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Plant Pathogen Name Game: Cross Kingdom Review for the Naming of Biotic Agents Associated with Plants

Carolee T. Bull,^{1,2} Catalina Salgado-Salazar,³
Megan K. Romberg,⁴ Cavan Allen,³ Mihail Kantor,¹
Zafar Handoo,³ Nina Aboughanem-Sabanadzovic,⁵
Sead Sabanadzovic,^{5,6} and Teresa Coutinho⁷

¹Department of Plant Pathology and Environmental Microbiology and the One Health Microbiome Center, The Pennsylvania State University, University Park, Pennsylvania, USA; email: ctb14@psu.edu

²Department of Plant and Soil Sciences, Faculty of Natural and Agricultural Sciences, University of Pretoria, Pretoria, South Africa

³Mycology and Nematology Genetic Diversity and Biology Laboratory, US Department of Agriculture, Agriculture Research Service (USDA-ARS), Beltsville, Maryland, USA

⁴National Identification Services, Plant Protection and Quarantine, US Department of Agriculture, Animal and Plant Health Inspection Service (USDA-APHIS), Beltsville, Maryland, USA

⁵Institute for Genomics, Biocomputing and Biotechnology, Mississippi State University, Mississippi State, Mississippi, USA

⁶Department of Agricultural Science and Plant Protection, Mississippi State University, Mississippi State, Mississippi, USA

⁷Department of Biochemistry, Genetics and Microbiology, Centre for Microbial Ecology and Genomics/Forestry and Agricultural Biotechnology Institute, University of Pretoria, Pretoria, South Africa

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Abstract

To communicate across scientific disciplines, regulatory bodies, and the agricultural community, the naming of plant pathogens assigned to specific taxa is critical. Here, we provide an overview of the nomenclatural systems governing the naming of plant-pathogenic nematodes, fungi, oomycetes, prokaryotes, and viruses. Although we focus on the nature of the nomenclatural codes, we briefly discuss fundamental principles of taxonomy, including

classification and identification. Key elements of the codes of nomenclature that ensure stability and clarity when naming species of pathogens are defined. When comparing the practice of nomenclature across different kingdoms, the classification and nomenclatural systems differ, and thus unique challenges are faced. We provide guidance from the codes and current practice for naming novel species. When there are nomenclatural conflicts, international committees play a critical role in their resolution. They also play a role in updating the codes to reflect new advancements in science. With this review, we aim to assist plant pathologists, journal editors, and those in related fields by providing an entrée to the legalistic requirements of the codes. Authors must consult and follow the rules of the appropriate code for any proposal of new or new combinations of names. To those interested in naming new species (or renaming the current ones), we recommend collaborations with experts in the field of taxonomy to ensure that rules for accurate and consistent naming practices and procedures are followed and to increase the likelihood that the proposed nomenclature is correct and acceptable.

INTRODUCTION

Phytopathologists have a rich history of exploring the diversity of microorganisms that impact plant health. Our earliest history includes investigations into the etiology and taxonomy of organisms causing disease because identifying and referring to pathogens was of critical importance (8, 14, 40, 57). Scientists, regulators, producers, and the public continue to require universal means of referring to specific organisms. Taxonomy is the process by which scientists compare the diversity of organisms to determine whether they are related (classification), determine whether organisms belong to previously named groups (identification), and name those organisms that do not belong to already recognized and named taxa (nomenclature). Although we aim to introduce the nomenclature of plant pathogens (nematodes, fungi and oomycetes, prokaryotes, and viruses), we briefly discuss classification and, in some cases, identification because the three branches of taxonomy are intimately associated.

This review is an overview of the current codes of nomenclature (**Table 1**) and some of the requirements for proposing names of nematodes, fungi and oomycetes, prokaryotes, and viruses. We also provide generalized definitions of vocabulary important to codes of nomenclature to help with understanding. Readers must consult the specific codes for the exact requirements and definitions, as they differ and are continually being updated. Codes of nomenclature are quasilegal documents produced by international scientific bodies that regulate the naming and recognition of taxa. They provide regulations on altering the codes and adjudicating conflicts. Despite the pedantic nature of codes, naming new organisms holds an incredible mystique that makes sifting through the codes worthwhile. These codes operate independently and try to avoid names that are regulated by the other codes at the ranks of genus and higher. Although our discussion occasionally mentions other ranks, we primarily refer to the naming of species, as species are the fundamental unit of biology and of interest to most plant pathologists. Taxa of other ranks generally follow the same principles.

There are several important universal principles and goals of all nomenclatural codes. Nomenclatural codes provide regulations that aim to promote the stability of names. They help to ensure that the names of taxa are unambiguous. Codes regulate names and can reject names. They avoid the creation of useless names and those that may cause error or confusion. Effective publication helps to ensure widespread access to information about new and reclassified taxa (and their names), promoting universality. It should be noted that although there are some universal goals

Principles:

foundations on which the codes are built and from which rules and recommendations are derived

Effective publication:

published in scientific outlets that are widely available to scientists globally

Table 1 Codes on nomenclature and distinguishing features

Regulating organization	International Commission on Zoological Nomenclature (https://www.iczn.org/)	International Code of Zoological Nomenclature for algae, fungi, and plants (Shenzhen Code) (https://www.iaptglobal.org/)	International Committee on Systematics of Prokaryotes (ICSP) (https://www.the-icsp.org/)	International Standards for Naming Pathogens of Phytopathogenic Bacteria (Standards) International Society of Plant Pathology-Committee on the Taxonomy of Plant Pathogenic Bacteria (ISPP-CTPPB) (https://www.isppweb.org/about_tppb.asp)	The International Code of Virus Classification and Nomenclature (ICVCN) International Committee on Taxonomy of Viruses (ICTV) (https://ictv.global/)
Current version of the code^a	International Code of Zoological Nomenclature (Zoological Code; 68)	International Code of Nomenclature for algae, fungi, and plants (Shenzhen Code; 93)	International Code of Nomenclature of Prokaryotes. Prokaryotic Code (2022 Revision; 59)	International Standards for Naming Pathogens of Phytopathogenic Bacteria (The Standards; 105)	The International Code of Virus Classification and Nomenclature (ICVCN) March 2021 revision (100)
Major components	Introduction, Preamble, Chapters 1–18, Glossary, Summary, Appendices	Preface, Preamble, three Divisions, followed by a Glossary, two Indexes, and seven Appendices	Preface, General Considerations, Principles, Rules with Notes and Recommendations, Advisory Notes, and 13 Appendices	Statement on behalf of the Executive Committee, International Standards, Supplement	Statutory Basis for the ICTV; Principles of Nomenclature, Rules of Classification and Nomenclature
Adjudicating Body	International Commission on Zoological Nomenclature	International Association for Plant Taxonomy (IAPT)	The Judicial Committee of the ICSP	The ISPP-CTPPB	
What taxonomic levels does the code cover	Domain, Kingdom, Phylum, Class, Order, Family, Genus, Species, Subspecies	Kingdom (regnum), Division or Phylum (division or phylum), Class (classis), Order (ordo), Family (familia), Genus (genus), and Species (species).	Domain, Kingdom, Phylum, Class, Order, Family, Genus, Species, Subspecies	Pathovar	Realm, Kingdom, Subkingdom, Phylum, Subphylum, Class, Subclass, Order, Suborder, Family, Subfamily, Genus, Subgenus, Species (15-rank system of classification)
Nomenclatural types	Paratype and/or holotype specimens/gene sequences	Specimens or cultures preserved in metabolically inactive states	Pure cultures of single organisms (type strain for species)	Pure cultures of single organisms (pathotype strain)	Genome sequence
Requirement for depositing types	Specimens must be publicly available in two international collections, which are based in two distinct countries (e.g., USA, Belgium), fixed specimens	Specimens must be metabolically inactive and deposited in one fungarium or herbarium	Pure cultures of single organisms must be publicly available in two international collections, which are based in two distinct countries	Designated living culture and decedents maintained as a living pure culture and deposited in at least one international collection	Genome sequence of the exemplar isolate must be deposited in one of the International Nucleotide Sequence Database Collaboration (INSDC) member databases (GenBank, ENA or DDBJ) and be publicly available
Registry of names	https://zoobank.org/	Mycobank, Fungal Names, Index Fungorum	Approved List of Bacterial Names (78) and International Journal of Systematic and Evolutionary Microbiology (IJSEM) ^b	Comprehensive List of Names and List of Names published since last Comprehensive List, as cited on committee website	ICTV Master Species List (MSL) (https://ictv.global/msl)

(Continued)

Table 1 (Continued)

	International Code of Zoological Nomenclature (Zoological Code)	International Code of Nomenclature for algae, fungi, and plants (Shenzhen Code)	International Code of Nomenclature of Prokaryotes (Prokaryotic Code)	International Standards for Naming Pathogens of Phytopathogenic Bacteria (Standards)	The International Code of Virus Classification and Nomenclature (ICVCN)
Effective publication	To be considered published, a work issued and distributed electronically must have been issued after 2011; state the date of publication in the work itself and be registered in the Official Register of Zoological Nomenclature (ZooBank) (see Article 78.2.4) and contain evidence in the work itself that such registration has occurred	Printed matter: Distribution to the general public or at least to scientific institutions with generally accessible libraries Electronic material: Published on or after 1 January 2012 in Portable Document Format (PDF) in an online publication with an International Standard Serial Number (ISSN) or an International Standard Book Number (ISBN)	Publications that are generally available (do not need to be free) to the scientific community in print or electronic form for the purpose of providing a permanent record	Generally available to the scientific community for the purpose of providing a permanent record	The Official ICTV/MSL is updated every year following the ratification vote on taxonomic proposals submitted a year before. MSL contains the list of all currently approved taxa
Valid publication of names	Appears in ZooBank and follows guidelines in Chapter 6, Articles 23 and 24	Effective publication plus correct designation of holotypes or basionyms and registration of names	Appears in Approved List of Bacterial Names (78) or in IJSEM as a primary manuscript or in the Validation Lists	Correct, legitimate names that are effectively published and considered validly published	Appears in the ICTV/MSL and designated official ICTV publications (e.g., reports)
Protologue requirements	Description of the new species, illustrations, molecular information, and type specimen information, plus details on the etymology and diagnosis of the new species	Everything associated with a name at its valid publication, e.g., description, diagnosis, illustrations, references, synonymy, geographical data, citation of specimens, discussion, and comments	Name clearly stated followed by sp. nov. or comb. nov., etymology of the name or combination, synonyms with authors and dates of publication, basionym indicated, properties of the taxon, clear designation of the type and location of deposit indicated with international culture collection numbers	Name clearly stated followed by pv. nov. or comb. nov., and etymology of the name or combination, properties of the taxon, clear designation of the pathotype and location of deposit indicated with international culture collection numbers	Not applicable
Priority	The valid name of a taxon is the oldest available name applied to it, unless that name has been invalidated or another name is given precedence by any provision of the Code or by any ruling of the Commission	For any taxon from family to genus, inclusive, the correct name is the earliest legitimate one with the same rank, except in cases of limitation of priority by conservation or protection	Based on date of valid publication in Approved Lists on January 1, 1980, or valid publication in IJSEM. Principle 6: Chapter 3, Section 5	Based on established names of Dye et al., (21) followed by the dates of effective publication of correct, legitimate names	Not applicable
Sections of the code dealing with formation of names	Follows guidelines in Chapter 7, Articles 25–29 of the Code	San Juan Chapter F	Section 3: Naming Taxa	Standards 6–8	Section 3: Rules of Classification and Nomenclature

^a Codes of nomenclature are continually updated through various processes, and these will soon no longer be the current version. However, the current versions are usually available on the websites of the governing bodies.

^b The List of Prokaryotic Names with Standing in Nomenclature (22, 63) provides an easy-to-use informal list of validly published names.

or themes presented, virus nomenclature differs from that of the cellular organisms and some of the generalizations do not apply to viruses.

Novel species names are required when one discovers an organism(s) that does not belong to any previously named species (not identifiable). Each code is prescriptive in how names are formed, and although there are some similarities, especially for cellular organisms, readers will need to consult specific codes (**Table 1**) for the exact rules for devising names. Whereas names of taxa above the rank of species are single words, species names are Linnaean binomials. Species names are constructed by a Latinized generic epithet (name), which starts with an upper-case letter, and a specific epithet, which is not capitalized, and species names are followed by a designation of authorship, except in virology. For cellular organisms, new names must clearly be designated as new species or new combinations [e.g., species nova (sp. nov.)] to ensure that new species names and combinations are recognizable as such. In the case of cellular organisms, a nomenclatural type (type), which incorporates the description of the taxon (e.g., type species for a genus or type strain for a bacterial species), must be designated and archived for public accessibility. The type serves as the name-bearing entity for the taxon and is the entity to which the name is permanently associated. Thus, for taxonomic studies, it is critical that researchers include all relevant types. In accordance with the recently adopted principle of sequence-based taxonomy in virology (76), publicly available annotated genome sequences of the exemplar isolate play the role of the type for a given species.

Although stability is an important goal of all codes discussed, the binomial system (species names are binomial consisting of genus name and the specific epithet indicating the species) obligates changes in species names when a type (e.g., strain) from a species is moved to a different genus (13, 15, 83). For example, the transfer of the economically important bacterial wilt pathogen from *Burkholderia* (*Burkholderia solanacearum* Smith 1896) to *Pseudomonas* (as *Pseudomonas solanacearum* Smith 1914) and to *Ralstonia* [*Ralstonia solanacearum* (Smith 1896) Yabuuchi et al. 1996] resulted in new species names (consisting of both the genus name and the specific epithet).

Not all changes in classification require changes in names. For those classifications of cellular organisms that do, the determination of the correct name to be used is based on a valid publication, legitimacy, and priority of publication, in addition to the placement of the type in the new classification. The principle of priority preserves the oldest names, except in virus nomenclature, as described below. Because taxa can have only one correct name in each classification, the principle of priority determines the earliest legitimate name from among those being combined. For example, in fungi, the sexual morph-typified name *Calonectria* De Not. 1867 [type: *Calonectria pyrochroa* (Desm.) Sacc. 1878] and asexual morph-typified name *Cylindrocladium* Morgan 1892 (type: *Cylindrocladium scoparium* Morgan 1892) circumscribe the same group of species. Following the principle of priority, *Calonectria* is the older name and thus should be used for this genus. The genus *Cylindrocladium* is considered a synonym of *Calonectria* (71). An illegitimate name is one that is not published in accordance with the code that governs it and should not be used or considered for determining priority. Valid publication refers to the publication that serves as the citation for priority and official registration or cataloging of the name. The rules for valid publication differ among the codes. For example, in some codes, the effective publication of correct names serves as the valid publication, whereas in other codes, publication in a specific registry after effective publication is valid publication.

Below, we describe the intricacies of each code and select the rules that must be followed to ensure that the names that are published are legitimate. After giving a brief history of the codes and a description of current practices in classification, we guide researchers to the appropriate parts of the codes that must be consulted for publication of names.

Rules:

required practices that operationalize the principles. Rules are the parts of the codes that are regulated

Nomenclatural type (type): the materials to which a taxon name is permanently linked. They vary by rank and code

Type strain: publicly available pure culture of a species or subspecies with which the name is permanently associated

Correct name: the name that must be adopted for a newly circumscribed taxon according to the codes of nomenclature

Valid publication: the publication that sets the date for priority. For most codes, this is the effective publication

Priority: method for determining the correct name of a taxon of cellular organisms, which gives precedence to the earliest legitimate name

Legitimate: published in accordance with the rules of the appropriate code

NEMATODES

The Zoological Code

With an estimated number of species up to 10 million, the Nematoda phylum is one of Earth's most diverse animal groups (65). Plant-parasitic nematodes (PPNs) are important agricultural pests that can cause significant economic losses totaling more than 100 billion dollars worldwide (36). Nematodes are the most abundant animals on Earth, and their naming is mandated by the International Commission on Zoological Nomenclature (ICZN). The ICZN is dedicated to crafting, releasing, and regularly updating the International Code of Zoological Nomenclature (Zoological Code) and was first published in 1961. Since then, three updates to the Zoological Code have been published, with the latest being published in 1999 and in effect starting January 1, 2000 (68). Between 2000 and 2012, several amendments were made to the Zoological Code, particularly expanding the refined publication methods for electronic formats. The Zoological Code provides guidelines for establishing new names and rules for determining the availability and priority of previously proposed names. Principle 6 of this code allows for name amendments and ensures that the name-bearing type of the taxon is identifiable. In cases of nomenclature ambiguity, the ICZN evaluates and adjudicates based on the Zoological Code. Decisions made by the ICZN on specific cases are published in the Bulletin of Zoological Nomenclature.

Classification

Nematode classification has evolved over the centuries with various systems based on morphology, ecology, and molecular data, yet no single method has been widely accepted. Early efforts, such as those by Cobb (19), who used the structure of the buccal cavity, and Schneider (72), who focused on musculature, relied on largely artificial systems that did not account for evolutionary relationships (3). Later, Chitwood's (17) classification introduced distinctions based on the presence of phasmids, which are chemoreceptors on the tail of the Hoplolaimina, later evolving into the Secernentea and Adenophorea classes (3). The quest for a natural classification system gained traction with Lorenzen's (46, 76) cladistic approach, which, despite some limitations, aimed to group nematodes phylogenetically based on morphological similarities, such as metanemes in certain free-living species (3, 32). However, morphological characters alone have proven insufficient for robust phylogeny, as homologous traits are often challenging to identify.

Molecular approaches have advanced nematode systematics significantly, yet many nodes remain unresolved because of limited genomic data and variability in sequence comparability (32). The latest comprehensive classification of the entire Phylum Nematoda was published by Hodda in 2022 (32), following his previous 2007 and 2011 classifications. Integrative taxonomy, combining morphology and molecular data, offers a promising solution for species delimitation, overlapping morphology, and morphometry (29). For example, some of the major groups of nematodes like stunt nematodes are characterized by phenotypic plasticity, which involves the ability of an organism to change its characteristics in response to environmental stimuli. These changes tend to result in physiology, morphology, and behavioral variants of an organism that need to be considered. Nevertheless, the complexity and time investment involved in using integrative taxonomic approaches limit its practical application. As a result, despite many advances, a fully resolved phylogenetic tree for nematodes remains elusive, with alternative classifications potentially representing the evolutionary relationships equally well.

Requirements for Describing a New Nematode Species

As with all organisms, describing a new PPN taxon requires a combination of meticulous specimen collection and preservation, detailed morphological and optional molecular analyses,

comprehensive literature review, and careful preparation of a formal description that follows the Zoological Code (68). Adhering to these requirements ensures that the new taxon is validly published and recognized within the scientific community. Valid publication of a new taxon requires that the publication be effective. An effective publication is issued for the purpose of providing a public and permanent scientific record that is obtainable and durable (68).

To describe a new nematode species, at least one type specimen and a description including detailed morphological characteristics, DNA sequences, illustrations, and other diagnostic features pertaining to the type specimen and the species must be provided. Preserved nematode type specimens should be deposited in at least two internationally recognized collections. For example, the USDA Nematode Collection has one of the largest nematode collections in the world with more than 40,000 permanent slides (28). The Zoological Code allows parts of animals to serve as types. Therefore, according to guidelines, DNA extracted from a specimen and sequenced can serve as type (61, 68); this is because DNA that has not been amplified prior to sequencing is considered part of the animal (68). As outlined in Articles 37.1, 44.1, and 47.1 of the ICZN code, the name-bearing type of a nominal taxon (species) also serves as the name-bearing type for its nominotypical or the subspecies carrying the same epithet name for subspecies and species (68). For example, for the burrowing nematode, the type is the same for *Radopholus similis* (Cobb, 1893) Thorne, 1949 and the subspecies *Radopholus similis* subsp. *similis* (Cobb, 1893) (Thorne, 1949) (Siddiqi, 1986). The Zoological Code also outlines how type status is retained if taxa change rank.

The Zoological Code provides guidelines on naming conventions, such as italicizing and capitalizing the genus name but not capitalizing the specific epithet. Also, a newly published name must be clearly indicated as new, and appropriate Latin abbreviations should be used (e.g., n. sp.). The Zoological Code grants considerable freedom in devising new names, with the main limitation being that the names should not offend (35). Additional guidance on formulating nematode names is given in Chapter 7, Articles 25–29 of the Code.

In addition to the description of the new species, illustrations, molecular information, and type specimen information, the protologue should also include details on the etymology of the name and diagnosis of the new species. The new taxa names should be compact, euphonious, and memorable. The Zoological Code lays out the rules describing species under multiple chapters (the criteria of publication, Chapter 3; criteria of availability, Chapter 4; and formation of names, Chapters 7 and 16). The original description should highlight the morphological diagnostic characters that set apart the new species from closely related described species to aid identification. Additionally, the molecular diagnosis based on multiple markers and the phylogenetic relationship of the new species should be provided.

FUNGI AND OOMYCETES

International Code of Nomenclature for Algae, Fungi, and Plants (Shenzhen Code)

As fungi were originally considered part of the plant kingdom, the rules for fungal nomenclature are inextricable from the history of botanical nomenclature (109). Guidance for the naming of plants (including fungi) was first written and organized in 1867 by A. de Candolle, a Swiss botanist (84). The document that eventually became the Code of Botanical Nomenclature debuted at the International Botanical Congress in Paris in 1867 and by the early 1900s, the code's language changed from French to English (104). Despite some early tension between American and European botanists, a unified International Code of Botanical Nomenclature was presented in 1950 at the Botanical Congress in Stockholm. From 1950 to 2012, major provisions of fungal nomenclature included a variety of statements concerning the valid and legitimate publication

Protologue: formal presentation of names and descriptions as required by codes

Etymology: explanation of origins and development of the name

Recommendations:
explanatory and
supplemental
comments to guide
practice without the
force of the rules

of names referring to different states of fungi with pleomorphic life cycles (88). During that time, only the name associated with the sexual state (ascospore-bearing states for ascomycetes and basidiospore-bearing states for basidiomycetes) was considered the correct name of a fungus. However, the use of names referring to asexual states was a useful concession and necessary given the varied ways in which fungi reproduce and is the reason why major changes to the code occurred in 2012 and 2018 (31).

In 2012, the name was changed from the International Code of Botanical Nomenclature (Vienna Code) to the International Code of Nomenclature for algae, fungi, and plants (Melbourne Code) (30). Until 2012, a Latin diagnosis or description was required to support the valid publication of a new name; however, this requirement was changed to allow for descriptions in either Latin or English. In addition, a unique identifier from a recognized repository (e.g., a MycoBank number) was required as part of the description of a new taxon. Most notably, the correct name applicable to an individual taxon with both asexual and sexual states could be the name of either the asexual state or the sexual state, with one of them having priority based on the first date of publication (66). For example, the sexual state *Guignardia* was described in 1892, whereas the asexual state *Phyllosticta* was described in 1818. Before 2012, the name *Guignardia* would have taken priority as the sexual state name even though it is a later name. Because *Phyllosticta* is the earlier name, it has priority and, after approval by the nomenclatural committee needed for asexual types, it is now the only name that should be used for this taxon (70). Prior to 2018, the article dealing with fungal names, Article 59, was part of Chapter 8 of the Melbourne Code, with other fungal-specific guidance scattered throughout the code. A separate chapter, Chapter F, was introduced in the 2018 Code (Shenzhen Code) (93) and was updated at the eleventh International Mycological Congress in Puerto Rico to become the San Juan Chapter F (51).

The International Code of Nomenclature for algae, fungi, and plants (currently the Shenzhen Code) is the set of rules and recommendations that govern the scientific naming of all organisms traditionally treated as algae, fungi, or plants, whether fossil or nonfossil, including blue-green algae (cyanobacteria), chytrids, oomycetes, slime molds, and photosynthetic protists with their taxonomically related nonphotosynthetic groups (but excluding microsporidia) (93). The current edition is the Shenzhen Code, which embodies the decisions of the Nomenclature Section of the XIX International Botanical Congress, which took place in Shenzhen, China in July 2017. This Shenzhen Code supersedes the Melbourne Code (93) and is updated every six years during an International Botanical Congress; however, nomenclatural amendments dealing with fungi are amended by the Nomenclature Session of the International Mycological Congress, which takes place every 4 years (50). Chapter F is the section of the Shenzhen Code that brings together provisions that deal solely with names of organisms treated as fungi (51). Chapter F was revised and is now the San Juan Chapter F, published on December 27, 2019 (51). It incorporates changes to the previous version of Chapter F that was part of the Shenzhen Code (93) in which a separate Chapter F was first introduced (31).

To actively participate in events related to the governance of fungal nomenclature, individuals, national or international societies, associations, or other groups with mycological interests can become members of the International Mycological Association (IMA) (<https://www.ima-mycology.org>). The IMA with various committees is in charge of the planning and organization of the International Mycological Congress as well as the Fungal Nomenclature Session, which is the forum in which formal proposals to amend Chapter F of the code are considered (51).

Classification

To know whether a set of fungal isolates correspond to a new taxon (i.e., delimit fungal species), researchers are encouraged to be aware of the different species recognition criteria that exist for

fungi and their advantages and disadvantages and to recognize that best practices can be defined only in the context of each fungal group studied and its particular genetic and evolutionary traits (16, 17). Contemporary mycologists usually determine the novelty of a taxon by inferring putative boundaries using phenotypic or phylogenetic data first, then associating those initial characters with diverse biological attributes, such as morphology, ecology, pathology, or geographic distribution; this two-step process circumscribes novel taxa with multiple independent lines of evidence (17). Methods or assays recommended to obtain multiple lines of evidence to support a new taxon include but are not limited to multilocus DNA phylogenetic analyses using multiple phylogenetic inference methods, macro- and micromorphology observations of multiple specimens from multiple collections when possible, isolation of specimens in pure culture when possible, and ecology, biogeography, or description of mating types (4).

Holotypes: individual specimens selected as the best example upon which the description and concept of a species (or type species) is based

Nomenclature

To describe and publish a new taxon according to the rules contained in the Shenzhen Code, a set of formal requirements and best practices for authors have been provided in detail by several publications elsewhere (4, 7, 44, 45, 73, 74, 92). In summary, names of new taxa must follow the San Juan Chapter F of the Shenzhen Code and can be available for use only if they are “effectively,” and “validly” published and are “legitimate” (4). Effectively published names are in accordance with Articles 29–31, which require the name to be published as printed material distributed to at least two publicly accessible libraries or institutions; as of 2012, this can also include PDF format to an online-only publication with an ISSN or ISBN number (93). Valid publication (Articles 32–45) refers to the correct designations of holotypes or basionyms and the registration of names in name databases such as Fungal Names, Index Fungorum, or MycoBank (4, 74). As of 2007, illustrations cannot serve as holotype species, and holotypes must be deposited at only one repository (93). A core rule of validly publishing a new taxon is that the name must be a binomial composed of letters of the Latin alphabet and otherwise comply with Articles 16–27 (92). Lastly, legitimate names are those that follow the rules of Article 6.5, in which for example, a name cannot include homonyms or be based on the same type as a distinct species (93).

Following best taxonomic practices when describing a new taxon helps reduce the likelihood nomenclatural issues will arise in the future. Authors must ensure the chosen name of a taxon has not already been used and that these names are formed by adding a termination (ending) appropriate to the rank of the name (92). Additionally, any new species must be assigned to a genus that is itself validly published (Shenzhen Code, Article 35.1), and any new species that is not assigned to a valid genus inherits the invalid status of that genus. New taxa are also required to have a description, which precisely describes the physical properties of the organism, or a diagnosis, in which it is differentiated from similar species (93). Even though the Shenzhen Code does not require the inclusion of both a diagnosis and a species description, it encourages the inclusion of the two written in English or Latin. Inclusion of images or illustrations for new taxa is strongly encouraged and should include diagnostic morphological features, such as culture characteristics and morphology of sexual and asexual states. A more recent addition to the Shenzhen Code, Article 40.8, specifies that if a holotype is a culture, it must be explicitly stated that it is preserved in a biologically inactive state, such as freezing or lyophilization (4).

Among the elements authors of new taxa are encouraged, although not required, to include are DNA barcode sequences, which must be deposited in public repositories, especially those associated with holotype specimens or ex-type strains. To abide by the Convention on Biological Diversity and Nagoya Protocols agreements, preservation of ex-type cultures is required in at least two publicly accessible culture collections residing in more than one country or continent and deposition of one or more isotypes or paratypes in different herbaria when possible (4, 74).

Orthography: dealing with the construction of names, including spelling, grammar, and Latinization

An abundance of online sources and databases are available for researchers who wish to describe new fungal or oomycete taxa, including extensive guidelines on how to describe new species (4, 74, 92), how to identify fungal species boundaries depending on the kind of data used (16, 49, 85, 86), and which DNA barcodes are most useful for fungal and oomycete species description (8, 47, 99). *IMA Fungus* (<https://imafungus.biomedcentral.org>) is mandated as the journal in which formal proposals relating to the rules on the naming of fungi or protected lists of names are to be published, and it is an excellent resource of information regarding fungal taxonomy and nomenclature.

PROKARYOTES

Prokaryotes are single-celled organisms that lack a nucleus and membrane-bound organelles. There are more than 20,000 named species with more than 1,000 species published each year (87). Among these are more than 300 species of plant-pathogenic bacteria that may, in some genera, be further divided into pathovars (9, 11, 12; C. Bull, M. Fischer-Le Saux, C. Brady, T. Coutinho, B. Dutta, et al. preparation).

The Prokaryotic Code

Bacterial nomenclature has its roots in the International Code of Botanical Nomenclature (41). Subsequent specific codes for bacteria continue to be influenced by the Botanical and Zoological Codes (62). The International Code of Nomenclature of Bacteria (ICNB) was published in 1958 (34) and was revised in 1975 (42) and 1990 (43). Major changes in the 1975 revision include the establishment of the List of Approved Bacterial Names (Approved List) (78). The January 1, 1980, publication date of the Approved List became the official starting date for bacterial nomenclature and the date of priority for names on the list. In 2019, the 2008 revision of the code was published changing the name to The International Code of Nomenclature of Prokaryotes (Prokaryotic Code, 2008 Revision; 62), which was revised in 2022 (59). Although the Prokaryotic Code primarily regulates how names are formed, mechanisms for revisions and adjudication of conflicts by the International Committee on Systematics of Prokaryotes (ICSP, formerly the International Committee on the Systematic Bacteriology) (**Table 1**) are stipulated. Voting members of the ICSP are largely representatives of national microbiological societies belonging to the Bacteriology and Applied Microbiology Division of the International Union of Microbiological Societies. However, experts can publish recommendations in the *International Journal of Systematics and Evolutionary Microbiology* (IJSEM) and participate in public discussions that impact proposed changes (59, 60). The Judicial Commission of the ICSP issues opinions that clarify the Prokaryotic Code in response to Requests for Opinions authored by experts and published in IJSEM. The Judicial Commission recently published a handy how-to guide for writing Requests for Opinions (6).

The Prokaryotic Code provides detailed guidelines on the rules for the formation of new names of species (Section 3, Rule 12), subspecies (Rule 13), and other ranks that must be followed. The Prokaryotic Code provides strict rules on orthography (Section 9), etymology (Rule 6), and the Latinization of names. Other useful guides exist on orthography, etymology, and forming Latin names (90, 91). Names are less likely to be changed through correction if the rules are carefully followed. The Prokaryotic Code provides guidance for forming correct names when new combinations are proposed (Section 7). Name changes may occur when taxa are divided (Rule 40), transferred (Rule 41), combined (Rules 42–44 and 47b), or changed in rank, i.e., elevated or placed in lower taxa (Rules 48, 49, 50), and the Prokaryotic Code provides guidance for each case. Rule 14 provides guidance on infrasubspecific divisions such as pathovars and how

to handle the elevation of a pathovar to species (Rule 14b). Rules related to priority (Section 5, Rule 38) and type strains (Section 4, Rules 18, 37a, 40b, 40c) guide these actions. Although there is no substitute for the code, there are several guides available on the List of Prokaryotic Names with Standing in Nomenclature (LPSN) website (<https://www.bacterio.net/>) (22, 63).

Classification of Prokaryotes

Prokaryotic taxa are circumscribed using a polyphasic approach that shows agreement between a variety of genetic, chemotaxonomic, and phenotypic characters (94). Additionally, diagnostic phenotypes that distinguish newly described species from previous species are required (60) despite pressure to rely solely on sequence analysis for species discrimination and sequences as type material (61, 95). Through the latter half of the twentieth century, species delimitation was based on members of the same species having at least 70% DNA–DNA hybridization values and a difference in melting temperature of less than 5°C (81, 89, 102). Cost-effective sequencing has led to equivalent criteria for species using single genes, multiple genes, and whole genomes, and minimal standards for using genomic data in prokaryotic taxonomy are now available (18, 69). An average nucleotide identity (ANI) of approximately 95–96% provides similar species demarcations as 70% DNA–DNA hybridization, and ANI is now frequently used as the genetic basis for species boundaries (27, 38, 67). Species are unlikely to have members that have less than 97% 16S rDNA identity (82). Although even more rigorous species boundaries of 98.7–99% have been defined (80), data from the 16S rRNA gene are often used to confirm genetically distinct species and not to circumscribe them. Multilocus sequence analyses have been used as the genetic basis for species circumscription, with cutoff values for genetic distances being estimated between established species within a genus prior to using multilocus sequence analysis as a genetic criterion [e.g., multilocus sequence analysis was used in the taxonomic refinement of *Xanthomonas arboricola* (106)]. Regardless of the sequence-based methods used, phenotypic results need to support the proposal, and a species cannot be formally named without providing criteria for distinguishing it from other species in the genus (Recommendation 29) (59). In addition, there are minimum standards established for some genera, types of organisms (e.g., Methanogenic Archaea), and methods (genome sequences), which are available in Appendix 6 of the latest version of the Prokaryotic Code.

Valid Publication of Prokaryotic Names

The following are requirements for valid publication of a new species (59). New legitimate names not in the Approved Lists or new combinations (e.g., transfer of a species from one genus to another such that the species name is a new combination of genus name and specific epithet) are validly published when they are cataloged in IJSEM either as an effective publication or on the IJSEM Validation Lists. The effective or valid publication must include a formal description as a protologue containing a clear proposal of the new species name followed by sp. nov. or comb. nov., the etymology of the name and appropriate synonyms, descriptive and diagnostic characters or reference to publications of accessible data, unambiguous designation of a type strain, and proof of deposition in international collections from two countries for distribution. The LPSN website (Table 1) provides an easily searchable unofficial catalog of valid publications of bacterial names (22, 63).

Candidatus Nomenclature

The category of *Candidatus* is used for uncultivated prokaryotes (55, 56, 58). The category *Candidatus* is currently beyond the scope of the Prokaryotic Code because conventional

descriptions, including distinguishing phenotypes and axenic cultures serving as type cultures, are unavailable. Recommendations for classification and nomenclature of some uncultured plant pathogenic prokaryotes have been made (25). Type strains are usually designated using reference sequences (16S rDNA or other) that must be available for comparisons by researchers. For plant pathogens, descriptions often include plant host, symptoms, and insect vectors. *Candidatus* names are presented in quotation marks with the category *Candidatus* in italics and species names are not italicized (e.g., ‘*Candidatus* Liberibacter americanus’ Teixeira et al. 2005). *Candidatus* nomenclature is currently in flux, as there is a proposal to integrate *Candidatus* names into the Prokaryotic Code (5).

Pathovar Nomenclature

In 1980, the Approved Lists of Bacterial Names excluded many species of recognized plant pathogens. In response, a special purpose nomenclature was codified in the International Standards for Naming Pathovars of Phytopathogenic Bacteria [the Standards (21) and its most recent 2001 revision (105)]. Pathovar designations were created to provide a nomenclature for distinct pathogens within species and ensure continuity with literature prior to 1980. Pathovar nomenclature is regulated by the International Society of Plant Pathology Committee on the Taxonomy of Plant Pathogenic Bacteria (ISPP-CTPPB). To date, this system remains the only method for distinguishing and naming distinct bacterial plant pathogens, and it is tied to the historical record.

The Standards explicitly prescribe that pathovars are circumscribed on the basis of pathogenicity (Standard 5). A pathovar is defined as a “strain or set of strains with the same or similar characteristics, differentiated at the infrasubspecific level from other strains of the same species or subspecies on the basis of distinctive pathogenicity to one or more plant hosts” (21, 105). Thus, a strain or set of strains must first be shown to belong to a given species and then be shown to have a distinct host range from other pathovars in the species or from the type strain of the species if no pathovars were previously designated. Pathovars may be shown to be distinct through natural and artificial host range testing conducted according to the principles of Koch’s postulates (13). Other phenotypes or genetic relatedness may or may not correlate with pathovars within a species.

Pathovar names are formed by the addition of an italicized intrasubspecific epithet to the species name (105), for example, *Pseudomonas amygdali* pv. *loropetali* Harmon et al. 2018. Rules outlined in the Standards for the formation of new and correct names after combining, splitting, transferring, or changing ranks largely follow the Prokaryotic Code after which it was modeled. These processes were reviewed by the ISPP-CTPPB to help demystify the nomenclature of plant-pathogenic bacteria (10). To be validly published, the publication must be effective, the pathovar name must be unambiguously designated and followed by pv. nov. or comb. nov., a nomenclatural type, called the pathotype, must be designated as part of the description and present in at least one registered international strain collection (**Table 1**), and a description for the pathovar that distinguishes it by host range or disease from other pathovars or the type strain of the species must be provided and include the demonstration of Koch’s Postulates. Effective publication serves as valid publication of correct names. The ISPP-CTPPB periodically publishes comprehensive lists or updated lists of names of plant pathogens and indicates which published names are correct and a list of culture collections from which the pathogens are available (**Table 1**).

VIRUSES

Viruses, obligate intracellular parasites infecting all life forms, were originally discovered as filterable agents at the end of the nineteenth century during the study of an important disease

of tobacco in Europe (8, 33, 52). Today, they are universally recognized as the most abundant biological entities on planet Earth and as a source of incredible genetic diversity. Unlike cellular organisms, virus genomes can be of either RNA or DNA in various variants (single- or double-stranded, positive- or negative-sense, linear or circular, segmented or nonsegmented). Viruses are polyphyletic and are not part of the tree of life. These peculiarities make virus taxonomy a uniquely exciting and challenging scientific endeavor that needs a coordinated international effort. The classification of viruses and the naming of taxa are governed by the International Committee on Taxonomy of Viruses (ICTV).

The International Committee on Taxonomy of Viruses and Its Remit

The ICTV is an official committee of the Virology Division of the International Union of Microbiology Societies whose responsibilities are outlined by statutes: (a) to develop and oversee internationally agreed taxonomy for viruses, viroids, and other mobile genetic elements¹ (for the sake of this article, generally termed viruses); (b) to develop international nomenclature for virus taxa; (c) to communicate taxonomic updates to the international virology community; and (d) to maintain an index of accepted names of virus taxa.

The ICTV operates through a large network of committees, subcommittees, and study groups (SGs) (23, 39, 75). The ICTV is currently composed of the Executive Committee (EC), Life Members, National Society Representatives, and Subcommittees with currently more than 120 taxon-specific SGs, usually responsible for family/order level taxonomy (for the organizational chart, see Reference 75). The EC membership is subjected to elections every three years and to statutory limits of service duration.

The International Code of Virus Nomenclature

The first internationally accepted system for virus nomenclature consisted of a set of 12 rules, approved during the foundational meeting of the ICTV in July of 1966 (48). That initial set of guidelines was modified and amended (24, 103) to become the International Code of Virus Classification and Nomenclature (ICVCN) (53). The ICVCN evolved over the past three decades to reflect developments in virus taxonomy (1, 37, 54, 97, 100, 101, 107).

Despite changes and a general tendency to align with other biological taxonomies, some ICVCN rules still conflict with principles widely adopted in other biological taxonomies. For example, the rule of priority in naming taxa is not observed. Furthermore, the rule prohibiting the use of a person's name in virus species nomenclature has only been partially reversed in 2020. Nevertheless, the recent adoption of the 15-rank hierarchy (26) and freeform binomial species nomenclature (100, 108) has made the current virus taxonomy reminiscent of the Linnaean system.

How to Name Viruses and Viral Species

Viruses continue to be named by scientists in the original papers, whereas species nomenclature is under the remit of the ICTV. Therefore, vernacular virus names are not subjected to strict rules on format and length and are not regulated by the ICVCN. They usually include description of the host and symptoms (e.g., tobacco mosaic virus, plum bark necrosis stem pitting-associated virus), geographic origin (e.g., artichoke Italian latent virus, sweet potato leaf curl Sao Paulo virus), or simply consist of the host name with an addition of a letter or number (potato virus Y, mint virus 1).

¹The remit of the ICTV extends beyond viruses to other mobile genetic elements such as viroids, satellites, viriforms, etc. Accordingly, the same rules described here for viruses apply to viroids as well and thus viroids are not discussed separately.

The same type of nomenclature was adopted for viral species when this concept was universally introduced in 1991. The only distinction between virus and species names was in the orthography (see 96, 98).

Recently, the ICTV changed this practice and adopted a freeform version of the binomial system of nomenclature for virus species (100). Accordingly, a virus species name is now composed of two words, written in italics, with the first word (the genus name) capitalized. However, the second word (species epithet or identifier) is in freeform. This allows the species epithet to be devised following the format used in other taxonomies (a Latinized single lowercase word, e.g., *Carlavirus trifolii*) or that may include acronyms instead (a combination of letters and numbers, e.g., *Bromovirus PrV2*). Species names in virology must never be abbreviated (108). Furthermore, the names of all higher taxa are written in italics with a first letter capitalized and ending in rank-specific suffixes. A simple guide on how to correctly devise the Latinized virus species names is available (64). Importantly, the adoption of binomial species nomenclature does not and should not affect the crucial use of English vernacular names or their development by scientists in naming newly discovered viruses.

Virus Classification

Viruses are classified into species based on their comparison with closest known relatives. An informed decision on whether a given virus belongs to an already recognized species or a new species is made by applying species demarcation criteria (SDC) recommended by the appropriate expert ICTV SG. SDC are taxon-specific (usually family level), are periodically revised/updated, and vary greatly across the entire virus taxonomy framework. The criteria traditionally included biological, epidemiological, serological, and/or physico-chemical features, and these can still be useful in specific scenarios (borderline cases). However, the degree of genomic sequence divergence and phylogenetic relationships have become standard for virus classification (76, 77). Therefore, to be classified, a given virus must have a genome sequence that meets certain quality standards (genome coverage, quality of assembly, etc.) and is annotated and deposited in one of the public databases (2). The overarching criterion for any ICTV-recognized taxon is that it must be monophyletic (77). Accordingly, because of their overall polyphyly, currently classified viruses are grouped into seven distinct Realms (two for RNA viruses and five for DNA viruses).

The ICTV has developed standardized procedures (**Figure 1**) for taxonomic changes/updates on an annual basis using specific templates (<https://ictv.global/taxonomy/templates>) for generating taxonomic proposals (taxoprops). Taxoprops can be prepared and submitted by any taxonomy enthusiast. In practice, however, it is mostly done by specific expert SGs. The submitted proposals are subjected to evaluation and a vote for approval by the EC. The proposals with insufficient scientific support are rejected. The taxoprops that are accepted by the EC are further scrutinized in a ratification vote by the full ICTV membership. The ratified changes become part of the official ICTV virus taxonomy and are reported in the ICTV Master Species List.

Official International Committee on Taxonomy of Viruses Publications

The traditional way of disseminating updates in virus classification and nomenclature was done by periodically publishing books called ICTV Reports. Currently, the printed format of these reports has been replaced with a freely accessible online version of live documents (<https://ictv.global/report>) that are being regularly updated by members of numerous ICTV SGs as primary authors and edited by members of the Editorial Board (mostly EC Members). Also, the ICTV has partnerships with *Archives of Virology* (79) and the *Journal of General Virology* (20) for regular publishing of virus taxonomy-related papers in the specialized sections of these journals. Finally, an

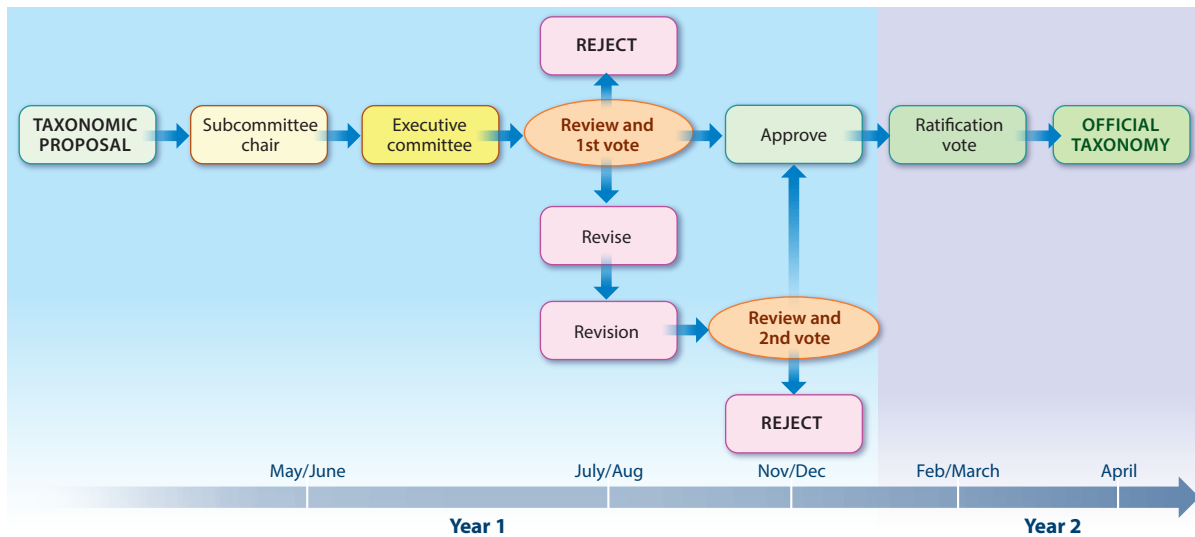


Figure 1

Flowchart of annual taxonomic procedures adopted by the International Committee on Taxonomy of Viruses (CC BY 4.0).

ICTV website (<https://ictv.global/>) is an invaluable reference for virus taxonomists, as it contains, among other information, an official list of all approved species and higher taxa.

CLOSING REMARKS

For the uninitiated, codes of nomenclature can be intimidating in part because, unlike other parts of the scientific endeavor, there are rules applied only to the process of naming. Fortunately, taxonomists and those involved in nomenclatural organizations are, generally, willing to collaborate. Taxonomic experts for specific taxa are the best resources and should be engaged as collaborators. Alternatively, hundreds of taxonomists work as volunteers for organizations that regulate and adjudicate the codes as well as maintain lists of validly published names. Members of these organizations (Table 1) and scientists at international specimen collections that accept and distribute type specimens are experts and are often willing to collaborate. These collaborations would help to prevent some of the numerous nomenclatural errors made in the literature, especially for virus and virus species names. To further ameliorate nomenclature errors in the literature, editorial boards should have members or a team of ad hoc reviewers that include taxonomic experts for the organismal groups for consultation.

DISCLOSURE STATEMENT

C.B. is a member of the Judicial Commission of the International Committee of Systematics of Prokaryotes. T.C. and C.B. are vice-convenor and a member, respectively, of the International Society of Plant Pathology Committee on the Taxonomy of Plant Pathogenic Bacteria. N.A.-S. is a member of the Executive Committee of the International Committee on Taxonomy of Viruses (ICTV), chair of the ICTV Subcommittees on Fungal and Protist Viruses, and member of the ICTV Subcommittee on Plant Viruses. The authors are not aware of any other affiliations, memberships, funding, or financial holdings that might be perceived as affecting the objectivity of this review.

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