Phylogenomic analysis of a 55.1 kb 19-gene dataset resolves a monophyletic *Fusarium* that includes the *Fusarium solani* species complex. *Phytopathology*. 111:1064-1077.
- Haridas, S., Albert, R., Binder, M., Bloem, J., LaButti, K., Salamov, A., Andreopoulos, B., Baker, S. E., Barry, K., Bills, G., Bluhm, B. H., Cannon, C., Castanera, R., Culley, D. E., Daum, C., Ezra, D., González, J. B., Henrissat, B., Kuo, A., Liang, C., Lipzen, A., Lutzoni, F., Magnuson, J., Mondo, S. J., Nolan, M., Ohm, R. A., Pangilinan, J., Park, H.-J., Ramírez, L., Alfaro, M., Sun, H., Tritt, A., Yoshinaga, Y., Zwiars, L.-H., Turgeon, B. G., Goodwin, S. B., Spatafora, J. W., Crous, P. W., and Grigoriev, I. V. 2020. 101 *Dothideomycetes* genomes: a test case for predicting lifestyles and emergence of pathogens. *Stud. Mycol.* 96:141-153.
- Hawksworth, D. L., Crous, P. W., Redhead, S. A., Reynolds, D. R., Samson, R. A., Seifert, K. A., Taylor, J. W., Wingfield, M. J., et al. 2011. The Amsterdam Declaration on fungal nomenclature. *IMA Fungus* 2:105-111.
- Hawksworth, D. L., and Lücking, R. 2017. Fungal diversity revisited: 2.2 to 3.8 million species. Pages 79-95 in: *The Fungal Kingdom*. J. Heitman, B. Howlett, P. W. Crous, E. Stukenbrock, T. James, and N. Gow, eds. ASM Press, Washington, DC.
- Hebert, P. D. N., Cywinska, A., Ball, S. L., and deWaard, J. R. 2003. Biological identifications through DNA barcodes. *Proc. R. Soc. Lond. B Biol. Sci.* 270:313-321.
- Hofstetter, V., Buyck, B., Eyssartier, G., Schnee, S., and Gindro, K. 2019. The unbearable lightness of sequenced-based identification. *Fung. Div.* 96:243-284.
- Hou, L. W., Groenewald, J. Z., Pfenning, L. H., Yarden, O., Crous, P. W., and Cai, L. 2020. The phoma-like dilemma. *Stud. Mycol.* 96:309-396.
- Jiang, N., Fan, X. L., Chenming, T., and Crous, P. W. 2020. Reevaluating *Cryphonectriaceae* and allied families in *Diaporthales*. *Mycologia* 112:267-292.
- Kijpornyongpan, T., and Aime, M. C. 2016. Rare or rarely detected? *Ceraeosorus guamensis* sp. nov.: A second described species of *Ceraeosorales* and the potential for underdetection of rare lineages with common sampling techniques. *Antonie van Leeuwenhoek* 109:1127-1139.
- Lévesque, C. A., and De Cock, A. W. A. M. 2004. Molecular phylogeny and taxonomy of the genus *Pythium*. *Mycol. Res.* 108:1363-1383.
- Lombard, L., Sandoval-Denis, M., Lamprecht, S. C., and Crous, P. W. 2019. Epitypification of *Fusarium oxysporum*: clearing the taxonomic chaos. *Persoonia* 43:1-47.
- Lombard, L., van der Merwe, N. A., Groenewald, J. Z., and Crous, P. W. 2015. Generic concepts in Nectriaceae. *Stud. Mycol.* 80:189-245.
- Lücking, R., Aime, M. C., Robbertse, B., Miller, A. N., Aoki, T., et al. 2021. Fungal taxonomy and sequence-based nomenclature. *Nat. Microbiol.* 6:540-548.
- Lücking, R., Aime, M. C., Robbertse, B., Miller, A. N., Ariyawansa, H. A., Aoki, T., Cardinali, G., Crous, P. W., Druzhinina, I. S., Geiser, D. M., Hawksworth, D. L., Hyde, K. D., Irinyi, L., Jeewon, R., Johnston, P. R., Kirk, P. M., Malosso, E., May, T. W., Meyer, W., Öpik, M., Robert, V., Seifert, K. A., Stadler, M., Thines, M., Vu, D., Yurkov, A. M., Zhang, N., and Schoch, C. L. 2020. Unambiguous identification of fungi: Where do we stand and how accurate and precise is fungal barcoding? *IMA Fungus* 11:14.
- Marin-Felix, Y., Groenewald, J. Z., Cai, L., Chen, Q., Marinowicz, S., Barnes, I., Bensch, K., Braun, U., Camporesi, E., Damm, U., de Beer, Z. W., Dissanayake, A., Edwards, J., Giraldo, A., Hernandez-Restrepo, M., Hyde, K. D., Jayawardena, R. S., Lombard, L., Luangsa-ard, J., McTaggart, A. R., Rossman, A. Y., Sandoval-Denis, M., Shen, M., Shivas, R. G., Tan, Y. P., van der Linde, E. J., Wingfield, M. J., Wood,

- A. R., Zhang, J. Q., Zhang, Y., and Crous, P. W. 2017. Genera of phytopathogenic fungi: GOPHY 1. *Stud. Mycol.* 86:99-216.
- Marin-Felix, Y., Hernández-Restrepo, M., Iturrieta-González, I., García, D., Gené, J., Groenewald, J. Z., Cai, L., Chen, Q., Quaedvlieg, W., Schumacher, R. K., Taylor, P. W. J., Ambers, C., Bonthond, G., Edwards, J., Krueger-Hadfield, S. A., Luangsa-ard, J. J., Morton, L., Moslemi, A., Sandoval-Denis, M., Tan, Y. P., Thangavel, R., Vaghefi, N., Cheewangkoon, R., and Crous, P. W. 2019a. Genera of phytopathogenic fungi: GOPHY 3. *Stud. Mycol.* 94:1-124.
- Marin-Felix, Y., Hernández-Restrepo, M., Wingfield, M. J., Akulov, A., Carnegie, A. J., Cheewangkoon, R., Gramaje, D., Groenewald, J. Z., Guarnaccia, V., Halleen, F., Lombard, L., Luangsa-ard, J., Marincowitz, S., Moslemi, A., Mostert, L., Quaedvlieg, W., Schumacher, R. K., Spies, C. F. J., Thangavel, R., Taylor, P. W. J., Wilson, A. M., Wingfield, B. D., Wood, A. R., and Crous, P. W. 2019b. Genera of phytopathogenic fungi: GOPHY 2. *Stud. Mycol.* 92:47-133.
- Maryani, N., Lombard, L., Poerba, Y. S., Subandiyah, S., Crous, P. W., and Kema, G. H. J. 2019. Phylogeny and genetic diversity of the banana Fusarium wilt pathogen *Fusarium oxysporum* f. sp. *cubense* in the Indonesian centre of origin. *Stud. Mycol.* 92:155-194.
- McCarthy, C. G., and Fitzpatrick, D. A. 2017. Phylogenomic reconstruction of the oomycete phylogeny derived from 37 genomes. *MSphere* 2:e00095-17.
- McNeill, J., Barrie, F. F., Buck, W. R., Demoulin, V., Greuter, W., Hawksworth, D. L., Herendeen, P. S., Knapp, S., Marhold, K., Prado, J., Prud'homme Van Reine, W. F., Smith, G. F., and Wiersema, J. H., eds. 2012. International Code of Nomenclature for Algae, Fungi, and Plants (Melbourne Code) [Regnum vegetabile no. 154]. Koeltz Scientific Books, Königstein, Germany.
- McNeill, J., Barrie, F. R., Burdet, H. M., Demoulin, V., Hawksworth, D. L., Marhold, K., Nicolson, D. H., Prado, J., Silva, P. C., Skog, J. E., Wiersema, J. H., and Turland, N. J. 2006. International Code of Botanical Nomenclature (Vienna Code) adopted by the Seventeenth International Botanical Congress, Vienna, Austria, July 2005 (electronic ed.). International Association for Plant Taxonomy, Vienna, Austria. <https://www.iapt-taxon.org/icbn/main.htm>
- McTaggart, A. R., and Aime, M. C. 2018. The species of *Coleosporium* (*Pucciniales*) on *Solidago* in North America. *Fungal Biol.* 122:800-809.
- Quaedvlieg, W., Binder, M., Groenewald, J. Z., Summerell, B. A., Carnegie, A. J., Burgess, T. I., and Crous, P. W. 2014. Introducing the consolidated species concept to resolve species in the Teratosphaeriaceae. *Persoonia* 33:1-40.
- Quaedvlieg, W., Kema, G. H. J., Groenewald, J. Z., Verkley, G. J. M., Seifbarghi, S., Razavi, M., Mirzadi Gohari, A., Mehrabi, R., and Crous, P. W. 2011. *Zymoseptoria* gen. nov.: a new genus to accommodate septoria-like species occurring on graminicolous hosts. *Persoonia* 26:57-69.
- Raja, H. A., Miller, A. N., Pearce, C. J., and Oberlies, N. H. 2017. Fungal identification using molecular tools: a primer for the natural products research community. *J. Nat. Prod.* 80:756-770.
- Reeleder, R. D. 2003. Fungal plant pathogens and soil biodiversity. *Can. J. Soil Sci.* 83:331-336.
- Rossmann, A. Y., and Palm-Hernandez, M. E. 2008. Systematics of plant pathogenic fungi: Why it matters. *Plant Dis.* 92:1376-1386.
- 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.
- Rush, T. A., Golan, J., McTaggart, A., Kane, C., Schneider, R. W., and Aime, M. C. 2019. Variation in the internal transcribed spacer region of *Phakopsora pachyrhizi* and implications for molecular diagnostic assays. *Plant Dis.* 103:2237-2245.
- Sandoval-Denis, M., Lombard, L., and Crous, P. W. 2019. Back to the roots: A reappraisal of *Neocosmospora*. *Persoonia* 43:90-185.
- Santini, A., Ghelardini, L., De Pace, C., Desprez-Loustau, M. L., Capretti, P., Chandelier, A., Cech, T., Chira, D., Diamandis, S., Gaitniekis, T., Hantula, J., Holdenrieder, O., Jankovsky, L., Jung, T., Jurc, D., Kirisits, T., Kunca, A., Lygis, V., Malecka, M., Marçais, B., Schmitz, S., Schumacher, J., Solheim, H., Solla, A., Szabò, I., Tsopeles, P., Vannini, A., Vettraino, A. M., Webber, J., Woodward, S., and Stenlid, J. 2013. Biogeographical patterns and determinants of invasion by forest pathogens in Europe. *New Phytol.* 197:238-250.
- Schoch, C. L., Seifert, K. A., Huhndorf, S., Robert, V., Spouge, J. L., Levesque, C. A., and Chen, W., and Fungal Barcoding Consortium. 2012. Nuclear ribosomal internal transcribed spacer (ITS) region as a universal DNA barcode marker for *Fungi*. *Proc. Natl. Acad. Sci. USA* 109:6241-6246.
- Seifert, K. A., and Rossman, A. Y. 2010. How to describe a new fungal species. *IMA Fungus* 1:109-111.
- Stadler, M., Lambert, C., Wibberg, D., Kalinowski, J., Kolařík, M., and Kuhnert, E. 2020. Intragenomic polymorphisms in the ITS region of high-quality genomes of the Hypoxylaceae (Xylariales, Ascomycota). *Mycol. Prog.* 19:235-245.
- Stielow, J. B., Lévesque, C. A., Seifert, K. A., Meyer, W., Irinyi, L., Smits, D., Renfurm, R., Verkley, G. J. M., Groenewald, M., Chaduli, D., Lomascolo, A., Welti, S., Lesage-Meessen, L., Favel, A., Al-Hatmi, A. M. S., Damm, U., Yilmaz, N., Houben, J., Lombard, L., Quaedvlieg, W., Binder, M., Vaas, L. A. I., Vu, D., Yurkov, A., Begerow, D., Roehl, O., Guerreiro, M., Fonseca, A., Samerpitak, K., van Diepeningen, A. D., Dolatabadi, S., Moreno, L. F., Casaregola, S., Mallet, S., Jacques, N., Roscini, L., Egidi, E., Bizet, C., Garcia-Hernoso, D., Martín, M. P., Deng, S., Groenewald, J. Z., Boekhout, T., de Beer, Z. W., Barnes, I., Duong, T. A., Wingfield, M. J., de Hoog, G. S., Crous, P. W., Lewis, C. T., Hambleton, S., Moussa, T. A. A., Al-Zahrani, H. S., Almaghrabi, O. A., Louis-Seize, G., Assabgui, R., McCormick, W., Omer, G., Dukik, K., Cardinali, G., Eberhardt, U., de Vries, M., and Robert, V. 2015. One fungus, which genes? Development and assessment of universal primers for potential secondary fungal DNA barcodes. *Persoonia* 35:242-263.
- Turland, N. J., Wiersema, J. H., Barrie, F. R., Greuter, W., Hawksworth, D. L., Herendeen, P. S., Knapp, S., Kusber, W.-H., Li, D.-Z., Marhold, K., May, T. W., McNeill, J., Monro, A. M., Prado, J., Price, M. J., and Smith, G. F., eds. 2018. International Code of Nomenclature for Algae, Fungi, and Plants (Shenzhen Code) adopted by the Nineteenth International Botanical Congress Shenzhen, China, July 2017 [Regnum Vegetabile 159]. Koeltz Botanical Books, Glashütten, Germany.
- Ullah, S., Abbasi, M., Khalid, A. N., Ishaq, A., Fiza, M., and Aime, M. C. 2019. *Allodus prostris* comb. nov., causal agent of tulip rust. *Nova Hedwigia* 109:225-232.
- Urbina, H., and Aime, M. C. 2018. A closer look at *Sporidiobolales*: Ubiquitous microbial community members of plant and food biospheres. *Mycologia* 110:79-92.
- Uzuhashi, S., Tojo, M., and Kakishima, M. 2010. Phylogeny of the genus *Pythium* and description of new genera. *Mycoscience* 51:337-365.
- Videira, S. I. R., Groenewald, J. Z., Braun, U., Shin, H.-D., and Crous, P. W. 2016. All that glitters is not *Ramularia*. *Stud. Mycol.* 83:49-163.
- Videira, S. I. R., Groenewald, J. Z., Nakashima, C., Braun, U., Barreto, R. W., de Wit, P. J. G. M., and Crous, P. W. 2017. *Mycosphaerellaceae*: Chaos or clarity? *Stud. Mycol.* 87:257-421.
- Vu, D., Groenewald, M., de Vries, M., Gehrman, T., Stielow, B., Eberhardt, U., Al-Hatmi, A., Groenewald, J. Z., Cardinali, G., Houben, J., Boekhout, T., Crous, P. W., Robert, V., and Verkley, G. J. M. 2019. Large-scale generation and analysis of filamentous fungal DNA barcodes boosts coverage for kingdom fungi and reveals thresholds for fungal species and higher taxon delimitation. *Stud. Mycol.* 92:135-154.
- Weresub, L. K., and Pirozynski, K. A. 1979. Pleomorphism of fungi as treated in the history of mycology and nomenclature. Pages 17-25 in: *The Whole Fungus* 1. B. Kendrick, ed. National Museums of Canada, Ottawa, ON.
- Wittstein, K., Cordsmeier, A., Lambert, C., Wendt, L., Sir, E. B., Weber, J., Wurzlner, N., Petrini, L. E., and Stadler, M. 2020. Identification of *Rosellinia* species as producers of cyclodepsipeptide PF1022 A and resurrection of the genus *Dematophora* as inferred from polythetic taxonomy. *Stud. Mycol.* 96:1-16.
- Yang, T., Groenewald, J. Z., Cheewangkoon, R., Jami, F., Abdollahzadeh, J., Lombard, L., and Crous, P. W. 2017. Families, genera, and species of Botryosphaeriales. *Fungal Biol.* 121:322-346.
- Zhang, N., Luo, J., Rossman, A., Aoki, T., Chuma, I., Crous, P. W., Dean, R., de Vries, R. P., Donofrio, N., Hyde, K. D., Lebrun, M., Talbot, N. J., Tharreau, D., Tosa, Y., Valent, B., Wang, Z., and Xu, J. 2016. Generic names in Magnaporthales. *IMA Fungus* 7:155-159.