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Systematics of Plant Pathogenic Fungi: Why It Matters

Systematics is the study of biological diversity; more specifically, it is the science that discovers, describes, and classifies all organisms. Taxonomy, nomenclature, and phylogeny are all part of systematics. Fungal systematic studies result in the discovery and description of fungi, the principles of nomenclature guide the naming of organisms, and phylogenetic studies contribute to the classification of taxa into genetically related groups. A taxon (pl. taxa) is a taxonomic group at any rank, e.g., order, family, genus, species, and subspecies among others.

Systematics is a dynamic science. As systematists obtain new data about fungi, they use that to more accurately determine the concept of a taxon and relationships among taxa. When new relationships are discovered or old relationships are found to be incorrect, systematists must account for those discoveries. Necessarily, this new knowledge may result in changes of scientific names. Centuries ago, fungal specimens were described simply by looking at them with the unaided eye, and then macroscopically using a ×20 hand lens. This approach was followed by the use of the compound light microscope that could magnify the image of structures up to ×1,000. In the late twentieth century, the scanning electron microscope allowed the close observation of external features of morphological structures such as ascospore ornamentation, while the transmission electron microscope led to the discovery of internal organelles and structures of cells. All of these tools for observing specimens are still useful. Today, sequencing and comparison of portions of the genome are also used to characterize fungi, especially in determining species concepts and relationships among fungi at all levels ranging from population genetics to the phylogeny of major groups of fungi as well as fungal-like organisms.

What's in a name?

Names are the means by which information is communicated about an object, in this case an organism. The name of an organism may be a common name or scientific name. Common names of organisms can vary considerably from place to place and among different languages and are therefore much less precise than scientific names. Scientific names are used to accurately define an organism or set of organisms and to communicate about them. As systematic scientists learn more about each species or other taxon and the relationships among them, scientific names change to reflect this increased knowledge. Based on the knowledge associated with the name, it is possible to predict the behavior or biology of that organism. For example, if one isolates and identifies a *Phytophthora* from woody plant material, the name *Phytophthora* suggests a potentially destructive plant pathogen. On the other hand, if a *Chaetomium* is found, one can predict that this fungus is unlikely to cause a disease, and knowledge associated with that name suggests that this organism is more likely to decay dead cellulosic material.

As an example of scientific names changing to reflect increased knowledge, one can examine a fungal pathogen causing root rot of woody plants known for many years as *Armillaria mellea* (Vahl:Fr.) Karst., which has the common names in English of honey mushroom, shoestring, or bootlace fungus (Fig. 1). Decades ago, *A. mellea* was considered to be just one ubiquitous species infecting many different hosts (60). Hints of the fact that *A. mellea* was a species complex came from mating experiments in which several groups were shown to be genetically isolated by a complex mating system (3,67,68). More recently, molecular sequence data have confirmed the existence of the groups defined by mating studies (17,18). Upon careful examination of specimens representing the different groups, morphological characters were discovered that reflected the distinctiveness of the groups.

As a result of scientific advances in systematics, at least eight species in North America and five species in Europe are recognized that would previously have been called by one name, *Armillaria mellea* (2). Combining morphological, biological, and genetic data, narrow species have been defined that reflect knowledge including the biology of each species

Fig. 1. Species of *Armillaria*. A, *Armillaria mellea sensu stricto*, associated with *Fagus grandifolia* (beech), North Carolina, Schenck Forest, October 1998. B, *Armillaria ostoyae* on *Quercus coccinea* (scarlet oak), North Carolina, Bent Creek, October 1998. Photos by Larry F. Grand, North Carolina State University.

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(9,14,33). For example, *Armillaria luteobubalina* Watling & Kile occurs only in Australia, where this fungus is a primary pathogen of *Eucalyptus* causing decline and death especially in plantations (36). Now recognized as distinct, this species was recently reported from Chile (17). Another segregate species, *Armillaria ostoyae* (Romagn.) Herink, occurs in the Northern Hemisphere (Fig. 1B). Making the distinction between these species using their scientific names is essential for preventing the movement of *A. luteobubalina* to South Africa or spreading *A. ostoyae* to New Zealand. If a pest risk assessment were based on *A. mellea* as it was defined 50 years ago as one cosmopolitan species, it is possible that conifers would be moved from the Northern Hemisphere to New Zealand, not knowing that this posed the risk of introducing a pathogenic species not known to be present in that country. Species previously recognized as *Armillaria mellea sensu lato* (in the broad sense) are now known as precisely defined species with names that communicate their biological differences, including host range, pathogenicity, and geographic distribution.

What rules govern the scientific names of fungi?

Nomenclature is the branch of systematics that determines the correct scientific name for a taxon. The naming of fungi is governed by the International Code of Botanical Nomenclature (ICBN) (42) because of the historical assumption that fungi and plants were closely related. We now know fungi in the traditional sense comprise a diverse range of organisms including true Fungi (Kingdom Fungi), stramenopiles (Kingdom Chromista), and various kinds of slime molds (Kingdom Protozoa). True Fungi represent a distinct kingdom that is more closely related to animals than to plants (see below). Nevertheless, the naming of fungi in the traditional sense is still governed by the ICBN. A different set of rules called the International Code of Zoological Nomenclature governs the naming of animals, while bacteria and other prokaryotic organisms are named according to the International Code of Nomenclature of Bacteria.

The International Code of Botanical Nomenclature has been developed over many decades based on principles that have remained relatively stable since about the 1950s. These basic principles are: (i) the first scientific name applied to a species or other taxon has priority; (ii) each name must be based on a type that represents that entity. In the case of a species, the type is a specimen; for a genus, the type is a species; for a family, the type is a genus, etc.; (iii) a name must be published in a specific manner, i.e., with a Latin description, a type designated, the publication widely distributed, among other requirements; and (iv) a species can have only one correct scientific name except in the case of fungi that have alternate states (Article 59, ICBN). The ICBN also governs how to transfer a species name from one genus to another as the concept of the genus or species changes, as well as many more details about the naming of plants and fungi. Changes are made to the ICBN following much discussion, debate, and a vote at the Nomenclature Session during the International Botanical Congresses held every six years. Although the details and complexity of the ICBN have changed over time, the basic principles have remained the same. The stability of scientific names of plants and fungi is facilitated through application of the ICBN to issues of nomenclature.

Each scientific name for a species consists of two or more portions, minimally, a genus and a species epithet. A specific name is placed in a defined hierarchy that usually includes the family, order, class, phylum, and kingdom. Species may also be given a subspecific designation such as variety or subspecies. Of interest to plant pathologists, the subspecific taxon *forma specialis,* or form species, is often used to indicate a physiological difference based on adaptation to a different host. Although this designation is recognized by the ICBN, its use is not governed by those rules.

The first time a scientific name is mentioned in a research article, the author(s) who initially described a taxon, often a species, is associated with that name, as is the author(s) who may later transfer that name to another genus. As an example, we will use *Neonectria coccinea* (Pers.:Fr.) Rossman & Samuels, cause of beech bark canker in Europe. This name was originally described as *Sphaeria coccinea* Pers.:Fr. by Persoon in 1800 (49) and then listed in Fries's 1823 *Systema Mycologicum* (27). Because this name is mentioned by Fries (27), it is sanctioned according to the ICBN. This sanctioned status is denoted by the ":Fr." and, because it is sanctioned, this name has priority over other names for this species published prior to Fries (27). According to the ICBN, Fries's major publications are considered the starting point for the nomenclature of ascomycetes and certain other groups of fungi. Later, Fries (28) revised his concept of *Sphaeria*, a genus that initially included all perithecial ascomycetes, and placed this species in *Nectria*, a genus that included fleshy, colored, uniloculate, perithecial ascomycetes. With that taxonomic decision, the scientific name of this species became *Nectria coccinea* (Pers.:Fr.) Fr. The abbreviation Fr. outside the parentheses refers to the author who placed the species name in that genus. Later, when Rossman et al. (54) placed this species in the genus *Neonectria* as *N. coccinea* (Pers.:Fr.) Rossman & Samuels, their names were placed outside the parentheses. Notice that the generic name may be abbreviated with the first letter, occasionally two or three letters, always referring to the previously listed generic name. Thus, the *N.* listed above refers to *Neonectria,* not *Nectria*. The author name(s) is often included when a species name is first mentioned in a publication, especially in taxonomic papers, in order to define precisely

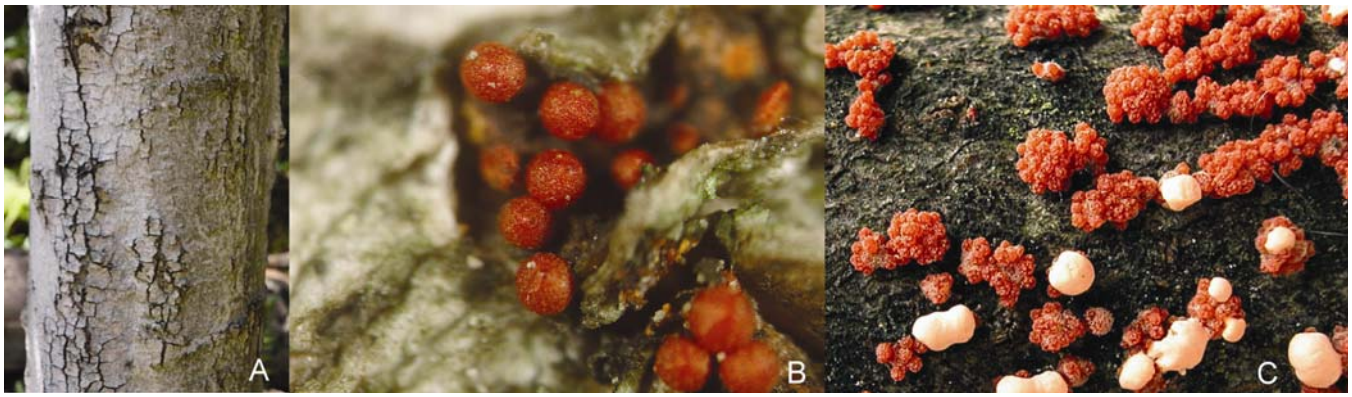

Fig. 2. Beech bark canker in North America caused by *Neonectria faginata;* type of genus *Nectria, N. cinnabarina*. A, Beech bark canker disease in North America caused by *Neonectria faginata.* Photo by Martin MacKenzie, USDA-Forest Service, Salinas, CA. B, Ascomata of *Neonectria faginata* BPI 864079. Photo by Gary J. Samuels, USDA-ARS. C, *Nectria cinnabarina*, cause of coral canker disease of hardwood trees, showing ascomata and *Tubercularia* asexual state. Photo copyrighted by Jeff Keller, Switzerland.

the concept of that name. For all scientific names governed by the ICBN, the authors associated with scientific names are abbreviated according to agreed-upon standards published in Brummitt and Powell (12), a list that is updated and available online at http://www.ipni.org/.

Why do scientific names change?

Scientific names change as systematists learn more about a species, including its morphology, biology, and evolutionary relationships.

Changes in scientific names can be annoying to users of those names. However, if one knows the reasons behind name changes and understands that a new name provides more information about that taxon than the old name, these changes are easier to accept. Continuing the example from above, we discuss the fungi that cause beech bark canker in North America (*Neonectria faginata*, Fig. 2A and B) and Europe (*Neonectria coccinea*).

Early in mycological history, fungal species were very broadly defined such that all pyrenomycetes (ascomycetes with tiny fruiting bodies often seen as bumps protruding on the plant surface) were placed in the genus *Sphaeria* and all little red perithecial fungi were called *Sphaeria coccinea*. With the use of microscopes and the study of fungi in culture, mycologists observed that some little red perithecial fungi were different from others based on characteristics of the ascomata, asci, and ascospores. Thus, *Sphaeria coccinea* was placed in the genus *Nectria* as *Nectria coccinea,* with other bright-colored, fleshy, uniloculate perithecial species with unitunicate asci. Further comparison of microscopic characteristics of species of *Nectria* revealed that *N. coccinea* was distinct from other red perithecial species such as *Nectria cinnabarina, N. episphaeria*, and many other species. Most recently, differences in ascomatal wall structure, asexual states, and biology have been noted among species of red *Nectria*-like fungi such that these species are placed in several newly defined or described genera (54).

The genus *Nectria* is based on the type or defining species *Nectria cinnabarina* (Tode:Fr.) Fr. (Fig. 2C). Species in the genus *Nectria sensu stricto* (in the narrow sense) are those most closely related to *N. cinnabarina.* Species in the genus *Nectria sensu stricto* have certain morphological characteristics in common such as a *Tubercularia* asexual state, a specific ascomatal wall structure, and similar biology as well as grouping with *N. cinnabarina* when molecular sequences are analyzed. On the other hand, *Nectria coccinea*, now known as *Neonectria coccinea*, has a *Cylindrocarpon* asexual state, an ascomatal wall structure that is different from *N. cinnabarina*, and does not group with *N. cinnabarina* using molecular sequence data. Rather, it is morphologically similar to the type species of *Neonectria, N. ramulariae* Wollenw., that also has a *Cylindrocarpon* asexual state and similar ascomatal wall structure. Therefore, *Nectria coccinea* is now placed in the genus *Neonectria* as *Neonectria coccinea* (54).

Most recently with the use of molecular sequence data, the concept of *Neonectria coccinea* has been even more narrowly defined. Using a multigene phylogeny, Castlebury et al. (13) demonstrated that the species name *N. coccinea* should be restricted to a group of fungi that occur only on *Fagus* (beech) in Europe. In this research, several genes were sequenced and analyzed from isolates of fungi appearing similar to *N. coccinea* on various plant hosts throughout the world. These data revealed the existence of several lineages of related but distinct species, only one of which could be *N. coccinea.* All were determined to belong in the genus *Neonectria.*

How can the "real" *Neonectria coccinea* be determined? When *Sphaeria coccinea* was described in 1800 by Persoon, he designated a particular specimen as the type specimen that serves as the standard or definition of that species. This type specimen occurs on *Fagus sylvatica* in Germany, and a portion of the type specimen is housed at the U.S. National Fungus Collections in Beltsville, MD. This portion of the type specimen was examined to determine the precise morphological characteristics of *Neonectria coccinea*. The type specimen of *N. coccinea* was determined to agree morphologically with a living culture from a similar looking, recently collected specimen on *F. sylvatica* in Germany. A single ascospore isolate was made from this specimen that produced a living culture. This specimen and derived culture were used to interpret and characterize the dead type specimen. In the publication by Castlebury et al. (13), this specimen was designated the epitype specimen with the living culture considered the ex-epitype culture. An epitype specimen is one that is used to interpret a type specimen that may not have all the characteristics needed to define a species such as DNA that can be sequenced. Using the epitype specimen and the ex-epitype culture that agree with the original type specimen on *Fagus* in Germany, the species *Neonectria coccinea* is now well-characterized based on morphology and molecular sequence data. In the molecular sequence study, isolates of *Neonectria* that group with the ex-epitype isolate of *N. coccinea* are considered to be the same species, while isolates distinct from those grouping with *N. coccinea* are considered different species. Thus, it was determined that *N. coccinea* occurs only on *Fagus* in Europe and does not occur on any other host plants, nor does it occur in North America.

This research included many isolates of related fungi associated with beech bark canker and other hardwoods in North America (Fig. 2A and B). The analyses of multiple genes from these isolates demonstrated that a different species is associated with beech bark canker on *Fagus* in North America. One of the pathogens causing beech bark canker in North America had been recognized as *Neonectria coccinea* var. *faginata* Lohman et al. Castlebury et al. (13) suggest that *N. coccinea* is distinct from *Neonectria coccinea* var. *faginata*, and that this variety should be recognized at the species level as *Neonectria faginata* (Lohman et al.) Castl. & Rossman (Fig. 2B). Based on the more precise definition of this species, it is found to occur only on *Fagus* in North America. Although many isolates from *Fagus* in Europe were included in this study, none of them proved to be the same as *N. faginata* that occurs in North America.

A second species, *Nectria galligena* Bres., also referred to as *Neonectria galligena* (Bres.) Rossman & Samuels, has been associated with beech bark canker in North America. Many isolates of *N. galligena* from *Fagus* and many other hardwood hosts and the closely related *N. ditissima* (Tul. & C. Tul.) Samuels & Rossman were included in the study. Analyzing the sequences of multiple genes, Castlebury et al. (13) determined that the isolates of *N. ditissima* including one representing the type specimen and those of *N. galligena* were genetically closely related. They are so closely related that Castlebury et al. (13) made the taxonomic decision that *Neonectria galligena* and *N. ditissima* are synonyms, i.e., they are the same species. Because the name *Nectria ditissima* Tul. & C. Tul. 1865, the basionym of *Neonectria ditissima* (Tul. & C. Tul.) Samuels & Rossman, was described prior to *N. galligena* Bres. 1901, the principle of priority from the ICBN dictates that the earliest name should be used. Thus, the correct name for this species known for many years as *Nectria galligena* is now *Neonectria ditissima.*

What does this research with the resultant name changes mean for plant pathologists and plant quarantine officials? Actually, quite a bit! First, *Neonectria faginata* associated with beech bark canker only occurs on *Fagus* in North America. Apparently, this species was not introduced into North America as had been previously thought. Second, *N. ditissima*, another species associated with beech bark canker, occurs on a wide range of hardwood trees in North America and Europe. *Neonectria ditissima* causes diseases of various hardwoods, such as birch canker and apple canker disease, suggesting that breeding these host trees for resistance to diseases caused by *N. ditissima* may be difficult because of the broad host range of the pathogen. Finally, *Neonectria coccinea sensu stricto* occurs only on *Fagus* in Europe. This is important information for

plant regulatory officials when considering the movement of beech germplasm between North America and Europe.

Accurate scientific names based on narrowly defined species reflect what is known about the biology, host range, and geographic distribution of the species. The knowledge associated with accurate scientific names is important for plant pathologists, for example, in developing strategies to control fungal diseases or determining actions to prevent the introduction of new pathogens.

Why does it matter whether scientific names reflect the phylogeny of fungal pathogens?

Accurate scientific names should convey as much information as is known about an entity, including its classification and phylogeny, also referred to as evolutionary history. An accurate name that reflects phylogeny will allow a prediction about a plant-associated fungus, including its potential pathogenicity and appropriate control measures. For example, species in the genus *Erysiphe* are obligate parasites that cause powdery mildew diseases on living plants. On the other hand, an isolate determined to be a species of *Phomopsis* may be pathogenic or harmlessly endophytic depending on the health of the host. An accurate generic classification implies information about the biological characteristics of the species included in that genus. An accurate identification of the causal agent of a plant disease is essential for determining the appropriate choice of control measures. As an example, consider the fungi that cause two serious diseases of cacao or the chocolate plant (*Theobroma cacao*, Malvaceae) in the Western Hemisphere.

Witches'-broom of cacao is caused by a fungus that until recently was known as *Crinipellis perniciosa* (Stahel) Singer. This pathogen causes an abnormal growth on the host; thus, the name witches'-broom has been given to the disease. This fungus produces a mushroom-type reproductive structure. Another serious cacao disease known as frosty pod appears as a whitish bloom on cacao pods with the associated fungus reproducing as a single layer of spore-bearing structures giving the pods a "frosty" appearance. The fungus causing frosty pod was originally identified as *Monilia roreri* Cif. (35). The generic name *Monilia* suggests that this is the asexual state of the ascomycete *Neurospora*. Upon close microscopic examination, Evans (23) and Evans et al. (24) determined that the spores produced by *M. roreri* were actually basidiospores; thus, to reflect this observation, they established the genus *Moniliophthora* with the type species, *Moniliophthora rorei* (Cif.) H.C. Evans et al. (24). The generic name *Moniliophthora* carries the knowledge that this pathogen is not an ascomycete related to *Neurospora crassa* and, for example, frosty pod disease probably could not be controlled by benomyl.

Knowing that the cause of frosty pod is a basidiomycete suggests that perhaps it is related to the other basidiomycete cacao pathogen in spite of the fact that *Crinipellis perniciosa* produces conspicuous mushrooms on decaying cacao pods (Fig. 3) while *M. roreri* produces only a single layer of spores on the cacao pods. Aime and Phillips-Mora (1) analyzed molecular sequence data from isolates of species in the genus *Crinipellis* including the type species as well as isolates of *C. perniciosa* and *M. roreri*. They used this approach to determine the relatedness of the two basidiomycete pathogens and if *Crinipellis perniciosa* was placed in the correct genus.

This research showed that the two species causing diseases of cacao were closely related to each other; that is, the fungus known as *Crinipellis perniciosa* causing witches'-broom was closely related to the fungus causing frosty pod, *Moniliophthora roreri*, even though the latter species does not produce a mushroom-like structure. This was a surprise! However, close observation of microscopic characteristics of these two species revealed less conspicuous similar structures that confirmed this relationship. In addition, *Crinipellis perniciosa* was determined to be only distantly related to the type and other species of the genus *Crinipellis,* a genus that includes primarily saprobic tropical fungi. To reflect this evolutionary relationship, Aime and Phillips-Mora (1) transferred *C. perniciosa* to *Moniliophthora* so that the two closely related species are in the same genus. The etiological agent of witches'-broom is now known as *Moniliophthora perniciosa* (Stahel) Aime & Phillips-Mora, reflecting the close relationship to *M. roreri* and the similar biology of these two pathogenic fungi. As a result of this knowledge, a plant pathologist should suspect that strategies for controlling frosty pod caused by *M. roreri* may also be effective against witches'-broom caused by the closely related, but macromorphologically different, *M. perniciosa*.

How can I find the most accurate, up-to-date name for my fungal pathogen?

Keeping up-to-date on the most accurate scientific names of fungi can be difficult and time-consuming. In order to make this as easy as possible, resources have been established for this purpose. Increasingly, this information is available on the Internet and can be rapidly accessed, but at present none of these sources are complete with the up-to-date scientific names for all fungi.

Several resources exist to help a user determine the accurate scientific name of a fungus. One is the *Index Fungorum* http://www.indexfungorum.org/Names/Names.asp developed by CAB International. This is a list of all described fungal names, over 400,000 of them, with a family placement for each name. An attempt is made to provide the currently accepted scientific name, although for many names an update is unavailable or inaccurate and the date or rationale for the updated name is not given. Complementary to *Index Fungorum* is the Catalog of Life http://www.catalogueoflife.org/search.php, which includes a phylogeny for most groups of true Fungi and Oomycota. This site is useful for determining the higher level relationships of all organisms and it is updated annually. However, the Catalog of Life includes only the most common species of fungi with even fewer synonyms. The Centraalbureau voor Schimmelcultures (CBS) Fungal

Fig. 3. *Moniliophthora perniciosa*, the fungus that causes witches'-broom disease of cacao. A, Mushroom-type fruiting body of *M. perniciosa*. Photo by USDA-ARS. B, Cacao pods with beans destroyed by *M. perniciosa*. Photo by USDA-ARS.

Biodiversity Centre has initiated a database of accurate scientific names of fungi along with descriptions and literature. In addition, this database provides access to the most recently described fungal species through an initiative known as MycoBank (http://www.mycobank.org/). New names for fungi are entered into the MycoBank database, and the name is given a number that is used in the publication. In that way, all new scientific names for fungi will be known without the need to access all the literature in which fungal names might have been published. Plans have been made to combine these databases of fungal names along with the one mentioned below. This would greatly help to meet the needs of plant pathologists who want to know the correct scientific names for fungal pathogens.

A resource for determining the accurate scientific name of fungal plant pathogens as well as the host range, geographic distribution, literature, and, for some species, descriptions and illustrations, is the fungal database at the USDA ARS Systematic Mycology & Microbiology Laboratory (SMML) (http://ars.usda.gov/ba/psi/smml). The nomenclatural part of this database has the advantage of documenting taxonomic information and decisions so that one can consult the literature upon which the taxonomic decision was based. The number of species names that have been reviewed is limited, about 40,000 species at present; however, the emphasis is on disease-causing fungi associated with plants worldwide. All of the 13,000 accepted species of fungi that were included in *Fungi on Plants and Plant Products in the United States* (25) are treated. Scientific names for important groups of plant pathogens such as *Phytophthora* and those on the APHIS Regulated Plant Pest List have been evaluated and published (15,16). The scientific names of plant pathogenic fungi will continue to be evaluated and updated as additional changes occur and new species are described.

At the SMML website, information in addition to nomenclature can be retrieved such as host range, worldwide distribution, disease and plant part affected as well as recent literature about the species and specimens in the U.S. National Fungus Collections, Arthur Herbarium of Purdue University, and Plant Pathology Herbarium of Washington State University. Although determining the accurate scientific name for a fungus can be a time-consuming process, once the nomenclature of a species has been evaluated and updated, data from each of the databases for that species under all of its scientific names can be retrieved at once. Information about the host range and geographic distribution can be determined using any of the various synonyms of both the sexual and asexual states of a species. By selecting the Quick Search option http://nt.ars-grin.gov/fungal databases/index.cfm, one can search for the accurate scientific name with synonyms and alternative state name, the reports of that species on plant hosts anywhere in the world under all synonyms, literature about that species, and data on specimens in three different herbaria. This resource relies on accurate nomenclature because the ability to gather information about any particular fungus depends on the ability to search for information using all synonyms.

In addition to the accurate names of and information about plant associated fungi, the SMML website provides several resources for the identification of plant pathogenic fungi. These include interactive keys with descriptions and illustration to species of bunt-fungi (*Tilletia*) in North America (26), rust fungi on legumes potentially confused with soybean rust (47), species of the rust genus *Ravenelia* (34), and species of *Trichoderma* used in the biological control of plant pathogenic fungi. In addition, descriptions and illustrations are available for invasive plant pathogens, http://nt.ars-grin.gov/sbmlweb/fungi/diagnosticfactsheets.cfm, such as *Puccinia horiana* Henn., cause of chrysanthemum white rust; *P. hemerocallis* Thüm., cause of daylily rust; and *Peronospora radii* de Bary, cause of downy mildew of marguerite daisy, among others (50).

Recent Advances in Systematics

The revolution resulting from the ability to obtain molecular data has greatly influenced the field of systematics such that an increasing body of genetic information about organisms exists. Following are some advances in knowledge that have been made as the result of applying molecular sequencing data to the understanding of relationships among fungi and other organisms.

Fungi are more closely related to animals than to plants. Although some evidence existed several decades ago to suggest that fungi were quite unlike plants in many ways, molecular sequence data have now been used to prove that the true Fungi are more closely related to animals than to plants (8,69; Fig. 4). This discovery explains why it has been so difficult to develop antimycotic pharmaceuticals that are effective against human fungal pathogens without negatively affecting the human host.

Oomycetes are related to the yellow-brown algae. The Oomycota or Peronosporomycetes consist of more than 800 species that may be saprobic or parasitic on terrestrial or aquatic plants and animals. The oomycetes, including *Phytophthora, Pythium,* and downy mildews, have long been considered to be fungi because they obtain their nutrients via absorption and many of them produce the filamentous threads characteristic of most fungi. As new tools for determining phylogenetic relationships were developed, they have been applied to questions such as whether

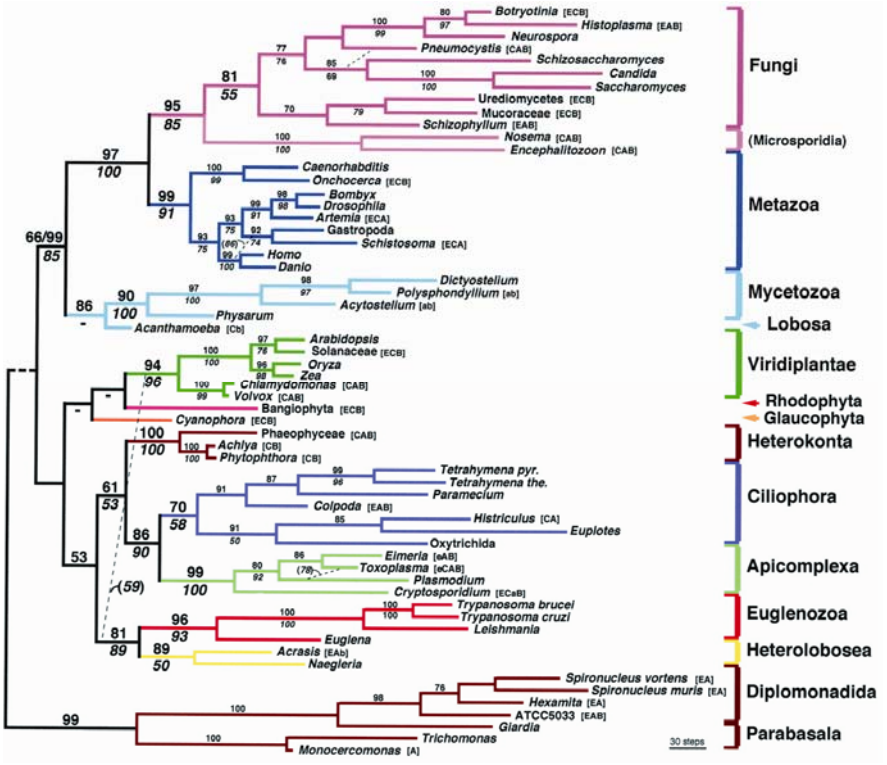

Fig. 4. A kingdom-level phylogeny of Eukaryotes based on combined protein data showing that fungi are most closely related to animals (Metazoa) and the Oomycota belong in the Heterokonta. Figure taken from Baldauf et al., Science 290:972-977 (3 November 2000). Reprinted with permission from AAAS.

the Oomycota are more closely related to the heterokont algae or the true Fungi (Chytridiomycota, Glomeromycota, Zygomycota, Ascomycota, Basidiomycota). Results from a number of studies using molecular sequence data combined with ultrastructural observations confirm unequivocally that the Oomycota share a common ancestor with the other members of the heterokont algae. The heterokont algae include the Phaeophyta or brown algae, Xanthophyta or yellow-green algae, Chrysophyta or golden algae, and Bacillariophyta or diatoms as well as several smaller groups. Some controversy still remains about exactly what to call this group of organisms. Most authors refer them to the Kingdom Chromista, Phylum Heterokonta (37), while others place them in the Kingdom Stramenopila (also spelled Straminipila) (48).

A number of characteristics distinguish the Oomycota from the true Fungi. These include differences in sexual reproduction, the nuclear state of the vegetative mycelium, cell wall composition, type of flagellae, and mitochondria (Table 1 from 52).

Five major classes of true Fungi are recognized, including arbuscular mycorrhizae in a class of their own. Two NSF-funded initiatives called Deep Hypha and Assembling the Fungal Tree of Life (AFTOL) produced a comprehensive review of the classification of true Fungi with the results published in Mycologia 98(6), 2006. In this issue, the latest phylogeny of all major groups of true Fungi is presented with an overview article by Blackwell et al. (10). The Ascomycota and Basidiomycota are two of the major classes of fungi along with the Chytridiomycota and Zygomycota. The arbuscular mycorrhizal fungi were determined to be distinct from these major classes and are now recognized as the class Glomeromycota along with a number of smaller groups of unusual fungi. Some evidence suggests that the Microsporidia are true Fungi as well, but these results are still equivocal.

Powdery mildews are defined by conidial state characters. As each group of Fungi is scrutinized using molecular tools, concepts of taxa at every level from class and order down to family, genus, and species are more precisely and sometimes differently defined. One example that was a surprise to many concerns a major group of plant pathogens, the Erysiphales or powdery mildews, in which new concepts of genera have been recognized based on the analyses of molecular sequence data. Many species of Erysiphales produce a sexual fruiting structure known as a chasmothecium (a closed fruiting body), often with appendages that are curved, hooked, branched, or straight (Fig. 5). In the past, genera were defined based on these appendages thought to influence the mode of distribution. Fairly nondescript asexual structures were also produced, mostly placed in the anamorphic genus *Oidium*, but relatively little attention had been paid to them as taxonomic characters. With the application of molecular sequence data (57,64–66), this classification system has been considerably revised. Molecular data demonstrated that the morphological signal, i.e., the morphological characteristics that correlate with the phylogeny, is exhibited by the asexual state. Today, the generic concepts in the Erysiphales are based primarily on characteristics of the conidiophores and conidia rather than on the appendages of the chasmothecia.

***Fusarium*: Molecular systematics results in more precisely defined species.** The concept of a species has changed considerably since the time of the father of mycology Elias Fries (1794–1878) and the father of American mycology David Schweinitz (1780–1830). The example of *Neonectria coccinea* presented above demonstrates a change in species concept over time based on available tools. Below we will use the genus *Fusarium* to further illustrate changing species concepts and why it is important to apply accurate scientific names to meaningfully defined species.

The genus *Fusarium* was first described in 1809 and was sanctioned by Fries in 1821 based on *Fusarium roseum* Link for "species with fusiform, non-septate spores borne on a stroma" (11). Species were added to *Fusarium,* but no monographic treatments, i.e., comprehensive accounts based on systematics, were published for this genus until a German plant pathologist Wollenweber (70) and later Wollenweber and Reinking (71) published landmark papers about *Fusarium* that laid the groundwork for future, premolecular stud-

Table 1. Major distinctions between the Oomycota (Kingdom Chromista) and the true Fungi

Character	Oomycota	True Fungi
Product of sexual reproduction	Produces oospores	Oospores not produced; sexual reproduction results in zygospores, ascospores, or basidiospores
Nuclear state of vegetative mycelium	Diploid	Mostly haploid or dikaryotic
Cell wall composition	Beta glucans-cellulose	Chitin, cellulose rarely present
Type of flagellae on zoospores, if produced	Heterokont, of two types, one whiplash directed posteriorly, the other fibrous, ciliated, directed anteriorly	If flagellae produced, usually of only one posterior whiplash type
Mitochondria	With tubular cristae	With flattened cristae

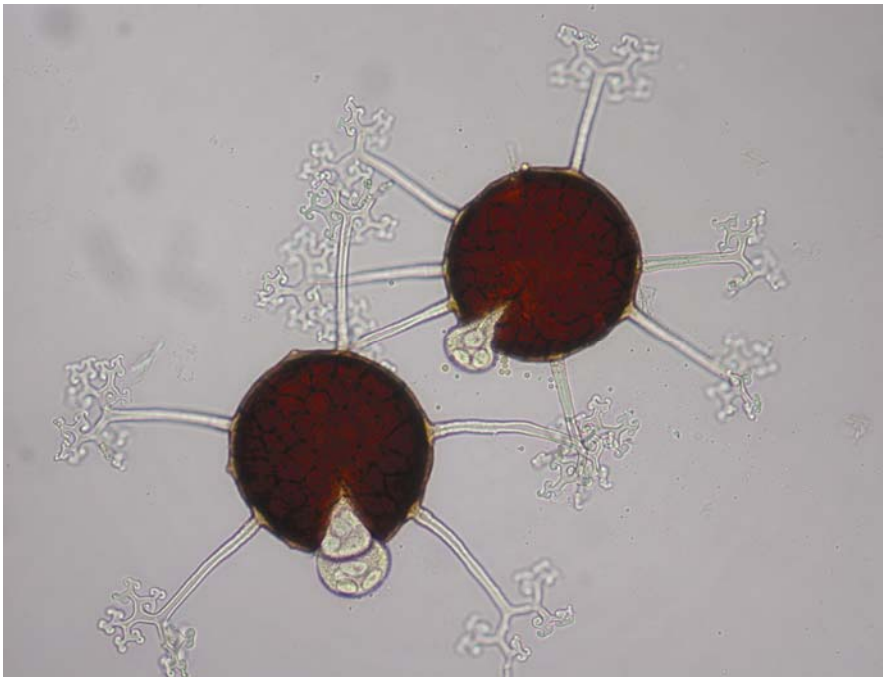

Fig. 5. Ascomata of powdery mildew, *Erysiphe magnifica,* showing branched appendages and asci emerging from ruptured ascomata. Photo by Larry F. Grand, North Carolina State University.

ies recognizing 142 species in 16 groups and six subgroups. A few years later, two Americans, Snyder and Hansen (61–63), reduced all *Fusarium* taxa to nine species more or less roughly equivalent to Wollenweber and Reinking's groups (11). While the identification of species was relatively easy using the Snyder and Hansen system, little distinction was made between species that, for example, were plant pathogens causing cereal diseases or root rots and those useful in biological control of scale insects and other fungi.

In the 1970s and 1980s, Booth (11), Gerlach and Nirenberg (31), Marasas et al. (40), and Nelson et al. (43) were in relative agreement about the major groups within *Fusarium*. These groups correlated with the biology of species as well as their known sexual states, although for some groups no sexual states are known. The cereal pathogens of *Fusarium* in Sections *Discolor, Elegans*, and *Liseola* have *Gibberella* sexual states, while the root rot pathogens including *F. solani* were placed in Section *Martiella* having *Haematonectria* sexual states (54). The unusual species *F. decemcellulare* Brick and related species in Section *Spicarioides* have sexual states placed in *Albonectria* (54). Species in Section *Epispheria* including slow-growing species that occur on other fungi and section *Coccophilum* on scale insects have sexual states placed in *Cosmospora* (54).

Fig. 6. Symptoms of soybean sudden death syndrome in South America caused by *Fusarium tucumaniae*. A, Leaf symptoms. B, Root symptoms. Photos by Takayuki Aoki, Tsukuba, Japan.

With the advent of non-morphological approaches to systematics including mating type studies and molecular sequence analyses, the genus *Fusarium* was tackled by several mycologists with a resulting proliferation of more narrowly defined species (5,38,46), often reflecting biological differences. As an example, one can examine *Fusarium solani* (Mart.) Appel & Wollenw. *sensu lato*, the only species in the section *Martiella* based on the nine-species system proposed by Snyder and Hansen (62). Mating type studies were undertaken in which at least seven reproductively isolated biological species of *Fusarium solani* were characterized, often referred to as its sexual state *Nectria haematococca* Berk. & Broome (41). Analyzing molecular sequences of mating type loci suggested that each of these represented a different species but that many more species existed. Eventually, O'Donnell (45) recognized 26 phylogenetically distinct species within *Fusarium solani,* many of which have a distinct biology.

The causal agent of soybean sudden death syndrome (56) was referred to as *Fusarium solani sensu lato* or *F. solani* f. sp. *glycines* (39,55). This is a disease (Fig. 6) that occurs throughout the world and now is known to be caused by four different species of *Fusarium*. To more accurately determine the causal agents of this disease, multiple genes were sequenced and analyzed from a diversity of isolates representing *Fusarium solani sensu lato*. Those isolates known to cause soybean sudden death syndrome in North America have been segregated as a distinct species named *F. virguliforme* O'Donnell & T. Aoki (6) (Fig. 7). Three related but different species of *Fusarium,* including *F. tucumaniae* T. Aoki et al. and *F. virguliforme,* are associated with this disease in South America (7). Pairings of these

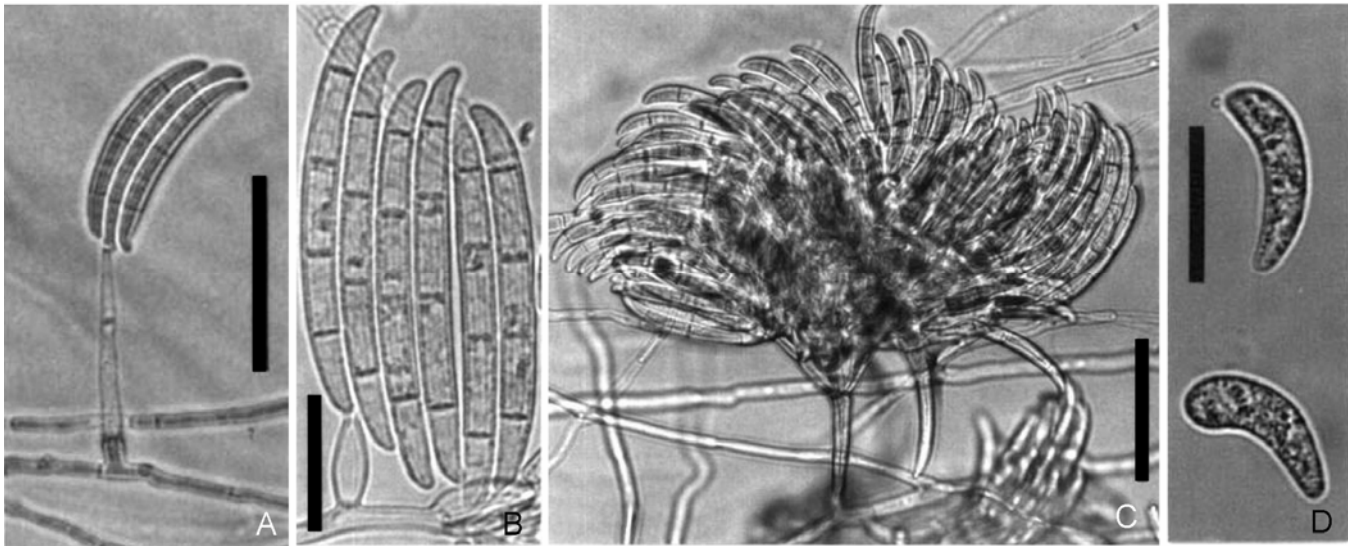

Fig. 7. Conidiophores and two kinds of conidia of *Fusarium virguliforme*, cause of soybean death syndrome in North America. A, Macroconidia on solitary conidiophore of *F. virguliforme*. B, Macroconidia of *F. virguliforme*. C, Aggregated conidiophores of *F. virguliforme*. D, Comma-shaped conidia of *F. virguliforme*. Photos by Takayuki Aoki, Tsukuba, Japan.

closely related species resulted in sexual reproduction among isolates of *F. tucumaniae* but not between *F. tucumaniae* and *F. virguliforme.* These mating studies are another confirmation of the validity of these species distinctions (19). Based on the putative existence of only one mating type, this research also suggests that *F. virguliforme* might have been introduced into North America and is still the only species known to cause soybean sudden death syndrome in North America. The hypothesis that the fungus causing sudden death syndrome in North America was introduced could not have been proposed without these accurately defined species distinctions.

Why break up large, well-known species into narrowly defined taxa with new names? The benefit is in the precise information conveyed by the scientific name. In the case of *Fusarium solani sensu lato* associated with soybean sudden death syndrome, no distinction was made among the biologically distinct and geographically separated entities. Once *F. virguliforme* was defined and named, the scientific name conveys the knowledge that this species alone causes sudden death syndrome of soybean in North America but that other species of *Fusarium* could also be accidentally introduced. Without this knowledge, the epidemiology, control strategies, timing, and breeding programs would be targeted at a species complex representing broad fungal genetic diversity. Once narrowly defined, control strategies can be designed based on the narrow genetic diversity of the causal agent. In addition, this information can be used by plant quarantine officials to develop appropriate regulatory policies.

Most asexually reproducing fungi are ascomycetes. Most species of plant-associated fungi are predominantly asexual or have no sexual state. Traditionally, they have been placed in artificial groups such as the hyphomycetes and coelomycetes based on the manner in which the conidia are produced and the presence or absence and kind of fruiting body. The molecular revolution has been extremely useful in determining relationships of asexually reproducing fungi to sexually defined groups. Most anamorphs have been determined to be ascomycetes, although some are basidiomycetes. Knowledge of the relationship of the asexual species to sexual fungi may assist in discovering the sexual state, thereby completing knowledge of the life history of a plant pathogenic fungus. For many asexual fungi, a sexual state may not exist, but knowledge of the phylogeny allows scientists to make predictions about the biology especially pathogenicity of these species.

In integrating the asexual species into an ascomycete phylogeny, some surprising relationships have become evident. One example of a relationship revealed using molecular sequence data is the inclusion of *Macrophomina phaseolina* (Tassi) Goid., cause of charcoal rot and ashy stem blight, in the ascomycete family Botryosphaeriaceae (21). *Macrophomina phaseolina* produces large numbers of sclerotia, but no spores. For this reason, the fungus was considered to be related to other common sclerotial-forming fungi such as *Rhizoctonia solani* J.G. Kühn, a basidiomycete. Knowing that *Macrophomina phaseolina* is an ascomycete rather than a basidiomycete means that different strategies should be used to control the diseases caused by this fungus.

Another surprising example of integrating asexual plant pathogenic fungi into the ascomycetes concerns the cause of barley and rye leaf spot and leaf scald, *Rhynchosporium secalis* (Oudem.) Davis. This fungus is asexually reproducing, with only simple unbranched conidiogenous structures that produce hyaline, 1-septate conidia. No sexual state has ever been encountered for this fungus. Molecular sequence studies of *R. secalis* revealed that this asexual fungus belongs in the Helotiales or inoperculate discomycetes related to the genus *Pyrenopeziza* and *Tapesia* (32). At about the same time, another group of scientists demonstrated that this asexual pathogen is related to the serious grass pathogen, *Tapesia yallundae* Wallwork & Spooner, cause of eyespot of cereals and grasses, subsequently placed in its own genus as *Oculimacula yalludae* (Allwork & Spooner) Crous & W. Gams in the Helotiales (20).

Theoretically, asexual fungi can be integrated both taxonomically and nomenclaturally into a known phylogeny. In reality, the nomenclatural integration of asexual fungi into an ascomycete phylogeny is proving difficult. The acceptance of two names for one species of fungus is allowed by Article 59 of the ICBN. The name for the asexual state is considered a form-taxon, and the correct name for the fungus as a whole must be based on a teleomorph. Many genera of sexual fungi correlate one-for-one with genera of asexual fungi. The ICBN indicates that teleomorph names must be used in most cases. Are plant pathologists willing to give up some of the commonly used names such as *Botrytis cinerea* Pers.:Fr. in favor of *Botryotinia fuckeliana* (De Bary) Whetzel in order to use just one name for this species? Or should the rules of the ICBN be changed to allow the name *Botrytis* to have priority over *Botryotinia*? Most scientists would agree that closely related species should be placed in the same genus, but which generic name should be used if one species has a sexual state while the other species is known only as an asexual species? These are questions that mycologists have been and still are pondering and discussing. In the long run, use of one name for each species may best serve the plant pathology community, but making the switch to one name will not be easy (29,53).

Initiatives will provide tools for the accurate identification of fungi. The DNA Barcode of Life Initiative seeks to provide a unique DNA sequence for the identification of all biological species (http://barcoding.si.edu/). The unique DNA sequence would be from a standardized position in the genome and would serve as a molecular diagnostic tool for species-level identification. Progress has been made toward developing DNA barcodes for specific groups of fungi. Among most groups of animals, the mitochondrial cytochrome oxidase I (COI) gene can be used to distinguish and rapidly identify species. Although the COI gene works for the nonfungal Oomycota and a few groups of true Fungi (59), the existence of introns of variable lengths and other problems eliminate it as the best gene for a universal DNA barcode for true Fungi. An international workshop was held in May 2007 to coordinate these efforts and decide on the best gene to use for DNA barcodes for fungi. A consensus was reached that the most appropriate gene known at present for DNA barcoding of true Fungi is the ITS region of the nuclear rDNA (51). Some DNA barcoding resources exist for the rapid identification of Fungi including one for *Fusarium* using the ITS region (30) and another for the biocontrol fungus *Trichoderma* using both ITS and EF1alpha for accurate species identification (22; http://www.isth.info/).

Identification using standardized known DNA barcodes requires accurate systematic knowledge of the group of organisms involved. At the same time, developing and applying DNA barcodes unveils cryptic species, i.e., species that are difficult to distinguish based on morphology, and thus contributes to an even more accurate understanding of a group of organisms. More sites for rapid identification of plant pathogenic fungi using DNA barcodes are anticipated.

At present, plant pathologists have used DNA sequences blasted to sequences in GenBank for the identification of some fungi. This method has serious limitations that merit caution. Many sequences deposited in GenBank, possibly as many as 27% of the ITS sequences, have been found to be from erroneously identified specimens or cultures (44) and will result in a wrong identification. GenBank is working to note which sequences represent reliable reference sequences for species as has been done for species in *Trichoderma* (58). To confirm an identification using a DNA sequence, one should always investigate the data associated with a GenBank sequence even examining a voucher specimen if one has been deposited and comparing the unknown with descriptions and illustrations of the sequenced known fungus. After all, most described species of

fungi have not yet been sequenced. Because a sequence does not match something in GenBank does not mean that one is working with an undescribed species. In fact, it is likely that the unknown is just one of the many described fungal species without a sequence deposited in GenBank.

Another initiative potentially useful to plant pathologists is the Encyclopedia of Life (http://www.eol.org/) in which a web page will be created for every biological species. Each species page will have basic information for either a layperson or a professional including general and technical data with links to sources of additional information. The first meeting to discuss how to develop such web pages for the fungi will take place in August 2008.

Document, Document, Document

Research involving fungal pathogens should be documented with voucher specimens and living cultures. One reason to do this is the possibility that the causal fungus is inaccurately identified or should be restudied as species concepts change. Given that species concepts are dynamic and will change as knowledge increases, the need to document research plant pathogenic fungi is critical. Such a requirement is more than of purely academic interest. When the United States is requesting permission to export a commodity to a foreign country, reports of pathogens and their distribution in the United States are scrutinized by the other country to determine if any pathogens in the United States are a threat to the country of import. For example, *Peronospora hyoscyami* (Rabenh.) deBary (=*P. tabacina* D.B. Adam), which causes tobacco blue mold, primarily infects tobacco, *Nicotiana tabacum* (Solanaceae). However, a few reports exist from the 1930s that this fungus occurs on *Solanum lycopersicum* (=*Lycopersicon esculentum*, tomato, Solanaceae) in Georgia, North Carolina, and South Carolina (4). Unfortunately, the basis for these reports is not known, nor are there specimens to document them. Because of these reports, Japan has been hesitant to accept tomatoes from the United States for fear of their infection with *Peronospora hyoscyami*. In order to prove the non-susceptibility of tomatoes, extensive pathogenicity tests have been made with negative results (http://www.uky.edu/Ag/kpn/kpn_97/pn971201.htm). Whether the initial reports of *P. hyoscyami* on tomatoes were accurate will never be known because they were not documented with voucher specimens. The expense and extensive testing could have been avoided if those reports had been documented, and thus could have been proven erroneous.

In plant pathology research, after Koch's postulates have been fulfilled, a representative of the causal organism should be deposited in a publicly accessible culture collection. Additionally, a dried specimen of the diseased tissue with diagnostic features should be placed in a publicly accessible collection. And, depositing cultures and specimens is free! Many institutions exist for documenting our science. For cultures, the American Type Culture Collection (ATCC) in Manassas, VA, and the Centraalbureau voor Schimmelcultures (CBS), Utrecht, The Netherlands, among others, accept living cultures without any charge to the depositor. Voucher specimens either as a fungal pathogen on the host plant or as a dried culture specimen should be deposited at the U.S. National Fungus Collections (BPI) in Beltsville, MD (Fig. 8A), New York Botanical Garden (NY), Bronx, NY, Oregon State University Herbarium (OSC), Corvallis, OR, or any number of fungal herbaria. Official abbreviations for herbaria are listed in *Index Herbariorum* (http://sciweb.nybg.org/science2/IndexHerbariorum.asp). Plant material with the pathogen can be pressed and dried, then sent with detailed collection data to an herbarium. Dried cultures for deposit are made by removing strips of fungus on agar in petri plates, then gluing them in cardboard slide mailers placed in silica gel to dry (Fig. 8B). Instructions for making specimens of diseased plant material and dried cultures are available at: http://www.ars.usda.gov/Services/docs.htm?docid=9403. Research in plant pathology should be documented so that future scientists can verify and build upon today's research results using these cultures and specimens.

Conclusion

The science of systematics that discovers, describes, and classifies organisms is essential for plant pathology. Systematic study of plant pathogenic fungi results in accurate scientific names that reflect knowledge and communicate information about these organisms including their evolutionary history. Accurate names of plant pathogens provide information essential for determining appropriate disease control measures and serve as the basis for making decisions that protect agricultural and natural resources from invasive fungal pathogens.

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Fig. 8. A, David Farr and Erin McCray looking at rust specimens among open herbarium cabinets in the U.S. National Fungus Collections (BPI). B, Making a dried culture specimen from a living culture for deposit in a permanent repository such as the U.S. National Fungus Collections (BPI). Photos by USDA-ARS.

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