

INVITED REVIEW

DEMYSTIFYING THE NOMENCLATURE OF BACTERIAL PLANT PATHOGENS

C.T. Bull¹, S.H. De Boer², T.P. Denny³, G. Firrao⁴, M. Fischer-Le Saux⁵, G.S. Saddler⁶, M. Scortichini⁷, D.E. Stead⁸ and Y. Takikawa⁹¹ USDA/ARS, Salinas, CA, 93905 USA² CFIA, Charlottetown, PE C1A 5T1 Canada³ University of Georgia, Athens, GA 30602, USA⁴ University of Udine, 33100 Udine, Italy⁵ INRA, UMR77 Pathologie Végétale, 49070 Beaucouzé, France⁶ SASA, Edinburgh, EH12 9FJ, UK⁷ CRA, Centro di Ricerca per la Frutticoltura, 00134 Roma, Italy⁸ Central Science Laboratory, Sand Hutton, York, YO41 1LZ, UK⁹ Faculty of Agriculture, Shizuoka University, 836 Ohya, Shizuoka 422-8529, Japan

SUMMARY

A unified approach to naming bacteria ensures accurate communication among scientists, regulators and the public. Rules for nomenclature, set out in the International Code of Nomenclature of Bacteria (ICNB), ensure that proposals for new names and combinations follow a logical and standardized progression that maintains the integrity of the established nomenclature while facilitating changes based on scientific inquiry into relationships among organisms. However, these Rules only apply to ranks at the level of subspecies and above and not to lower taxonomic ranks. The pathovar is one infraspecific rank that is widely used in the classification and nomenclature of plant pathogenic bacteria and is often included in legislation to provide statutory control of bacterial plant pathogens. Thus, phytobacteriologists must rely on two discontinuous but, complimentary systems: the Rules set forth in ICNB for naming down to subspecies level, and the Standards in the International Standards for Naming Pathovars of Plant Pathogenic Bacteria to name pathovars. A framework for determining the priority of names is provided by the Approved Lists of Bacterial Names, which gives genus, species and subspecies names and their corresponding type strains, and subsequent lists of validly published names appearing in the *International Journal of Systematic and Evolutionary Microbiology*. For pathovar names priority is based on the date of valid publication of legitimate names. A list of pathovar names and pathotype strains is maintained by the Committee on the Taxonomy of Plant Pathogenic Bacteria of the International Society of Plant Pathology. To help researchers avoid common pitfalls encountered when developing nomenclature for novel classification systems, this manuscript clarifies several key Rules and

Standards. It aims to promote best practice, in that names developed to conform to the ICNB should also consider precedents set by previous nomenclatural designations as per the International Standards for Naming Pathovars of Plant Pathogenic Bacteria, thus ensuring continuity across the nomenclature of all phytopathogenic bacteria.

Key words: Pathovars, taxonomy, systematics, nomenclature, phytobacteriology, plant pathogenic bacteria, The Code, prokaryotes, approved lists, international standards.

INTRODUCTION

Classification is the discipline of circumscribing groups of similar and, presumably, related organisms and assigning them to *taxa*¹ within a classification scheme. The practice of nomenclature involves assigning unique names to the taxa. The primary purpose of naming organisms is to have a universal means of referring to them (Lapage *et al.*, 1992; Knapp *et al.*, 2004). Additionally, scientific names direct the practitioner to relevant literature for organisms of interest. In the case of phytopathogenic bacteria, scientific names are useful in disseminating information about basic pathogen biology, emerging epidemics, and management options including statutory or quarantine action. Nomenclature and classification in combination with identification comprise the three branches of taxonomy. Although the primary subject of this article is bacterial nomenclature, classification is discussed in relation to its impact on nomenclature and to clarify rules of nomenclature that otherwise may seem confusing.

Corresponding author: C.T. Bull
Fax: +1. 831.755.2814
E-mail: Carolee.Bull@ars.usda.gov

¹ Nomenclatural terms given in italics when first used indicate that a definition of this or a related term is given in Table 1.

Classification is an iterative process based on the scientific method and is not governed by the rules of nomenclature (Sneath and Brenner, 1992; Tindall, 1999). Scientific inquiry may refine and/or change classification schemes to better represent relationships among organisms. The peer review process determines if the methods used and conclusions presented are adequate for publication. However, individual scientists contribute to scientific opinion by using the classification scheme and its associated nomenclature, which in their opinion, most accurately describe the taxa in question.

A universal approach to nomenclature is a prerequisite to ensure accurate communication among scientists, regulators, and the public. Ideally the name of a taxon should be unambiguous such that “all biologists should use the same name for the same taxon, and a name should not designate different taxa, nor a taxon be designated by different names” (de Queiroz and Gauthier, 1994). To this end, bacteriologists use the Rules set forth in the International Code of Nomenclature of Bacteria (Lapage *et al.*, 1992; which in future editions will become the International Code of Nomenclature of Prokaryotes) referred to as ‘*the Code*’ in this text, for naming taxa at the rank of *subspecies* and above. “The Rules are primarily for assessing the *correctness* of the names applied to defined taxa; they also prescribe the procedures for creating and proposing new names” (Lapage *et al.*, 1992). In addition to the Code, the Approved Lists of Bacterial Names (Skerman *et al.*, 1980; referred to as the ‘Approved Lists’) and the Validation Lists published in the *International Journal of Systematic and Evolutionary Microbiology (IJSEM)*, establish the *priority* of names published in accordance with the Code.

However, the naming and classification of plant pathogenic bacteria often necessitates the further differentiation of *species* and subspecies into *pathovars*, a taxonomic rank based specifically on pathogenic characteristics that is not governed by the Code. Consequently, the use of the International Standards for Naming Pathovars of Plant Pathogenic Bacteria (Dye *et al.*, 1980; referred to as ‘the Standards’) is required for naming many plant pathogenic bacteria. The role of the Standards is similar to that of the Code except that the Standards deal specifically with the naming of pathovars of plant pathogens. Similarly, the Lists of Names of Plant Pathogenic Bacteria produced by the International Society for Plant Pathology Committee on the Taxonomy of Plant Pathogenic Bacteria (*ISPP-CTPPB*) chronicle the valid publication of legitimate pathovar names. These lists also catalog all other phytopathogenic bacterial names published in accordance with the Rules of the Code.

Nomenclature is the only element of taxonomy that is conducted according to strictly defined rules and, furthermore, the rules for nomenclature are independent

of scientific opinion about classification. When the rules are applied properly, changes to names of taxa follow a logical progression that maintains as much of the previous nomenclature as possible while allowing for the proposal of new classification schemes based on additional scientific information. Although the Code and the Standards are comprehensive, scientists frequently have difficulty interpreting and applying them to their research (Tindall, 1999; Young, 2000; Knapp *et al.*, 2004). In this manuscript we provide an overview of the major elements of phytobacterial nomenclature. However, the authoritative references on bacterial nomenclature listed in Table 2 should be consulted for a more complete explanation.

THE INTERNATIONAL CODE OF NOMENCLATURE OF BACTERIA

The first definitive version of the International Code of Nomenclature of Bacteria was published in 1958 (Anonymous, 1958), then subsequently revised (Lapage *et al.*, 1975; Lapage *et al.*, 1992) and amended through publication of the minutes of the Judicial Commission of the International Committee on Systematics of Prokaryotes (*ICSP*, formerly the International Committee on the Systematic Bacteriology) in *IJSEM*. These amendments can be found online (<http://www.bacterio.cict.fr/code.html>). Additionally, the history of the Code is available in recent publications (Sneath, 2003; Knapp *et al.*, 2004).

The Code consists of *Principles*, *Rules* and *Recommendations* (Lapage *et al.*, 1992). The Principles are general concepts that form the basis and overall guidance for the Code. The Rules are derived from these Principles and provide the detailed methods for practical application of the Principles in the naming of bacteria. The Rules must be followed when proposing names for bacteria. The Recommendations provide additional guidance, but in contrast to the Rules are not obligatory.

The Code and its amendments are solely concerned with the correct application of names. It stipulates the process for designating names according to a natural hierarchy (class, order, family, genus, species and subspecies). The key function of the Code is to ensure that names are *legitimate*, and *effectively* and *validly published*. The Rules mainly deal with designating and making available name-bearing organisms (type strains), providing a description of the taxon, and publishing unequivocally proposed names in a journal or book that is readily available (*effective publication*). A legitimate name is in accordance with the Rules and only names in accordance with the Code may be validly published (Tindall, 2008). ***The legitimacy or validity of a name does not reflect on the quality of the classification scheme proposed, only on adherence to the Rules for the applica-***

Table 1. Definitions useful to understanding phytobacterial nomenclature.

Circumscribe – to delineate or indicate the limits of a taxon thus, describing which entities belong to or are outside of a given taxon.

Correct – the name of a circumscribed taxon that must be adopted for a new taxon according to the Rules or the Standards.

ISPP-CTPPB - International Society for Plant Pathology Committee on the Taxonomy of Plant Pathogenic Bacteria.

Effectively Published – A proposal that is published in printed source generally available to the scientific community.

Elevate – To move from a lower rank to a higher rank, for example from subspecies to species.

ICSP - International Committee on Systematic of Prokaryotes [formerly the International Committee on Systematic Bacteriology (ICSB)].

IJSEM - International Journal of Systematic and Evolutionary Microbiology [formerly International Journal of Systematic Bacteriology (IJSB)].

Illegitimate – a name that was not published according to the Rules and/or the Standards.

Infrasubspecific – refers to taxa below the rank of subspecies.

Junior Homonym – refers to the name of a taxon which is identical to a name that was previously given to a taxon (senior homonym) of the same rank with a different type.

Legitimate Name – a name published following the Rules and/or the Standards.

Lower - To move from a higher rank to a lower rank, for example from genus to species.

Neopathotype – proposed as the pathotype only when none of the strains that were used in preparing the original description are no longer extant.

Neotype – proposed as a type strain only when none of the strains that were used in preparing the original description are no longer extant.

Nomen Perplexum – A name which causes confusion such as two specific epithets in the same genus that are very similar.

Nomenclatural type – The entity to which the name is permanently associated. The nomenclatural type is a strain for a species of subspecies, a species for a genus, a genus for higher taxa.

Orthography – The system for developing correctly constructed names.

Pathotype – the nomenclatural type or name-bearing strain of a pathovar.

Pathovar – “a strain or set of strains with the same or similar characteristics differentiated at infrasubspecific level from other strain of the same species or subspecies on the basis of distinctive pathogenicity to one or more plant hosts” (Dye *et al.*, 1980).

Pathovarietas Nova – abbreviated pv. nov. and used to unequivocally indicate the proposal of a new pathovar.

Principles – The general concepts of the Code upon which the Rules and Recommendations are derived.

Priority – The method of determining the earliest legitimate name for a taxon which must be used because in a given classification a taxon can only have one correct name.

Recommendation – subsidiary points of clarification to the Rules of the Code, proposing a name contrary to a recommendation would not serve as grounds for rejection of a name.

Rejected Name – a name which must not be used to designate a taxon, listed by the Judicial Commission of the ISCP for various reasons generally related to ambiguity and confusion.

Rules – the instruction laid out in The Code that must be followed in order to develop or apply legitimate names with priority to taxa within novel classifications systems.

Species – The taxonomic group below genus and above subspecies. Species definitions change as a result of the scientific method.

Standards – the instructions laid out in The International Standards for Naming Pathovars of Phytopathogenic Bacteria for naming and delineating plant pathogenic bacteria with diverse pathogenicity.

Subspecies – The lowest official taxonomic ranking in the Code.

Taxon/taxa (pl) – a taxonomic unit describing a circumscribed group of organisms.

The Code – the International Code of Nomenclature of Bacteria (which will become the International Code of Nomenclature of Prokaryotes when the next edition is published).

Validly Published – According to the Code, a proposed name is validly published when the name appears in IJSEM either as an original manuscript proposing the name or through listing on the Validation Lists. The Standards do not have a criterion for valid publication.

Table 2. Essential publications for the nomenclature of plant pathogenic bacteria.**Specific to the naming and recording of subspecies, species and higher taxa.**

The International Code of Nomenclature of Bacteria (Lapage *et al.*, 1992; <http://www.ncbi.nlm.nih.gov/books/bv.fcgi?rid=icnb>).

The Approved Lists of Bacterial Names (Skerman *et al.*, 1980).

Validation Lists published by the International Committee on Systematics of Prokaryotes (ICSP; <http://www.the-icsp.org>) in the International Journal of Systematic and Evolutionary Microbiology (IJSEM; <http://ijs.sgmjournals.org>).

Specific to naming pathovars within species and recording plant pathogenic bacteria.

The International Standards for Naming Pathovars of Phytopathogenic Bacteria (Dye *et al.*, 1980) and its revision (Young *et al.*, 2001a; http://www.isppweb.org/about_tppb.asp).

Lists of Names of Plant Pathogenic Bacteria maintained by the International Society for Plant Pathology Committee on the Taxonomy of Plant Pathogenic Bacteria (ISPP-CTPPB; http://www.isppweb.org/about_tppb.asp).

tion of names outlined in the Code. The Code does not dictate the methods for circumscribing taxa, nor the assays on which descriptions should be based. It does require that each taxon be unambiguously distinguished from other associated taxa (Rule 28a) and recommends that determinative tests be provided in the descriptions (Recommendation 30b).

A. The Approved Lists of Bacterial Names.

The *Index Bergeyana* (Buchanan *et al.*, 1966) indicated the extent to which previously published bacterial names were *illegitimate*, synonyms, or lacked authenticating reference strains. Recognition of the enormity of nomenclatural confusion led to the decision to make a complete revision of bacterial names, embodied in the 1975 revision of the Code (Lapage *et al.*, 1975). Central to the revision was the creation of the Approved Lists of Bacterial Names that included only names that conformed fully to the revised Code (Skerman *et al.*, 1980). These names were effectively published, had a description differentiating the species from other species and at least one strain available to serve as the authentic type strain. Names not on the Approved Lists had “no further standing in nomenclature” (Rule 24a). This reduced the number of named species from ~ 28 000 (Buchanan *et al.*, 1966) to ~ 2000 (Skerman *et al.*, 1980). Adoption of the Approved Lists resulted in numerous names of plant pathogenic species being abolished. These included such names as *Pseudomonas fabae*, a pathogen on broad beans, *Pseudomonas tectonae* on teak, *Pseudomonas gardneri* on tomato and *Pseudomonas adzukicola* on adzuki beans. Furthermore, because there were differences in taxonomic opinion at the time, several bacterial species were included under two different names, i.e., with the same specific epithet but different genus names. For example, strain ATCC

11663 was listed as the type strain for both *Erwinia chrysanthemi* and *Pectobacterium chrysanthemi* (Skerman *et al.*, 1980).

B. Validation and Notification Lists

Valid publication ensures that names developed after publication of the Approved Lists are in accordance with the Code as verified by publication in *IJSEM* (Principle 7 and Rule 27), the official journal of the ICSP (for a review of valid publication, see Tindall *et al.*, 2006). A name can be published in *IJSEM* as an original peer reviewed manuscript. In this case the editors of *IJSEM* ensure adherence to the Rules of the Code. The resulting manuscript serves as the effective and valid publication of legitimate names. Since January 1991, these new names and combinations that were published in *IJSEM* and conform to the Rules, along with important taxonomic opinions published in *IJSEM* (i.e., creation of synonyms and emendation of circumscriptions) have been catalogued for easy reference in Notification Lists regularly published by *IJSEM*.

Alternatively, a name may be effectively published elsewhere, but *IJSEM* must be notified of the publication by the author so that it can be determined if the name was developed in accordance with the Code. Valid publication in *IJSEM* in this case is *via* the ‘Validation Lists’ (Rule 27). **The appearance of a name on the Validation Lists indicates only that the name conforms to the Code.** Scientists have mistakenly thought that the Validation Lists present officially approved classification schemes that must be used (Tindall, 1999). However, “the inclusion of a name on this list is not to be construed as taxonomic acceptance of the taxon to which the name is applied” (Euzéby, 2006).

Each year the Validation Lists serve as an important source of information for phytobacteriologists. For ex-

ample, recent publications listed in the Validation Lists (Euzéby, 2006) included a proposal to reclassify *Enterobacter dissolvens* causing stalk rot of maize, as *Enterobacter cloacae* subsp. *dissolvens* (Hoffmann *et al.*, 2005) initially published in *Systematic and Applied Microbiology*. Publication of this name in the Validation Lists signaled its legitimacy and served as valid publication of the previously effectively published name.

Although not directly related to nomenclature, important taxonomic opinions that do not involve the creation of new names and new combinations (i.e., creation of synonyms and emendation of circumscriptions) previously published outside the *IJSEM* are announced in 'Lists of changes in Taxonomic Opinion' published in *IJSEM*. This list and the Notification Lists, were created as a service to bacteriology and have no official role in regulating nomenclature. A useful, unofficial Website (<http://www.bacterio.cict.fr/>) provides easy access to these lists, associated literature and accession numbers of type strains.

C. The Role of Nomenclatural Types.

As stated above, for a name to be validly published, a *nomenclatural type* must be designated. The nomenclatural type (usually shortened to 'type') refers to "that element of the taxon with which the name is permanently associated" (Rule 15). For a genus, the type is a designated species. For a species or subspecies the type is a designated strain. A type must be designated when a new genus, species or subspecies is proposed. **The sole purpose of a nomenclatural type is to bear the name of the taxon.** To ensure the scientific community's permanent access to this material, pure cultures (Rule 18a) of type strains must be deposited in at least two publicly accessible service collections in different countries (Rules 27 and 30 as modified by the Judicial Commission; De Vos and Trüper, 2000). The preservation and availability of type strains are essential to taxonomic research (Tindall and Garrity, 2008).

The term 'type' is commonly misunderstood to imply that a type is "typical" or represents the "average" characteristics of the taxon (Starr and Heise, 1969; Sneath, 1984; Young, 2000). Type strains are initially chosen to be representative of a species. However, as more isolates are allocated to the species from diverse sources, as taxa are united, or as more characteristics are evaluated, it may be that the nomenclatural type no longer typifies the species as a whole. Nevertheless, once allocated, the type strain remains as the element of the taxon with which the name is permanently associated (Rule 15). During any reclassification the taxon to which the type strain is allocated will retain the name following the Rules of priority (see below). **Thus, all relevant types must always be included in taxonomic studies if nomenclatural proposals are to be made.**

Some strains selected as types for names in the Ap-

proved Lists (Skerman *et al.*, 1980) have subsequently been found to have characteristics inconsistent with the description of the taxon. Because they are living organisms, type strains may mutate to such an extent that they no longer conform in key elements of the published description. Other type strains have become contaminated in culture collections. When a type strain is found to be unrepresentative of the species as described, it can be replaced with an authentic representative of the taxon. Changes to nomenclatural type strains for taxa at the level of subspecies and higher (i.e., designations of *neotype* strains) can only be made by application to the Judicial Commission of the ICSP (Rule 18g). An example of this can be found in the recent Request for an Opinion on *Arthrobacter ilicis*, a pathogen of American holly, in which the designated type was shown to be unrepresentative of the pathogen (Young *et al.*, 2004b).

D. Priority of Publication

The Code gives priority to the oldest validly published names and describes how names are to be assigned (Principle 8; Rule 23). Priority provides a logical, unambiguous way to assign names. The Approved Lists (Skerman *et al.*, 1980) became a new starting point for bacterial nomenclature by designating January 1, 1980 as the earliest date that authority can be assigned to names, except in cases where two names on the Approved Lists compete for priority and in this case priority is determined by the date of the original description. For legitimate names not in the Approved Lists, the order of publication in *IJSEM* either as an original publication or on the Validation Lists determines priority (Rule 27).

Priority is dictated by the Principle that a taxon within a given classification scheme at a given position and rank can have only one name (Principle 8, Rule 23a) and one type. Priority is applied to the generic name and specific or subspecific epithets independently (Rule 23a). For example, the specific epithet remains the same (subject to correction of Latin and gender agreement) upon transfer of a species from one genus to another unless the specific epithet has already been used within the genus (Rule 41a).

Rule 23a must not be misinterpreted to mean "that a particular nomenclatural type can only be assigned one name, and the name to be used is that which has most recently been published" (Tindall, 1999). This rule, in fact, applies only to one particular classification proposal and not to all classification schemes simultaneously. Two or more names may correctly be in use in the literature for the same organism. For example, the type strain and the specific epithet for each of the separately proposed species *Erwinia chrysanthemi* (Skerman *et al.*, 1980), *Pectobacterium chrysanthemi* (Hauben *et al.*, 1998) and *Dickeya chrysanthemi* (Samson *et al.*, 2005)

are identical and these names are validly published binomials within the context of their respective classification schemes. Each practitioner must decide which classification and adherent nomenclature they will use.

In the process of developing a new classification scheme, the data may indicate that two or more type strains for taxa at the same rank (e.g., type strains of two different species) are placed in the same new taxon. The name assigned to this new taxon must be the name associated with the type strain with nomenclatural priority. For example, when Gavini *et al.* (1989) proposed the new genus *Pantoea* gen. nov., one species corresponded to a taxon formerly identified by Beji *et al.* (1988) and included the type strains of *Erwinia herbicola*, *Erwinia milletiae* and *Enterobacter agglomerans*. The specific epithet *agglomerans* had priority as it was ascribed to Beijerinck (1888) and as a consequence the species was named *Pantoea agglomerans*. At the genus level, the species *P. agglomerans*, which bore the oldest epithet effectively published, became the type species of the genus. Likewise, when many of the plant pathogenic coryneform bacterial species were transferred into one species in the new genus *Clavibacter*, the species *Clavibacter michiganensis* became the type species of the genus because the specific epithet *michiganensis* had nomenclatural priority within the newly circumscribed genus. The former type strain of *Corynebacterium michiganensis* was designated the type strain of the new species *Clavibacter michiganensis*, as well as the type strain for the subspecies *C. michiganensis* subsp. *michiganensis* (Davis *et al.*, 1984).

E. Development of New Names and Combinations.

The Code also deals with how to form names. Names are Latin words. Names of taxa above the rank of species are single words (Rule 6), whereas the species name is an italicized binary combination consisting of the genus name followed by a single specific epithet (Rule 12a).

Generic names are substantives (i.e., words functioning as a noun), in singular form and must be capitalized (Rule 10a). The gender of generic names is governed by Rule 65 and must be indicated with the etymology in the description. Specific epithets may be adjectives that agree in gender with the genus name, substantives in apposition (nominative case) or substantives in genitive case (Rule 12c). The Code recommends that the etymology of the name be provided (Recommendation 6(5)). For example the etymology for *Pseudomonas cannabina* is given as can.na'bi.na. L. fem. Adj. *cannabina* pertaining to *Cannabis*, the generic name of the host plant, *Cannabis sativa* L." (Gardan *et al.*, 1999).

Inaccuracy in the Latin rendering does not usually render a proposed name illegitimate. If a name is effectively published outside IJSEM, but is grammatically incorrect, then the *orthographic* error is usually corrected

with valid publication in IJSEM. Orthographic corrections cannot be made after publication in IJSEM except under particular circumstances (Rule 61 as amended; De Vos and Trüper, 2000). However, prior to amending Rule 61 a number of phytopathogenic bacterial names were corrected by Trüper and de' Clari (1997, 1998). For example, *Pantoea ananas* was corrected to *P. ananatis* and *Streptomyces scabies* was corrected to *S. scabiei*. Both of these corrections have been challenged [*P. ananas/anantatis* (Kilian, 2001) and *S. scabies/scabiei* (Lambert *et al.*, 2007)], largely based on the view that the community of bacteriologists was accustomed to using these names and correcting them would only cause confusion. The former challenge was denied by the Judicial Commission of ICSP (Saddler, 2005) and the latter has yet to be decided upon, although the proposal to reinstate *S. scabies* has been recently rebutted by Trüper (2008). Appendix 9 of the Code (see its new edition available online: <http://www.ifmb-a.uni-bonn.de/ICNP-Appendix-9.pdf> or <http://www.bacterio.cict.fr/Appendix-9.pdf>) gives practical advice on how to form correctly spelled Latinized words (requirement of Rule 57a). A list of Latin experts and tips are available to assist authors in the Latinization of scientific names (Trüper, 1996, 2007).

A new name may be formed from any source and may even be composed arbitrarily (Rules 10a, 12c). It is recommended that names be reasonably short and easy to pronounce (Recommendation 6). Names may be derived from geographic regions, such as the site from which the bacterium was first isolated. Alternatively, names may be chosen to recognize individual bacteriologists or pathologists, but names honoring individuals quite unconnected with bacteriology are discouraged (Recommendations 6, 10a, 12c). For example, a novel species of *Agrobacterium* from *Ficus benjamina* was proposed and named *Agrobacterium larrymoorei* (of Larry Moore) to honor the "renowned plant pathologist who spent his career studying the genus *Agrobacterium*" (Bouzar and Jones, 2001).

Although the Code recommends that authors choose epithets that give some indication of a property or source of the species (Recommendation 12c), **the name of a taxon does not describe characteristics that are necessarily universal to the taxon.** The name is solely a means of referring to the taxon and does not impart any real information about the taxon. For example, *Xanthomonas arboricola* was originally described for organisms isolated from trees (Vauterin *et al.*, 1995), but trees are not among the hosts of the strawberry leaf spot pathogen, *Xanthomonas arboricola* pv. *fragariae* (Janse *et al.*, 2001). More explanation regarding this commonly misunderstood recommendation and why the names of taxa are not descriptive is available in several detailed reviews (Starr and Heise, 1969; Sneath, 1984; Young, 2000).

Selected names must not have been rejected previ-

ously for specific reasons (Rule 56a; see Euzéby, 2005). For example, the genus name *Rhizomonas* is listed as a “rejected name of genera and subgenera of bacteria” (*nomina generum et subgenerum bacteriorum rejicienda*) because this genus name had earlier been assigned to a taxon of protozoa (*Rhizomonas* Kent 1880). According to Rule 51b, *junior homonyms* of a taxon of bacteria, fungi, algae, protozoa, or viruses are illegitimate. Thus, the proposal to use *Rhizomonas* as the genus name for the pathogen causing corky root of lettuce (*Rhizomonas suberifaciens*; Van Bruggen *et al.*, 1990) violated the Code. This bacterium has since been assigned to the genus *Sphingomonas* as *Sphingomonas suberifaciens* (Yabuuchi *et al.*, 1999). The nomenclature of this taxon is further complicated because the Code does not “clarify whether a species or subspecies epithet may be validly published if, at the time they were created, the genus name and resulting combination are not validly published” (Tindall, 2008). This has significant implications for the date of priority and attribution of the specific epithet.

To distinguish a formal proposal of a new name from a mere suggestion and to help the reader understand the history of the name being proposed, abbreviated indicators are added to the name upon first publication and are often included in the title of the manuscript proposing the name (Rule 33a). A new genus or species is indicated by following the new name with the abbreviations ‘gen. nov.’ or ‘sp. nov.’ for *genus novum* or *species nova*, respectively (e.g., *Agrobacterium larrymoorei* sp. nov.). Further, note that the formal proposal to place certain strains of *Erwinia carotovora* into a subspecies, *wasabiae*, was published with the indicator ‘subsp. nov.’ (Goto and Matsumoto, 1987) while, in contrast, another subset of *E. carotovora* strains was published as *E. carotovora* subsp. *brasiliensis* without the indicator (Duarte *et al.*, 2004), signifying that the later was a mere suggestion rather than a formal proposal.

Reclassification may result in the transfer of a species from one genus to another. Because the specific epithet would normally be maintained, the resulting name would be a combination of the new genus name and the former specific epithet. Such names are proposed as ‘comb. nov.’ (*combinatio nova*; Rules 33a, 34a). Thus, when *Pectobacterium chrysanthemi* and *Brenneria paradisiaca* were, respectively, renamed *Dickeya chrysanthemi* and *Dickeya paradisiaca* the requirement for the indicator comb. nov. was applicable upon first publication (Samson *et al.*, 2005). Reclassification also may result in alteration of distinguishing characters that should be indicated by the abbreviation ‘emend.’ for *emendavit* [Rule 35; e.g., *Xanthomonas campestris* (Approved Lists, 1980) emend. Vauterin *et al.*, 1995].

THE NEED FOR AN *INFRASUBSPECIFIC* SUBDIVISION FOR PLANT PATHOGENS

When the Approved Lists were adopted many of the named species of bacterial plant pathogens did not conform to the revised Code. Often, pathogens causing distinctive diseases could not be differentiated by phenotypic tests, and differences in pathogenic reactions were not considered adequate criteria for circumscribing species. Consequently, many plant pathogenic bacterial species were not included in the Approved Lists. According to the Code, the specific epithets from these species would thereafter be available for reuse to name new taxa. The loss of species designations for recognized plant pathogens and subsequent potential reuse of these names for different taxa, threatened to result in unnecessary confusion and loss of the knowledge previously published about these pathogens. The ISPP-CTPPB was formed in 1978 essentially to meet this challenge (see the ISPP-CTPPB website for information about the history of this committee, http://www.ispp-web.org/about_tppb_history.asp).

The ISPP-CTPPB petitioned to have species names for plant pathogens maintained due to their importance to the science and practice of phytobacteriology and agriculture, but the request to the ICSP was denied (Dye *et al.*, 1980). Therefore, to ensure that the plant pathogenic species published prior to 1980 remained recognizable, the ISPP-CTPPB adopted the infrasub-specific category *pathovar* to distinguish organisms of the same species that have different host ranges or cause different diseases (symptoms) on the same host (Young *et al.*, 1978). A special purpose nomenclature codified in ‘The International Standards for Naming Pathovars of Phytopathogenic Bacteria’ (described below; Dye *et al.*, 1980) was developed and published to coincide with the publication of the Approved Lists.

THE INTERNATIONAL STANDARDS FOR NAMING PATHOVARS OF PHYTOPATHOGENIC BACTERIA

The Standards are an internationally recognized code of nomenclature written to maintain nomenclatural continuity for established plant pathogen species that were consolidated upon publication of the Approved Lists (Dye *et al.*, 1980). The immediate intention of writing the Standards was to maintain a connection to the pre-1980 nomenclature *via* the use of pathovar epithets that were identical to the former specific epithets. For example, 41 nomenclatures in the genus *Pseudomonas* were consolidated into *P. syringae*. Pathovar epithets were derived from specific epithets of species not included on the Approved Lists (e.g., *P. syringae* pv. *maculicola* from *P. maculicola* and *P. syringae* pv. *morsprunorum* from *P. morsprunorum*). The Standards define a pathovar 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." The pathovar system has helped to maintain coherent order and differentiation of bacterial plant pathogens since 1980.

It was anticipated that future investigations would result in proposals in which some pathovars would be elevated to species (Dye *et al.*, 1980). Although the Code indicates that names not on the Approved Lists have no further standing and are available for reuse, one goal of the Standards was to ensure that the specific epithets be reserved for species that include the pathogens associated with the original name. Dye *et al.* (1980) exhorted researchers not to reuse names of phytopathogenic bacteria not on the Approved Lists for unrelated taxa on the grounds that the name would be a *nomen perplexum*. Although there are a few examples in which researchers have disregarded the intent, the majority of workers have used the recommendations in the Standards for phyto-bacterial taxonomy.

The Standards were adapted to the Code in a manner that allows both the Standards and the Code to be applied without conflict. The principal requirements from the Code for legitimate names (discussed above) are essentially the same for pathovars. Briefly, these include effective publication (Standard 15) with an unambiguous proposal for naming a new pathovar (Standard 18), including the addition of the abbreviation 'pv. nov.' for *pathovarietas nova* after the proposed name (Standard 19). A complete description of a new pathovar based on the characteristics of a pure culture of a designated *pathotype* strain is required (Standards 9 and 17). The Standards also closely follow the Code with regard to the conditions that make the publication of a new pathovar name *invalid*, and to the development and orthography of names. Although submission of the pathotype to one permanent readily accessible culture collection is required, the ISPP-CTPPB suggests that researchers follow the suggestion of the Code and submit new pathotype strains to at least two different international collections located in two different countries to ensure stability and access. Authors can propose *neopathotypes* for pathovars if the strain upon which the original description was based cannot be located (Standard 9(4)). However, if the original pathotype or neopathotype has become unsuitable due to changes in its characters, researchers must notify the ISPP-CTPPB to consider replacement (Standard 11).

Priority is assigned by the Standards in a manner very similar to the Code. January 1, 1980 represents the date for which priority is assigned to the pathovar names listed with the Standards (Dye *et al.*, 1980). The pathovar names included in the List of Pathovar Names published with the Standards (Dye *et al.*, 1980) are

treated as though they had been validly published for the first time on that date. Only if two pathovar names on the List of Pathovar Names are competing for priority will the publication of the previous nomen-species be evaluated.

However, the Code and the Standards differ on how priority is assigned for names published after January 1, 1980. For taxa at the level of subspecies and higher, priority is based on the date of publication of legitimate names in *IJSEM*. In contrast, no journal is specified for valid publication of pathovar names. Priority for pathovar names published after January 1, 1980 is therefore determined according to the date of effective publication of legitimate pathovar names.

The Standards differ most significantly from the Code in that the Standards are a special purpose nomenclature for taxa explicitly delineated by differences in pathogenicity (Standard 5), whereas, the Code is applicable regardless of the methods of classification used to delineate taxa. The requirement that pathovars be delineated by differences in pathogenicity, coupled to the recommendation that epithets give some indication of pathogenicity of the pathovar (Standard 8(4)), may lead to the misconception that pathovar epithets are descriptive. This misconception has been compounded by the use of pathovar epithets reflecting the host from which the pathogen was first isolated (e.g., *citri*, *phaseolicola*, *persicae*), falsely suggesting host specificity. Pathogens can have wide host ranges but be named after a specific host. For example, *Pseudomonas syringae* pv. *syringae* (referring to lilac, *Syringa vulgaris*) includes strains that cause diseases on a variety of different hosts. Pathovar epithets, like other scientific epithets, are only names and should not be construed to be descriptions shared by all members of the taxon or to indicate host specificity (Young, 2000).

LISTS OF NAMES OF PLANT PATHOGENIC BACTERIA

The ISPP-CTPPB has periodically developed lists of names of plant pathogenic bacteria as a centralized resource for legitimately published names of bacterial plant pathogens. The first list was an appendix to the Standards and only contained the names of organisms for which pathovar names and pathotype or neopathotype strains needed to be assigned (Dye *et al.*, 1980). Names of plant pathogenic species in the Approved Lists were not included in the ISPP-CTPPB list. These two documents together contained the names of all bacterial plant pathogens validly published as of 1980. Since then, the ISPP-CTPPB periodically publishes lists of recently published legitimate names (Young *et al.*, 1991; 2004a) and up-dates an annotated comprehensive list of names of plant pathogenic bacteria (Table 3;

Table 3. Lists of names of plant pathogenic bacteria.

The International Standards for Naming Pathovars of Phytopathogenic Bacteria (Dye *et al.*, 1980) includes the standards for nomenclature and the first list of Pathovars and Pathotype or Neopathotype strains. This and The Approved Lists of Bacterial Names (Skerman *et al.*, 1980) represent all of the names available for plant pathogenic bacteria in 1980.

Nomenclatural revisions of plant pathogenic bacteria and list of names 1980-1988 (Young *et al.*, 1991) represents the new names that had been proposed since 1980.

Names of plant pathogenic bacteria 1864-1995 (Young *et al.*, 1996) is a the first comprehensive list of names published by the ISPP-CTPPB in which all the names proposed for plant pathogenic bacteria were presented in one location. This was originally published in the Review of Plant Pathology and in 2000 was placed on the ISPP website. http://www.isppweb.org/names_bacterial_revised.asp

Names of Plant Pathogenic Bacteria Published Since 1995 (Young *et al.*, 2004a; http://www.isppweb.org/names_bacterial.asp) is a list of names published from 1995 to March 2004. It is only published online and includes all names from the list that were published during this period.

Names of Plant Pathogenic Bacteria, 1864-2006 (Bull *et al.*, 2008; http://www.isppweb.org/about_tppb.asp).

Young *et al.*, 1996; Bull *et al.*, 2008) that conform to the Standards and also, for completeness, those that conform to the Code.

Each list provides a comprehensive introduction describing its contents and providing directions on its use. Note that the names from the most recent proposals are listed in bold only to allow the reader to recognize newly proposed names (Table 4). ***The bold formatting does not indicate a preference by the committee for the newer nomenclature over the former. The Standards and the lists only evaluate the process of naming organisms and not the classification schemes that necessitate the new names.*** The ISPP-CTPPB requests that authors send a copy of the publication to the convener and complete the web-based notification system present on the ISPP-CTPPB webpage (Submit a New Name; http://www.isppweb.org/about_tppb.asp) to facilitate inclusion of recently published names in the lists.

CANDIDATUS NOMENCLATURE

Phytoplasmas and a few other phloem-restricted bacteria represent a special case in nomenclature. Because they cannot be cultivated, researchers are unable to provide conventional descriptions or to preserve type strains in axenic cultures in accordance with the Code. Nevertheless, the recent accumulation of information on the diversity and properties of these bacteria has created a need to unambiguously refer to them.

The category of *Candidatus* was introduced to provide a means for “describing procaryotic entities for which more than a mere sequence is available but for which characteristics required for description according

to the Code are lacking” (Murray and Schleifer, 1994; Murray and Stackebrandt, 1995). Delineation of an individual *Candidatus* relies heavily on sequence data and uses ecological and metabolic information when available. With reference to the phytoplasmas, the PCR amplified 16S rRNA gene sequences (basis of the present classification), the plant host(s), the insect vector(s) and other molecular data are usually included in the descriptions. To date, around 30 ‘*Candidatus* Phytoplasma’ species have been created (Firrao *et al.*, 2005).

The designation *Candidatus* is a category or status, not a taxonomic rank, and is not recognized by the Code. The names are not italicized because they contravene the Code. The names are preceded by the word *Candidatus* (italicized) and the entire designation is written between quotation marks (e.g., “*Candidatus* Phytoplasma asteris”). Type strains are not designed (long time preservation of strains can be challenging or impossible) although the identification of ‘reference strains’ (as infected plants or DNA samples) to be made available for comparative purposes is encouraged. Other examples of plant pathogenic *Candidatus* include “*Candidatus* Phlomobacter fragariae” within the *Gammaproteobacteria* (Zreik *et al.*, 1998) and “*Candidatus* Liberibacter spp.” within the *Alphaproteobacteria* (Jagoueix *et al.*, 1994).

CLASSIFICATIONS THAT REQUIRE NAME CHANGES

Although proposals for new taxa can arise from the discovery of new organisms, revisions of taxa are almost invariably the result of planned studies to clarify bacter-

Table 4. How to use the comprehensive lists of names of plant pathogenic bacteria (Bull *et al.*, 2008; Young *et al.*, 1996; 2004).

Scientists should carefully read the introduction to each list for complete explanations on how to use the lists.

The comprehensive lists contain the names of all plant pathogenic bacteria that have been legitimately, effectively and validly published according to the Code or legitimately and effectively published in accordance with the Standards (Dye *et al.*, 1980) and their revision (Young *et al.*, 1991a). Included are species names from the Approved Lists (Skerman *et al.*, 1980), pathovar names listed by Dye *et al.* (1980), and names of pathogens reported since 1980.

For some taxa there are several valid synonyms. Unless otherwise stated, the most recent name is used as the reference name (*in bold italic*) to which all other synonyms are referred. This does not mean that the reference name is always the preferred name.

Alternative valid names are listed in italic and are cross-referenced to their reference names; synonyms under a reference name are preceded by '='.

In order to avoid confusion, care must be taken to avoid using a range of valid names for the same taxon/taxa in the same publication without explanation and compelling reasons.

ial taxonomy. Revisions of taxa are usually proposed on the basis of new methods and forms of analysis available at the time. This research requires the inclusion of all relevant type strains. Unfortunately, many studies using new methods to evaluate genetic diversity among pathogen populations do not include type strains and thus, the nomenclatural implications of the research remains theoretical (Vinatzer and Bull, 2009).

Among the most complicated situations are cases in which pathovars whose names were derived from previous nomenclatures are subsequently elevated to species. Although the Rules and Standards concerning priority are applied independently to genus names and to species, subspecies, and pathovar epithets, renaming an organism may be complicated, because names of plant pathogenic bacteria can consist of ternary (e.g., *Pseudomonas syringae* pv. *tomato*) or quaternary combinations (e.g., *Pseudomonas syringae* subsp. *savastanoi* pv. *nerii*).

A. Union of Taxa

When a classification scheme requires that two taxa of equal rank be united, the two type strains from the original taxa will be in the new taxon. However, within a given proposed classification scheme, a taxon can only have one correct name (Rule 23a) and one type strain. The type strain whose name has priority remains the type strain for the new taxon even if the strain with priority is less representative of the new taxon than the other type strain(s). For example, Willems *et al.* (1992) proposed that *Pseudomonas avenae*, *Pseudomonas rubrilineans*, *Pseudomonas cattleyae* and *Pseudomonas pseudoalcaligenes* subsp. *citrulli* be transferred to the genus *Acidovorax* and united into a single species. The name of the new species became *Acidovorax avenae*, be-

cause among the species that were united the specific epithet *avenae* had nomenclatural priority and the type strain for *Pseudomonas avenae* Manns 1909 was designated the type strain for this new species.

B. Division and Transfer of Taxa

Taxa shown to be represented by two or more distinct populations may merit reclassification into two or more taxa of the same rank. At the species rank, formal revision will place the type strain in one species, which will take the name of the type (Rules 40b,c). The other population(s) will be recognized as novel species, with novel specific epithets and type strains. (e.g., *P. mediterranea* was proposed as a novel species from among *P. corrugata* strains; Catara *et al.*, 2002). The same process occurs when strains within a pathovar are shown to be heterogeneous and are different in host range and/or symptoms; they may remain in the same species but should be discriminated as separate pathovars (e.g., *P. syringae* pv. *coryli* was proposed as a novel pathovar from among *P. syringae* pv. *syringae* strains; Scortichini *et al.*, 2005).

It may not be obvious that division and transfer of taxa are the same nomenclatural process, but in both cases a previously described taxon is found to be heterogeneous and consists of two or more distinguishable groups. The difference between a division and a transfer is that in a division of taxa a new taxon is delineated in the process, while in a transfer of taxa organisms are moved to an already delineated taxon.

C. Changes in Rank - Lowering of Taxa

A taxon may be *lowered* in rank, as when two species are amalgamated, but are recognized as representing

distinct lineages (Rule 50b). The specific epithet of the lineage without priority is used as the subspecific epithet for that lineage. For example, *Enterobacter dissolvens* and *Enterobacter cloacae* were found to be in the same DNA-DNA hybridization group but formed two distinct lineages that were phenotypically distinguishable (Brenner *et al.*, 1986; Lindh and Ursing, 1991; Hoffmann and Roggenkamp, 2003; Hoffmann *et al.*, 2005; Grimont and Grimont, 2006). Thus, *E. dissolvens* was not merely melded into the *E. cloacae* species but was lowered in rank. Because *E. cloacae* had nomenclatural priority, *Enterobacter dissolvens* became *E. cloacae* subsp. *dissolvens*. The type strain for the new subspecies *E. cloacae* subsp. *dissolvens* is the same as that of *E. dissolvens* (ATCC 23373; NCPPB 1850), while the type strain for *E. cloacae* remains unchanged (ATCC 13047) and is shared by the subspecies having the same subspecific epithet, *E. cloacae* subsp. *cloacae*.

D. Changes in Rank - Elevation of Taxa

The subspecific epithet must be used as the specific epithet when a subspecies is elevated in rank to a species unless the resulting combination is illegitimate (Rules 50a, 51a). For example, the subspecific epithet *betavasculorum* became the specific epithet for *Pectobacterium betavasculorum* when *Pectobacterium carotovorum* subsp. *betavasculorum* was proposed as a separate species in the genus *Pectobacterium* (Gardan *et al.*, 2003). Because pathovar refers to a taxon below subspecies (Rule 5d), it follows that pathovar epithets would also be required to be used as the specific or subspecific epithets when pathovars are elevated. Although the Code allows former species names (maintained as pathovar epithets) to be elevated after additional taxonomic work (Rule 14b), this is, unfortunately, not required. Regardless of whether the species names are composed from pathovar epithets, the species names for elevated pathovars must be proposed as new names (*nomina nova*), in conformity with Rule 27 of the Code. Importantly, the date and authorship of the publication elevating the pathovar to a species or subspecies is used in considering priority of the epithet. For example, priority is assigned to the species epithet *tremae* based on the publication proposing the species name *P. tremae* (Gardan *et al.*, 1999) rather than its proposal as the pathovar epithet in *P. syringae* pv. *tremae* (Ogimi *et al.*, 1988).

COORDINATION BETWEEN THE STANDARDS AND THE CODE

While plant pathologists work to preserve the continuity of names published prior to 1980 for taxa causing distinct diseases on plants, the Code clearly indicates that the names not included in the Approved Lists are “available for reuse in the naming of new taxa” (Rule 24a), regardless of whether the new taxa being named

are related to the taxa to which they were previously assigned (Rule 28a). For example, according to the Code the species name, *Xanthomonas citri*, could be used without consideration of the status of the pathovar name and pathogenic characteristics of the organism with this name prior to 1980 (Gabriel *et al.*, 1989). Notwithstanding Rules 24a and 28a of the Code, to maintain an unambiguous nomenclature, the purpose of the Standards is to preserve the former nomenclature epithets as pathovar epithets for eventual reuse when additional research establishes an authentic species for that group of pathogens (Dye *et al.*, 1980). Reuse of specific epithets (maintained as pathovar epithets) for unrelated taxa and type strains runs counter to the goals of a coherent nomenclature.

Although the Code does not regulate infrasubspecific taxa, it does ‘encourage conformity’ in the application of these designations (Appendix 10). Additionally the Code states, “The reuse of a particular name cannot be recommended if such reuse is likely to result in confusion due to previous or continuing use of the name as a synonym, strain designation, or for other reasons” (Rule 24a). ***For continuity and clarity, the pathovar epithet should be used as the specific of subspecific epithet when pathovars are elevated to species or subspecies level unless it is illegitimate by rules of the Code, e.g., the epithet has been used previously in the genus.*** Neither the Rules nor the Standards mandate this, but authors should carefully consider the confusion likely to occur if a specific epithet in common use prior to 1980 is proposed for a bacterium with different pathogenic properties.

A complicating factor in maintaining nomenclatural continuity of plant pathogens and avoiding confusion in future classification, involves the selection of type strains. For example, when Gabriel *et al.* (1989) proposed *X. citri*, they chose a type strain other than that of *X. campestris* pv. *citri*, a decision supported by Schaad *et al.* (2005) in their emended description of the species. According to the Code this is acceptable, because the species was being newly proposed and validated. However, this resulted in a disjunction between pathovar and higher nomenclature, with two names (*X. citri* and *X. campestris* pv. *citri*) based on two different type strains for the same pathogen. Likewise, when Vauterin *et al.* (1995) combined several pathovars in *X. arboricola*, they could have chosen any strain within the circumscribed species as the type strain, because no previously designated type strains were allocated to this taxon. Had they done so, then this new species name would have been independent in nomenclature from the individual pathovars that comprise the species. Instead, they chose as type strain, the pathotype strain of pv. *juglandis* (probably because this pathovar was the earliest proposed name). The result in this case is that a taxon (*X. campestris* pv. *juglandis*) gave its pathotype strain (i.e., name bearing strain) without giving its name

to the new species *X. arboricola*. In these examples, if the authors had followed the intent of the Standards, the pathotype strain of *X. campestris* pv. *citri* would have been used as the type strain of the newly proposed *X. citri* and the epithet *juglandis* would have been used in forming the species name for which the pathotype of *X. campestris* pv. *juglandis* was designated as the type (i.e., *X. arboricola* would have been named *X. juglandis*).

These examples highlight the lack of connection that can occur between the higher nomenclature and pathovar nomenclature. The maintenance of a coherent and functional classification and nomenclatural scheme for plant pathogenic bacteria remains in the hands of users. Bacterial taxonomists should use the Standards in coordination with the Code to preserve the specific epithets of former nomenspecies (preserved as pathovar epithets) for their future elevation as species to avoid confusion and maintain continuity in the nomenclature of bacterial plant pathogens.

CONCLUSION: WHAT NAME SHOULD I USE?

Although the Code and the Standards govern the correct application and publication of names, there is no authority governing which classification and adherent nomenclature should be used. Peer review panels for scientific journals evaluate the scientific rigor of the methods and data used to formulate new classifications prior to publication. Researchers can choose among any of the validly published legitimate names that correspond to a particular bacterium. In choosing a name, researchers pass judgment on the classification schemes available. Thus, support for a classification scheme is expressed directly through the use of the nomenclature associated with a particular classification.

Sometimes, a lack of consensus about which classification (former or new) is most appropriate can lead to two or more legitimate names being used in the literature for the same organism. The reclassification of *Agrobacterium* spp. into *Rhizobium* is a case in point (Young *et al.*, 2001b). The authors proposed that strains of *Agrobacterium* spp. and *Rhizobium* spp. should be included in a single genus for which the name *Rhizobium* had priority. There is little use, as yet, made of the new nomenclature. This is probably because *Agrobacterium tumefaciens* is a familiar name in many disciplines, in addition to a lack of agreement with the newly proposed classification (Farrand *et al.*, 2003). In contrast, there is reasonably good acceptance of most if not all the new genera derived from *Erwinia* (Gardan *et al.*, 2003; Samson *et al.*, 2005). Unfortunately there is no easy rule to help decide which valid name to use. **Individual authors must critically examine the taxonomic literature to decide which classification is most appropriate and suitable for their needs.**

ACKNOWLEDGEMENTS

Special thanks to Drs. D. Gent, B. Vinatzer, and E. Roskopf for their comments on the manuscript.

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Received September 15, 2008

Accepted September 29, 2008

