Identifying and Naming Plant-Pathogenic Fungi: Past, Present, and Future

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Abstract

Scientific names are crucial in communicating knowledge about fungi. In plant pathology, they link information regarding the biology, host range, distribution, and potential risk. Our understanding of fungal biodiversity and fungal systematics has undergone an exponential leap, incorporating genomics, web-based systems, and DNA data for rapid identification to link species to metadata. The impact of our ability to recognize hitherto unknown organisms on plant pathology and trade is enormous and continues to grow. Major challenges for phytomycology are intertwined with the Genera of Fungi project, which adds DNA barcodes to known biodiversity and corrects the application of old, established names via epi- or neotypification. Implementing the one fungus–one name system and linking names to validated type specimens, cultures, and reference sequences will provide the foundation on which the future of plant pathology and the communication of names of plant pathogens will rest.

INTRODUCTION

Molecular phylogenetics: using DNA data to study evolutionary relationships, usually depicted via phylogenetic trees

The protection of plants against disease and, more specifically, research on plant pathogens rests primarily on accurate communication regarding the fungi that cause disease. We communicate about species of fungi causing diseases via the application of scientific names. These names provide the key to the accumulated knowledge on the biology, distribution, ecology, host range, and control of, as well as the risks associated with, fungal pathogens. Inaccurate characterization can lead to unnecessary control measures and restrictions being applied or, importantly, in no action being taken to control potentially devastating pathogens. Even when hitherto unknown fungi are encountered, an understanding of their relationships can predict whether they are likely to be a cause for concern.

Our understanding of the fungi and their relationships with plants and each other has seen an unprecedented and exponential growth over the past 10–15 years. This has been primarily fueled by advances in molecular phylogenetics, and the impact of this new technology continues to accelerate. Fungal systematics, the field concerned with classification and relationships, is becoming increasingly vibrant in diverse regions of the world and is no longer largely confined to Europe and North America, which was the case into the 1980s. It is also witnessing an unprecedented level of international collaboration and visibility, taking advantage of web-based systems to enhance the procedures for documenting and naming fungi, including those that cause plant disease.

Mycologists face a daunting challenge. Just 20 years ago, the notion that we knew only 6% of the fungi on Earth was treated with skepticism by many other biologists. Now, primarily as a consequence of the application of DNA sequence data to the identification of fungi, it has emerged that this was far from an exaggeration and is actually a conservative estimate of the huge problem facing our knowledge of global fungal species richness. There are at least 1.5 million and probably 3 million species to contend with (41, 44), although some estimates are even higher (98). It is thus unfortunate that only around 100,000 species are presently recognized. Fungi are surely the most diverse eukaryotes on Earth. Faced with this knowledge gap, mycologists are beginning to find new approaches to both document this megadiversity and reduce the time traditionally devoted to clarifying the application of old, insufficiently known names (see sidebar, How Many Fungal Species Are There on Earth?).

Plant pathologists and other users of fungal names are understandably often irritated and frustrated by name changes that can appear nonsensical. This frustration is often justified because

HOW MANY FUNGAL SPECIES ARE THERE ON EARTH?

In the premolecular era, Hawksworth (41) estimated that, conservatively, there were 1.5 million species of fungi on Earth. This estimate was based on three independent data sets, which indicated that the number of fungi in all habitats to be expected in a survey of a particular place was six times that of the vascular plants present, extrapolated to the global scale. Estimates of the number of plant species have risen from 250,000 to 400,000, suggesting that the estimate for fungal species should be increased to 2.4 million, and around 3 million is probable (44). However, some additional data on fungal numbers suggest that the ratio of fungi to plants could be at least 10:1 (8, 66); fungi occurring in unique habitats such as soil and insects or those on lichens have generally not been included in these later estimates. Recent molecular studies have shown that there could be more than a thousand species of fungal endophytes in a single plant host, most being unculturable (49), suggesting that there could be as many as six million species of fungi (86).

some of these changes are indeed senseless, arising from arcane rules devised in the early twentieth century that are no longer appropriate or necessary. Examples are versions of the International Code of Botanical Nomenclature (ICBN), which allowed different morphs of the same fungal species to be accorded separate scientific names and did not permit fungal species to be based on even permanently preserved cultures. Other changes in names, however, reflect a more logical understanding of relationships, arising from new research with molecular tools and so are more predictive of the biology and ecology of the fungi concerned; something plant pathologists should welcome.

Sporophore: spore-bearing organ of a fungus

In this review, we consider recent developments affecting the identification and naming of plant-pathogenic fungi. This is done in the context of past practices, in order that plant pathologists can better appreciate the background of changes now in the pipeline. In addition, we look to new developments and enhancements of the current systems and practices, which promise to provide further precision in the naming and identification of fungi. Through their positive impacts on the knowledge of plant pathology, mycologists are becoming increasingly recognized as world leaders in the organization of naming systems, envied by zoologists and botanists alike, who are now striving to follow suit.

Premolecular Phase

The fungi occurring on plants and plant parts were historically separated morphologically and were often misunderstood until microscopy began to be actively applied in the 1840s. The first convincing evidence that fungi were agents of plant disease was the case of *Phytophthora infestans* (6). The form of the spore-bearing structures and the color, septation, and dimensions of the spores were increasingly emphasized in classification systems into the early decades of the twentieth century.

In the mid-nineteenth century, it started to become clear that it was not uncommon for what appeared to be the same species to have stages with different sporing morphs. In some cases, through careful observation work, the links were inescapable (e.g., 102). With the emphasis on spore characters in classification, these different stages were nevertheless accorded separate scientific names (e.g., 30), and this became the accepted practice adopted in the major compendium of the time (83). This approach was also considered prudent, as in many cases the biological relationships were unclear. Surprisingly, the resultant dual nomenclature was maintained, even where the relationship between different morphs was proved by the culture of single spores. This outdated approach became a burden to mycology into the twenty-first century (see below).

Another unfortunate practice that developed and became more commonplace in the early decades of the twentieth century was to give very similar fungi growing on different plant genera, and sometimes plant species, separate scientific names (e.g., *Cercospora*; see 17). In some instances these were correlated with, for example, seemingly minor differences in spore sizes. The trend was also fueled by the emerging experience of plant pathologists with inoculation experiments, for example with rusts, showing that some morphologically apparently indistinguishable fungi could cause diseases on one plant species but not another. In some cases, fungi shown to be host-restricted experimentally but morphologically indistinguishable were distinguished as special forms [formae speciales (f. sp.)], as in *Fusarium*, but this approach has become obsolete with advances in molecular systematics.

More critical light microscopy (LM) revealed finer details of the hyphal structures making up sporophores and that categories of asci and conidiogenous cells could be separated. These newly appreciated features were also linked to differences in ontogeny, and it has become gradually accepted that the earlier spore-based systems were simplistic; families and genera started to

be rearranged in earnest in the later decades of the twentieth century. Transmission electron microscopy (TEM) not only substantiated LM observations but also led to the discovery of fundamental differences in the layering of hyphal walls between major groups, meaning that even in the absence of sexual structures, it was possible to assign conidial or yeast-like fungi to the ascomycetes or basidiomycetes (106). Further, the TEM revealed an unexpected range of septal pore structures, which were correlated with other features and came to be emphasized in basidiomycetes (104). The advent of scanning electron microscopy (SEM) in the mid-1960s enabled surface features, particularly spore ornamentation, to be critically examined for the first time, and these proved to be of immense value in the separation of otherwise very similar plant pathogens, most spectacularly in rusts and smuts. The SEM also played a major role in clarifying patterns of conidiogenesis, for example by visualizing annellations (percurrent proliferation) on conidiogenous cells (18).

The 1960s and 1970s were an exciting period for fungal systematics, as novel ways of discriminating between species began to be explored. A range of techniques and molecular approaches appeared promising in distinguishing plant pathogens, from thin-layer chromatography (TLC) and isozyme profiles to the study of chromosome numbers (e.g., 60, 88, 110). In subsequent years, it also emerged that diagnostic characters of fungi (including plant pathogens)—such as including their cardinal temperature requirements for growth, which is still presently being employed—could be obtained from pure cultures [e.g., *Ophiostoma* (11) and *Cercospora* (37)]. Working with fungi in culture in the early period included the recognition that population structure could be understood through defining vegetative compatibility groups (VCGs) that for some plant pathogens can be defined reasonably easily on agar in Petri dishes. Techniques to recognize VCGs in culture included pioneering work applying *nit* (nitrate) mutants for this purpose. These have, for example, been fundamentally important in many research studies on pathogenic *Fusarium* spp. (54, 55). In addition to understanding population structures in culture, considerable work was done to connect asexual and sexual morphs of fungi through studies in culture (50). Understanding fungal reproductive systems was also substantially advanced by tests in culture in which mating strains could be defined, and sexual barriers considered as defining species boundaries (i.e., in the biological species concept) could be tested (39, 63).

The increasing availability of powerful computers in the 1970s enabled organisms to be scored for large numbers of morphological, cultural, and physiological characteristics; similarities were then computed and analyzed by cluster analysis. This new numerical taxonomy, later commonly referred to as phenetics, proved particularly valuable in bacteria and was taken up by some botanists in the late 1960s, but it was rarely attempted by mycologists (15). An alternative methodology of character analysis, cladistics, in which groupings were made on the basis of shared ancestral characters, came to the fore in the mid-1970s, but again that was little used in mycology except at some of the higher levels (e.g., 101), largely because it was often uncertain whether characters were ancestral or derived because of the lack of a substantial fossil fungal record (100). Several studies coded morphological features and employed multiple correspondence analyses to test species hypotheses and generic limits (19, 72).

Despite attempts to increase the range of features used in species separations of fungi and to introduce more objective methods of analysis, identification continued to be based almost entirely on features that could be examined by LM. Even though LM had improved significantly by the 1980s, especially with the application of Nomarski differential interference contrast, the separation of almost identical fungi, one pathogenic and one not, often remained problematic. Fungal systematists were not yet able to reflect the level of discrimination required by plant pathologists in their classification systems. That situation was, however, set to change as the twentieth century came to a close and as DNA-based methodologies moved from occasional to common use.

Scanning electron microscopy (SEM): an electron microscope that produces high-magnification images by scanning samples via electrons

Annellations: a series of percurrent proliferations, usually at the tip of a conidiogenous cell proliferating via basipetal succession

Thin-layer chromatography (TLC): technique used to separate nonvolatile mixtures on a thin layer of adsorbent material, usually silica gel

Isozymes: enzymes that differ in amino acid sequence, activity, or physical properties; also known as isoenzymes

Vegetative compatibility groups (VCGs): mycelium of two isolates of a fungus fuse in a culture when the alleles at incompatibility loci are identical

Numerical taxonomy: a classification system that groups taxa by numerical methods based on all available character states

DNA Phase

The earliest attempts to use DNA data in fungal identification in the 1990s were based on techniques such as randomly amplified polymorphic DNA (RAPD) and restriction fragment length polymorphisms (RFLPs) (28, 113). These techniques were, however, difficult to standardize between laboratories, which was seen as a major drawback. Furthermore, it was also unclear whether similar fragment sizes equated to identical sets of genes, as a fragment could be the result of several similarly sized products from different parts of the genome.

The examination of proportions of different nucleotide bases, the so-called GC ratio, through DNA-DNA reassociation studies or flow cytometry, was also commonly used in studies, particularly those of medically important fungi (40). The ratio had become used widely in the characterization of bacteria and also proved of value in yeasts (95) but was not particularly widely applied for fungal pathogens.

Amplified fragment length polymorphism (AFLP) markers have commonly been used to differentiate closely related pathogens in genera such as *Colletotrichum* and *Fusarium* (32, 92), although problems encountered with this technique range from nonindependence of fragments, homology assignment of fragments, and asymmetry in the probability of losing and gaining fragments. In spite of this, AFLP markers have been found to be informative at somewhat lower taxonomic levels than what can be normally distinguished on the basis of internal transcribed spacer (ITS) region DNA sequence data.

Although various molecular techniques were used in attempts to provide insights into species boundaries, and some of these are discussed above, the advent of phylogenetic inference based on analyses of DNA sequence data is the approach that radically changed fungal taxonomy. Indeed, it is this approach that spurred the revolution that led to the currently accepted one name–one fungus situation.

The application of DNA sequence technology to resolve relationships was first exploited in fungi of medical importance and in yeasts and was based on the 18S and the ITS rDNA (5, 11). The most cited work on fungal protocols is the landmark paper of White et al. (109), which is where the primers for the ITS were first introduced, and these protocols remain widely used to this day (87). The more genes or gene regions that are used to assess phylogenetic relationships, the more likely the results will reflect reality. Thus, whereas single genes or gene regions were initially employed to assess species boundaries, today it is commonplace to test and use multigene phylogenies, often including a mix of particular mitochondrial, nuclear, ribosomal, and protein-coding genes, analyzed using different approaches, such as maximum parsimony, maximum likelihood, and/or Bayesian inference. These principles are currently employed to derive a better understanding of many important genera of phytopathogenic fungi, such as *Alternaria* (115), *Bipolaris* (56), *Botryosphaeria* (73, 93), *Ceratocystis* (26), *Colletotrichum* (14, 24, 25), *Phyllosticta* (112), *Pyricularia* (52), and *Teratosphaeria* (74), to name but a few.

In interpretation of phylogenetic trees, it is always necessary to bear in mind that the underlying algorithms that produce the trees do not allow for all possibilities, such as ancient or recent hybridization events, horizontal gene transfer, or loss of whole or parts of chromosomes. Thus, the resulting trees are only as informative as allowed by the specific loci chosen for sequencing and the alignment used as input data.

Comparisons of whole or extensive sections of genomes are becoming increasingly feasible and, in general, seem to support classifications based on a limited number of selected conserved genes (69). Whether they prove to be the Holy Grail of fungal molecular systematics remains to be seen, but that is likely to depend on the added value compared with the additional time and costs of obtaining results. The computational time for analyzing large data sets, the quality of the genome annotation, and the amount of storage space required to store the raw sequence reads are other

Nomarski differential interference contrast: an optical microscopy illumination technique that enhances the contrast in unstained samples

Randomly amplified polymorphic DNA (RAPD): a technique using PCR to amplify any genomic region containing an arbitrary sequence

Restriction fragment length polymorphisms (RFLPs): variation in the length of a DNA fragment produced by a specific restriction enzyme acting on DNA from different individuals

DNA-DNA reassociation studies: a molecular biology technique that measures the degree of genetic similarity between pools of DNA sequences

Amplified fragment length polymorphism (AFLP): the selective PCR amplification of restriction fragments from a total digest of genomic DNA

Horizontal gene transfer: acquisition by an organism of genetic information by transfer from a different organism, typically a different species

constraining factors. Additional advantages from whole-genome sequences for systematics other than phylogenomics include the ease with which mating-type primers and microsatellite markers can be developed and insights into, for example, horizontal gene transfer can be gained (80).

Next-generation sequencing: applies to genome sequencing, genome resequencing, transcriptome profiling (RNA-Seq), DNA-protein interactions (ChIP sequencing), and epigenome characterization

In all molecular approaches, DNA is most easily recovered from living cultures. Obtaining reliable DNA from historic specimens, including name-bearing types, is problematic because of degraded DNA, DNA contaminated with host DNA, and/or DNA from other microorganisms present in the specimen. However, there have been some successes, e.g., in *Septoria cytisi* (type of *Septoria*; 75) and *Heteroconium citharexyli* (type of *Heteroconium*; 17). Furthermore, DNA isolation from herbarium or dried specimens has also made it possible to revise major groups of obligate fungi that cannot be cultivated, such as the powdery mildews (97), rusts, and smuts (91). Other than for taxonomy, this approach has also made it possible to track invasive species of plant pathogens, confirming not only the species involved but also the clones and mating types (36, 82). DNA retrieved from museum specimens (ancient DNA) has also opened up a new field of research enabling plant pathologists to trace pathogens through time and correlate the amount of infection and pathogen composition on different hosts with other variables such as climate change (4). Whole-genome sequence analyses of major plant pathogens from old specimens have made it possible to describe sequence variation in nineteenth-century samples of the pathogen (*P. infestans*) responsible for the Irish potato famine of 1845–1847 (33, 57). This suggests that the millions of dried fungal specimens housed in collections of museums, research institutes, and universities internationally could hold great promise for understanding the evolution of many major fungal pathogens and their associated diseases and epidemics over time.

So-called next-generation sequencing represents nothing short of a paradigm shift in DNA sequencing technology. Remarkably, this technology, which is also advancing rapidly, has made it possible to determine the diversity of fungal pathogens in plant substrates, water, and soil. But it has also exposed mycologists to the startling unseen fungal diversity that is present in every imaginable niche, the majority of which cannot be cultured (1, 12, 49, 70, 71). We must now face the reality that these fungi are present even though we cannot see them and that new taxonomic schemes will need to be devised to accommodate them (46).

Until recently, there was no universally accepted DNA barcode for Fungi, which proved to be a serious limitation for ecological and biodiversity studies (see sidebar, DNA Barcoding). In a study involving several different laboratories, six genes were evaluated, leading to the conclusion that the ITS region has the highest probability of successful species identification, with the most clearly

DNA BARCODING

A DNA barcode represents a unique DNA sequence pattern 400–800 nucleotides in length that can be quickly processed from thousands of specimens or cultures and unambiguously analyzed by computer programs to identify species. Until recently there was no universally accepted DNA barcode for Fungi. In April 2011, the Fungal Working Group met in Amsterdam to discuss and evaluate the data generated with six markers from all major lineages of fungi. From the various markers evaluated, the internal transcribed spacer (ITS) appeared to be the main candidate because of its broad utility as a species marker in taxonomic and ecological studies and the ease of amplification across the kingdom. The ITS was subsequently proposed as a standard barcode for fungi (87). In spite of the fact that the ITS region cannot accurately identify species in many genera of plant-pathogenic fungi (e.g., *Alternaria*, *Botryosphaeria*, *Calonectria*, *Cercospora*, *Diaporthe*, *Fusarium*, *Ilyonectria*, *Teratosphaeria*, etc.), it always gets the user to at least the generic level (86). In such cases, secondary barcodes, frequently incorporating protein-coding genes, would need to be employed, but these vary depending on the genus being investigated.

Q-BANK

The Q-bank fungal database contains DNA barcodes supplemented by morphological, phenotypical, and ecological data for more than 725 species of relevance to phytopathology. Currently, the database focuses on species of quarantine importance to Europe and their closest relatives. Specific genera studied to date include *Ceratocystis*, *Colletotrichum*, *Melampsora*, *Monilinia*, the *Mycosphaerella* generic complex, *Phoma*, *Phytophthora*, *Puccinia*, *Stenocarpella*, *Thecaphora*, and *Verticillium*. The database continues to be actively expanded, and parties interested in participating or contributing can contact its curators (**http://www.q-bank.eu**).

defined barcode gap between inter- and intraspecific variation (87). Having settled on a primary barcode gene for the fungi and one that worked well for biodiversity studies, several mycologists were of the opinion that this gene could be used to identify a wide range of plant-pathogenic fungi (64). Unfortunately, however, this is not the case for many genera of phytopathogenic fungi (86), where secondary barcode genes must be used to reach an accurate identification. As a rule however, protein-coding genes [glyceraldehyde-3-phosphate dehydrogenase (GAPDH), beta-tubulin (*tub2*) gene, translation elongation factor 1-alpha (tef1), actin (act), and histone H3 (his3)], generally prove a valuable supplement to ribosomal genes at the species level. More conserved gene regions such as large subunit (LSU), small subunit (SSU), and RNA polymerase II (RPB2) gene provide a better discrimination at the generic and/or family level (38, 47, 107).

Although the majority of presently described fungal species still lack DNA data, GenBank and its collaborative partners in the International Nucleotide Sequence Databases Collaboration (INSDC), the DNA Data Bank of Japan (DDBJ) and the European Nucleotide Archive (ENA), have proven essential for validating fungal taxonomic research by providing DNA signatures linked to authentic type specimens or ex-type cultures. Mycologists have long been a vocal group arguing for improved accuracy of names used in GenBank (7, 65). A major advance in this regard was the development of curated databases for specific groups of fungi, such as human and animal pathogenic fungi (**http://www.mycologylab.org**) and ectomycorrhizal fungi (Unite; **http://unite.ut.ee/**). Other important fungal databases include The Barcode of Life Data System (BOLD; **http://www.boldsystems.org**) and its mirror website, EU-BOLD (**http://www.eubold.org**), MycoBank (**http://www.mycobank.org**), and Q-bank for fungi of plant quarantine concern (**http://www.q-bank.eu**) (see sidebar, Q-Bank).

It is estimated that there are at least 1.5 million (see above), probably 3 million, and perhaps as many as 6 million species of fungi (98), of which we presently recognize around 100,000. Barely a third (28,340) are to be found in GenBank (29). GenBank does not have the mandate to self-curate the database [only the original depositor(s) are allowed to request changes to records] and, therefore, it cannot correct records, even though some may clearly be incorrectly identified species. To offset this problem, a new robust initiative for type-related data, RefSeq (**http://www.ncbi.nlm.nih.gov/projects/RefSeq/**), aims to provide an additional curated and corrected-type-data database via a structured interface for depositors (86).

POLYPHASIC TAXONOMY AND SPECIES CONCEPTS

Presently there are more than 40 different species concepts in biology (58, 78). A recent overview concluded that there was no universal concept and that it was necessary to be pragmatic, keeping in mind that the primary purpose of names is communication (78). In recent years, genealogical concordance phylogenetic species recognition (GCPSR), which is an adaptation of the

Phylogenetic Species Concept, has become a common method employed by mycologists and plant pathologists to distinguish species (99). GCPSR uses the phylogenetic concordance of unlinked genes to indicate a lack of genetic exchange and thus, evolutionary independence of lineages (27, 67, 99).

Genealogical concordance phylogenetic species recognition (GCPSR): a multigene phylogenetic approach for recognizing fungal species on the basis of genealogical concordance

Consolidated species concept (CSC): a polyphasic approach to species recognition, incorporating morphological, biological, and phylogenetic characters

Using a polyphasic approach to identify species by combining morphological, ecological, and phylogenetic data has been common practice in bacterial taxonomy for many years. This approach has also been widely used in contemporary fungal taxonomy, predominantly in fungi of industrial importance (84, 105). It is also increasingly being applied to genera of phytopathogenic fungi, such as *Alternaria*, *Colletotrichum*, *Daldinia*, and *Phyllosticta* (2, 13, 35, 94, 96). In a recent study to elucidate genera and species in *Teratosphaeriaceae*, Quaedvlieg et al. (74) referred to the polyphasic approach for identifying species as the consolidated species concept (CSC), although no clear formula could be given as how to weigh the different components considered in reaching species consensus. This suggested that that the GCPSR still outweighed the ecological or morphological data combined in the CSC.

A pragmatic species concept that is effective is "Species are groups of individuals separated by heritable character discontinuities and which it is useful to give a species name to" (42, p. 32). This is especially true in relation to so-called cryptic species, where recognized morphospecies represent a suite of indistinguishable or almost indistinguishable taxa that are clearly different based on phylogenetic inference and that often also differ in ecology (including host range and pathogenicity) or distribution. Cryptic species are emerging rapidly and groups of fungi, including important plant pathogens, are now studied using DNA sequence-based phylogenetic inference. Examples include genera, such as *Phaeoacremonium*, in which one species has now proliferated into more than 20 (62) and *Colletotrichum*, in which *Colletotrichum acutatum* and *Colletotrichum boninense* now each represent approximately 20 species (24, 25). In some cases, subtle differences can be found when isolates are reexamined in the light of molecular groupings, such as in the case of the *Fusarium graminearum* complex, where some species could be separated by minor differences in conidium shape but also host range (68).

DUAL NOMENCLATURE

The separate naming of different morphological states of the same fungal species was formally included in the rules governing the nomenclature of fungi adopted by the 1905 International Botanical Congress (IBC) in Vienna (108). The provisions, which were restricted to nonlichenized ascomycetes and basidiomycetes, underwent modifications at subsequent congresses and became increasingly complex by the time of the 1981 Sydney Congress. At that date, names typified by an asexual morph were not permitted to be included in a genus with a sexual type, and any such names were ruled as illegitimate (see sidebar, Dual Nomenclature).

DUAL NOMENCLATURE

A diversity of fungal propagules (pleomorphism) is seen in many fungi but especially in Ascomycota. In the past, fungi have been primarily classified on the basis of their sporing structures, and separate names were given to the sexual structures (formerly called the teleomorph) and asexual structures (formerly called the anamorph or if there are several asexual morphs, synanamorphs). Together, they represent the holomorph, for which there is, since the end of dual nomenclature, only a single name. The merging of sexual and asexual generic and species names is currently being progressed by working groups under the aegis of the ICTF, including a newly established committee for names of plant-pathogenic fungi (see **http://www.fungaltaxonomy.org**).

This had the consequence, for example, that whenever a sexual morph was discovered, it had to be given a new and independent name, even though it was known to be a morph of a known species. Schoch et al. (85), for example, introduced new sexual genera for *Cylindrocladiella* (as *Nectricladiella*), *Gliocladiopsis* (as *Glionectria*), and *Xenocylindrocladium* (as *Xenocalonectria*). On the basis of the new ICN adopted in 2011, however, these genera are now treated as synonyms of the earlier, well-established asexual genera (81). Before that date, if a fungus had more than two morphs, as is the case in many rust fungi, all could theoretically be given separate names, but fortunately most mycologists showed restraint and avoided providing such names. Nevertheless, the increasingly labyrinthine rules resulted in a situation where all possible situations could not be covered. But importantly, these rules were being interpreted in different ways by different researchers, in some cases those working on the same genus.

The mycological community at that time considered two routes to regularize the situation: increasing the complexity to cover all conceivable situations or simplification. In 1971, a committee was established by the International Mycological Association to resolve the situation, and it opted for simplification and it also adopted the holomorph-teleomorph-anamorph (whole fungus, sexual state, asexual state, respectively) terminology (50). Their recommendations, adopted at the 1981 IBC, meant that many names that had previously been ruled as illegitimate and not for use, were to be taken up. As a direct result of this modification, numerous name changes were made in some groups of fungi, whereas in others they were fortunately never pursued.

But the 1981 changes to the rules provided no panacea. This was because a situation arose in which asexual and sexually typified species names that were established as belonging to the same genus continued to have separate scientific names. For example, *Diaporthe* species with a sexual type had names in *Diaporthe*, whereas *Diaporthe* species known only from asexual types were allowed names exclusively in *Phomopsis* (61). There were even greater complications, including one in which a *Diaporthe* with a sexual type could also have a separate name in *Phomopsis* for the asexual morph with an asexual type—but the name in *Diaporthe* could be used even where only the asexual morph was present. It is hardly surprising that plant pathologists and those concerned with plant-protection legislation were dissatisfied and frustrated with mycologists.

The advent of molecular systematics meant that fungi, even those failing to sporulate, could be unequivocally placed in classifications based on the sexual states. This led to proposals to delete the provisions for dual nomenclature entirely (77), but they were not accepted by the subsequent IBC in Tokyo in 1993. Many mycologists became increasingly dissatisfied with this untenable situation, and the topic was debated at subsequent International Mycological Congresses (IMCs), particularly at the Oslo 2002 IMC, but with no consensus (89). Proposals to drastically modify the provisions were made to the 2005 IBC in Vienna (43), but these were only partially accepted, and a committee was appointed to pursue the matter. In the meantime, the rules began to be ignored by mycologists frustrated by not being able to introduce names for naturally existing taxa even when the morphs were confirmed as belonging to a single species by DNA sequence data. For example, in a revision of genera in the *Botryosphaeria* complex, Crous et al. (23) introduced new taxa using previously applied generic names, irrespective of which morph (sexual or asexual) was observed in culture. This example might be considered one of the major catalysts that led to the monumental changes in fungal taxonomy that were to follow.

A poll of mycologists taken at the 2010 IMC in Edinburgh established that deletion of the provision allowing for dual nomenclature was gaining overwhelming support. These ideas were further developed at a special symposium held in Amsterdam in April 2011, leading to "The Amsterdam Declaration on Fungal Nomenclature" (45). This proposal, viewed as radical and unacceptable by some mycologists (31), among other recommendations called for the abolition of Article 59, which would result in fungi having only a single name. The Special Committee

The Amsterdam Declaration on Fungal Nomenclature: this included the view that each fungus should have a one name, with priority normally being given to that first published

appointed by the 2005 IBC to look into the matter had failed to agree on the deletion of Article 59, but some suggestions were made by its Secretary and considered along with The Amsterdam Declaration at the Melbourne IBC in July 2011. Proposals were developed at that Congress and voted on, and the provisions for the separate naming of fungal morphs came to an end on July 30, 2011. The proposals were retroactive, implying that asexually and sexually typified names had the same nomenclatural standing and competed equally when determining the correct name for a genus or species, which would normally be the first published name. Many cases would thus need to be reexamined in the light of this change, and difficult choices would have to be made between competing sexually and asexually typified, often well-established, pairs of generic names (114) (**Figure 1**).

Provisions to minimize the disruption emerging from the fact that all fungi would bear a single name were approved, including the ability to produce protected lists of names. These lists are currently under development (see 48, 51, 81, 111), initially concentrating on the generic names, and several drafts have been published for debate and discussed at pertinent international meetings. Recommendations on whether particular lists of names should be accepted for protection against other competing names will then be made by the Nomenclature Committee for Fungi (NCF) to the General Committee on Nomenclature for action at the next IBC in Shenzhen, China, in 2017.

MODERNIZING NOMENCLATURAL PRACTICES

Nomenclature is often confused with taxonomy, and it is important to recognize that these are separate activities. Nomenclature is concerned with the application of names to the biological units (taxa) that taxonomy (research into classification) demonstrates have merit for formal scientific names. Nomenclature is an activity to be applied when research is completed and being prepared for publication. The internationally agreed rules that regulate the naming of fungi aim to provide a mechanism to provide for only one correct name for the entity taxonomic research establishes (see sidebar, Requirements for Publishing a Fungal Species). We view nomenclature as a necessary evil, which must remain open to modification to meet the changing needs of both taxonomists and all users of the names. As a consequence of mycology being traditionally treated as a part of botany, an anachronism that surprisingly still persists even in some developed countries, the nomenclature of fungi has been regulated by successive editions of the *International Code of Botanical Nomenclature*. It is only very recently, in 2011, that this code was renamed the *International Code of Nomenclature for algae, fungi, and plants* (ICN; 59), and this came about largely due to the pressure of mycologists that were signatories to the Amsterdam Declaration (45).

REQUIREMENTS FOR PUBLISHING A FUNGAL SPECIES

1. A description must appear in a journal or book with an ISSN or ISBN number.
2. A new species must have a unique binomial.
3. A new species must have an English or Latin diagnosis or description and a permanently preserved type, which may be in a fungarium (dried specimens and slides) or a biological resource center (metabolically inactive cultures).
4. Nomenclatural data must be deposited in one the approved repositories (MycoBank, Index Fungorum, or Fungal Names) and the accession number cited.
5. Although not required at present, it is good practice to deposit DNA data in a repository such as GenBank and the alignment in TreeBASE (90).

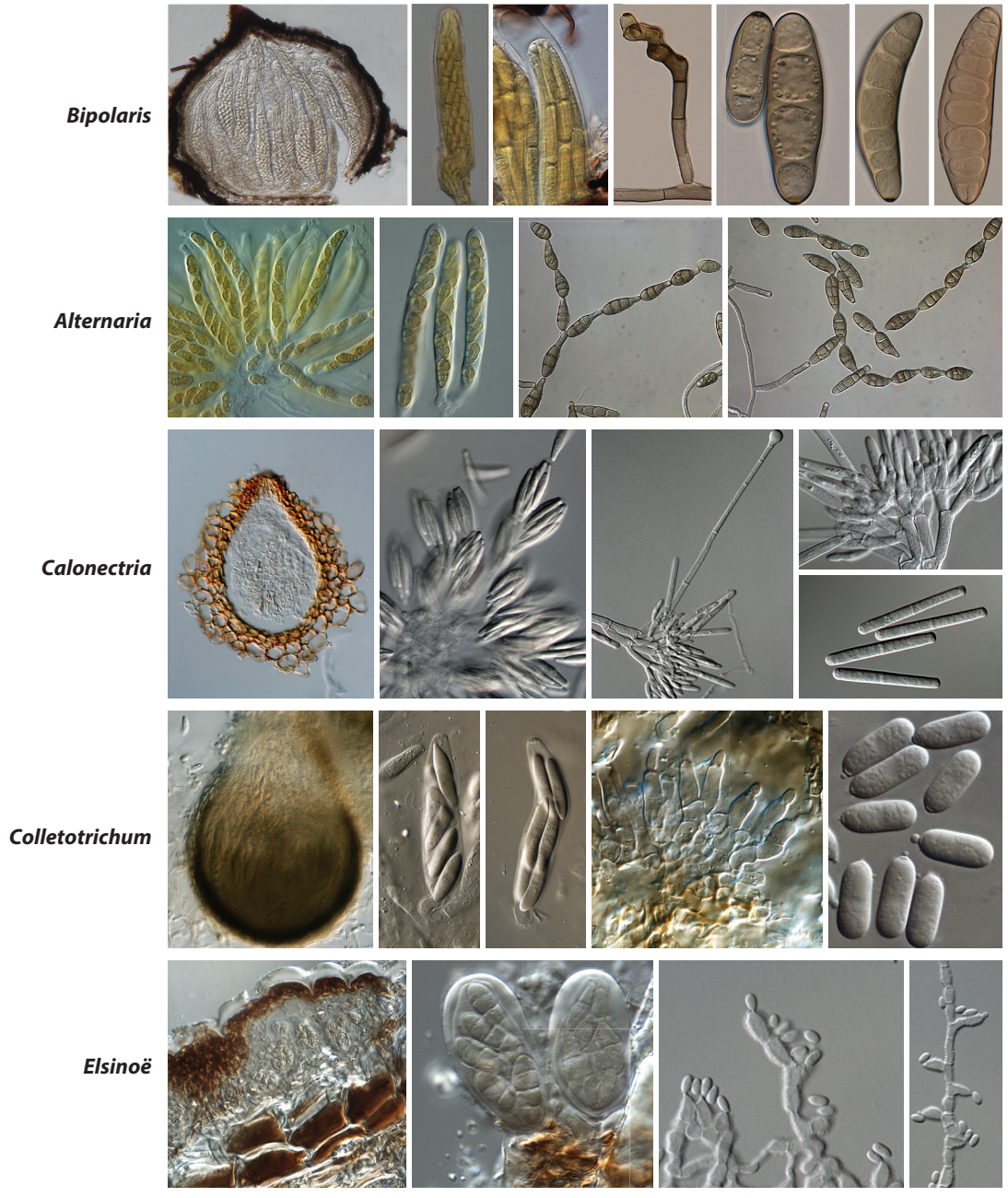

Figure 1

Morphological structures of genera of phytopathogenic fungi in which use of a single generic name (alternatives in parentheses) will simplify many aspects of dealing with them. The selection portrayed here include: *Bipolaris* (*Cochliobolus*), *Alternaria* (*Lewia*), *Calonectria* (*Cylindrocladium*), *Colletotrichum* (*Glomerella*), and *Elsinoë* (*Sphaceloma*). These images were taken by P.W. Crous and are published under the Creative Commons Attribution 3.0. Unported license in the following references: *Bipolaris* (56) and *Colletotrichum* (24, 25).

Epitype: material selected as an interpretative type when the existing type of a name cannot otherwise unambiguously fix the application of the name

Mycologists have been particularly active and successful in securing decisions important for fungal nomenclature in the ICN. These include the acceptance of cultures preserved in a metabolically inactive state as name-bearing types (i.e., the material to which the scientific name is fixed), the retention of well-known generic and specific names by conservation over other names that would have to be used by a strict application of the rules, the rejection of potentially disruptive names, and the possibility to protect lists of names at any rank against names that threaten them (see below). A category of name-bearing types, epitypes, is available to fix the application of names when that cannot be done using the existing name-bearing type material. At present, when epitypes or replacement types (neotypes) are necessary, they are ideally supplemented by a DNA barcode (3).

The most dramatic changes affecting the naming of fungi in the past decade were made at the 2011 IBC in Melbourne. Following proposals from mycologists, English was permitted as an alternative to Latin for validating diagnoses or descriptions, dual nomenclature (see above) was ended, publication in electronic form was accepted for the effective publication of names (subject to certain restrictions), lists of names for protection could be proposed, and the decision was made to require that all new scientific names be lodged in a designated repository and a unique identifier be obtained before they can be accepted as valid. These changes have all come about as a consequence of years of consideration by the mycological community, especially at successive IMCs, at some regional mycological congresses, various mycological society meetings (e.g., Mycological Society of America), and, more recently and particularly significantly, at the annual spring symposia in Amsterdam, convened by the CBS-KNAW Fungal Biodiversity Centre. It was the first Amsterdam symposium in 2011 that took the issues debated at the 2010 Edinburgh IMC and formulated these into The Amsterdam Declaration (45), which provided the basis for recent and ongoing changes as to how fungi will be named in the future.

Every IBC appoints a series of nomenclature committees to consider proposals for changes or for the conservation or rejection of names, including the Nomenclature Committee for Fungi (NCF). The NCF debates and votes on formal published proposals but does not have a responsibility for taxonomy or for being proactive in generating proposals. Since 1982, the work of the NCF has been complemented by the International Commission on the Taxonomy of Fungi (ICTF), which aims to develop guidelines for good practice and links to subcommissions or other groups concerned with particular fungi. The ICTF is currently assuming a major role in coordinating the preparation of lists of names for protection and making them available for comment by mycologists at large through its website (**http://www.fungaltaxonomy.org/**). It has also published guidance on describing new fungi, which may be particularly helpful to plant pathologists who encounter new fungal pathogens (90).

Not surprisingly, few mycologists attend IBCs, let alone the preceding week-long debates of the Nomenclature Section. In response, Nomenclature Sessions have been established at recent IMCs, and these include discussions on proposals and also the solicitation of views of all congress participants on topics of current concern. These occasions have proved valuable in conveying the views of mycologists to those making formal proposals for change. These sessions have been attended by 8–10% of the total number of delegates, as compared with just 2–4% of mycologists present at IBC Nomenclature Section meetings. The Amsterdam Declaration included the proposal to transfer decision-making on nomenclatural matters on fungi to IMCs and a request that the NCF be elected at each IMC. These proposals were not adopted at the Melbourne IBC, but a special subcommittee was established to consider the issue and is currently deliberating and scheduled to report to the 2017 IBC. If this proposal is implemented, the nomenclature sessions at the IMCs may need to be changed to encourage more people to actively participate. Additional proposals, mainly to fine-tune some of the decisions made at the Melbourne IBC, were debated

and voted on at IMC10; those with strong support will form the basis for future changes to the ICN to make it even more fit-for-purpose (76).

The option of an independent set of rules for naming fungi, a MycoCode, has been voiced (45). Because mycologists in general are content with the bulk of provisions in the ICN, and changes mycologists have desired in the past have been approved and included in the ICN, a separate code would not necessarily be a panacea. Further, an additional code would be contrary to the current move to a more unified approach to nomenclature for all groups of organisms, including prokaryotes, now being pursued with a single BioCode (34). In order for such a BioCode to be used, a system of protected names needs to be in place. With the possibility of having such lists for protected fungal names introduced under the latest ICN, if in time there was a need to part from the ICN, adoption of the BioCode would be the favored option.

The incremental improvements in the ICN to the present point mean that it is has now become possible to avoid the displacement of almost all established scientific names, subject to approval of formal proposals by the pertinent committee (for fungi, the NCF). The difficulty is that preparing and publishing proposals is extremely time-consuming, and it may take several years for the NCF to make a recommendation and for that to be endorsed by the overarching General Committee on Nomenclature. With the rapid and accelerating progress being made in fungal systematics today, mycologists are rarely able to spend time writing formal nomenclatural proposals and waiting long periods for a decision before publishing their research. Further, if a change is published, there can be counter proposals leading to a period of uncertainty and perhaps a rejection of the decisions of the original researcher. This problem is being addressed through the newly proposed Lists of Protected Names, provided that listed names are protected against all unlisted names. These lists will also deal with choices with respect to generic names arising from the ending of dual nomenclature for different morphs of the same fungus.

Compiling and refining lists of names for protection will be a lengthy process, but it is now in the pipeline and greatly facilitated by the names being held in freely accessible databases (see below). This will mean that plant pathologists will no longer need to be irritated by the resurrection of long forgotten names or be uncertain as to the generic name to be used in a particular case for a pleomorphic fungus. Further, fungal taxonomists will not be obliged to spend a disproportionate amount of time delving into old literature and trying to track down the whereabouts or ascertain the identities of never restudied name-bearing types. When the hurdle of list production has been cleared by the mycological community, taxonomists will be able to devote their energies to the priority task of documenting the diversity and resolving the relationships of the fungi around us—not least, those of particular concern as plant pathogens.

FUTURE DEVELOPMENTS

There have been several major milestones in fungal systematics in recent years (**Figure 2**). These include the first deposit of fungal DNA sequences in GenBank in 1991, the initiation of the registration process of taxonomic novelties in MycoBank in 2004 (21), the registration of typification events (79), the abandonment of dual nomenclature and obligatory Latin diagnoses (45, 59), the selection of an official DNA barcode for Fungi (87), and curated databases, such as Q-bank, UNITE (53), and RefSeq (86), for fungal data. Simultaneously, there has been a move to provide open access to fungal descriptions and novelties via MycoBank as well as through a range of other journal portals that have embraced different funding models, making these sources of information freely available to global developing nodes of mycology.

In recent years, there has also been an increased push to ensure that mycologists supplement fungal descriptions with DNA data (deposited in public sequence data centers) to facilitate rapid

Taxonomy	Year	Nomenclature (and organization)
	1753	Starting point for "botanical" nomenclature
Fungi recognized as a separate kingdom	1783	
Treatment of the known fungi started	1821	
Pleomorphism in fungi recognized	1851	
Asexual fungi classified separately	1870	
	1910	Category of special forms introduced
	1912	Separate naming of morphs permitted
Incompatibility as a species criterion	1927	
Keys to all known fungal genera	1931	
	1935	Latin diagnosis or description mandatory
	1940	Index of Fungi initiated
Ascomycete ontogeny linked to ascus types	1951	
Categories of conidiogenesis	1953	
	1954	Registration of fungal names proposed
Parasexual cycle discovered	1956	
	1958	Type designations mandatory
Numerical taxonomy of fungi	1964	
Scanning electron microscope	1965	
Taxonomy of Fungi Imperfecti conference	1969	
	1971	International Mycological Association founded
Sexual-asexual synthesis conference	1977	
	1981	Later starting points for fungal nomenclature ended
	1981	Rules on naming pleomorphic fungi revised
	1982	International Commission on the Taxonomy of Fungi founded
	1986	Systema Ascomycetum launched
Cladistics used in mycology	1988	
rDNA fungal primers introduced	1990	Specification of location of types became mandatory
	1991	Abandonment of dual nomenclature proposed
Ascomycete Systematics international workshop	1993	Metabolically inactive cultures permitted as types
	1993	Epitype concept introduced
Amplified fragment-length polymorphisms introduced	1995	
Saccharomyces cerevisiae genome sequenced	1996	
Phylogenetic species recognition	2000	Index Fungorum available online
Oomycota placed in kingdom Straminipila	2001	
	2004	MycoBank registration system launched
Phylogenomics	2006	
Assembling the Fungal Tree of Life project	2006	
Molecularly based ordinal classification of Fungi	2007	
Next-generation sequencing	2008	
DNA barcode primers for Fungi proposed	2011	Amsterdam Declaration on fungal nomenclature
1000 fungal genomes project launched	2011	Separate naming of morphs of pleomorphic fungi ended
	2012	English allowed as an alternative to Latin for diagnoses
	2012	Electronic publication permitted for new names
	2013	Registration mandatory for new fungal names
Reference Sequences for higher fungal taxa issued	2014	

Figure 2

Fifty key events in fungal systematics.

identification via various online portals and also to facilitate a range of metagenomic studies. In 2010, approximately 20% of all novel fungal species were provided with a DNA barcode, and this number rose to around 35% in 2013 (data extracted from MycoBank and GenBank). The process of fixing the application of old names via epitypification has also added much needed stability in moving from loosely applied names to the definitive application of names linked to fresh specimens, cultures, and DNA data. At the same time, this process has highlighted the problems encountered when dealing with old names that have since become important species in plant pathology and in trying to answer the "what is it exactly" question. Several studies have, for example, shown that names based on European or American specimens could not be loosely applied to similar-looking disease-causing organisms on the same hosts in Africa or Asia (20, 35), which in turn could have serious implications for global trade and food security.

It is of the utmost importance to fix the application of fungal names via their DNA sequence data. There needs to be a focus on recollecting described taxa and, where appropriate, subsequent epi- or neotypification (79). In cases where a formal typification cannot be justified under the present ICN, it has been proposed that sequenced reference specimens (RefSpecs) be designated (3). For instance, DNA data are presently still lacking for the majority of known species of plant-pathogenic fungi. Genera of phytopathogenic fungi will primarily be addressed via the Genera of Fungi project (**www.GeneraofFungi.org**), which will aim to recollect type species of known genera, and designate lecto-, neo- or epitype specimens, cultures, and DNA sequence data of these species (22).

An initiative now gaining momentum is the move toward sequence-based classification of fungi (46). How will plant pathologists and mycologists deal with new fungi being described that are known only from their DNA, i.e., lacking specimens and cultures, and morphology? This is a major issue in the case of sequences obtained directly from air, soil, and water that needs to be resolved, and some possibilities have been proposed (46). This will facilitate the understanding of the fungal diversity that remains unstudied and unidentified. Among problems also to be addressed is the question of how to deal with short sequences and cases in which no single locus to distinguish between cryptic taxa is known; these represent major hurdles that will need to be overcome. An exciting challenge lies in determining the value and impact of whole-genome comparisons in systematics, as these are starting to be generated at a rate unanticipated even two to three years ago (103).

A welcome and marked change in fungal systematics over the past 10–15 years has been a growing global collaboration between mycologists. The proportion of papers with single, or even two or three, authors has fallen as teams of researchers with complementary skills have come together to tackle problems relating to particular groups of fungi. More importantly, however, is the astonishing and growing collaboration between mycologists (including plant pathologists, where plant pathogens are involved) on an international scale in major revisions or synthetic works that could not have been envisaged even in the early 1990s. There were some earlier examples, most notably in *The Whole Fungus* (50) and its predecessors, but nothing on the scale of Assembling the Fungal Tree of Life (AFTOL) and Deep Hypha projects (9). Works with 30 or more authors are now appearing with increasing frequency, generating major syntheses and overviews such as *The Families of Dothideomycetes* (47), as are agreements on approaches such as barcodes, reference sequences, and repositories (see above). The move toward lists of protected names (see above) has accelerated this trend even in the past five years. It is also encouraging that such multi-authored works are becoming increasingly international with respect to the participants, with mycologists in China and Southeast Asia assuming important roles. Such collaboration also facilitates the acquisition of specimens and cultures representing broader taxonomic spectra and wider geographical areas than ever before, ensuring that investigations can be increasingly comprehensive, representative, and reliable.

Collaboration in mycological research at the species level, in particular that concerning genera of plant pathological, medical, or industrial importance (e.g., *Colletotrichum*, *Fusarium*, *Trichoderma*), has increased markedly, and this has been facilitated by the ICTF. Of particular relevance to the plant pathology community is a proposed ICTF Subcommission on Plant Pathogenic Fungi that, it is anticipated, will consider not only the common species of phytopathogenic fungi but also the generic names to be used. Fungal systematics is now a more vibrant and exiting international activity than at any time in its history. This augurs well for the production of an increasingly sound and stable base for the naming of all groups of fungi, not least those of importance in biological control, plant pathology, and crop storage.

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