BERGEY'S MANUAL® OF Systematic Bacteriology

Second Edition

Volume Three **The Firmicutes**

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Systematic Bacteriology

Second Edition

Volume Three
The Firmicutes

Paul De Vos, George M. Garrity, Dorothy Jones, Noel R. Krieg, Wolfgang Ludwig, Fred A. Rainey, Karl-Heinz Schleifer and William B. Whitman

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This volume is dedicated to our colleagues

James T. Staley and George M. Garrity,

who retired from the Board of Trustees of Bergey's Manual Trust

during preparation of this volume.

We deeply appreciate their efforts as editors, authors and officers of the Trust.

They have devoted many years to helping

the Trust meet its objectives.

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Preface to Volume Three of the Second Edition of Bergey's Manual® of Systematic Bacteriology

A number of important changes occurred at Bergey's Manual Trust during the preparation of this volume. In 2006, George Garrity retired from the Trust, and the Trust moved its offices from Michigan State University to the University of Georgia. We are deeply indebted to Professor Garrity, under whose supervision much of this volume was prepared. James T. Staley's wise council guided this transition until he retired from the Trust in 2008 after 32 years of service.

The officers of the Trust have also changed during this time. Barny Whitman became Treasurer and Director of the Editorial Office in 2006. Michael Goodfellow succeeded Professor Staley as Chair in 2008 and Peter Kämpfer succeeded Professor Goodfellow as Vice-Chair in 2008. The Trust was also fortunate to acquire the services of Dr Aidan Parte as Managing Editor in 2007.

Much as things have changed, prokaryotic systematics has remained a vibrant and exciting field of study, one of challenges and opportunities, great discoveries and gradual advances. To honor the leaders of our field, the Trust presented the Bergey Award in recognition of outstanding contributions to the taxonomy of prokaryotes to Jean Paul Euzéby (2005), David P. Labeda (2006), and Jürgen Wiegel (2008). In recognition of life-long contributions to the field of prokaryotic systematics, the Bergey Medal was presented to Richard W. Castenholz (2005), Kazau Komagata (2005), Klaus P. Schaal (2006), Fergus Priest (2008), and James T. Staley (2008).

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The Trust recognizes its enormous debt to Dr Aidan Parte, whose enthusiasm and professionalism have made this work possible. His expertise and good judgment have been extremely valued.

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We also thank the Department of Microbiology at Michigan State University and especially Connie Williams, for her assistance in bring this volume to completion, and Walter Esselman, the Chair of the Department of Microbiology and Molecular Genetics, who facilitated our move to the University of Georgia. We thank our current copyeditors, proofreaders and other staff, including Susan Andrews, Joanne Auger, Frances Brenner, Robert Gutman, Judy Leventhal, Linda Sanders and Travis Dean, whose hard work and attention to detail have made this volume possible. Lastly, we thank the Department of Microbiology at the University of Georgia for its assistance and encouragement in thousands of ways.

William B. (Barny) Whitman

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On using the Manual

NOEL R. KRIEG AND GEORGE M. GARRITY

Citation

The *Systematics* is a peer-reviewed collection of chapters, contributed by authors who were invited by the Trust to share their knowledge and expertise of specific taxa. Citations should refer to the author, the chapter title, and inclusive pages rather than to the Editors.

Arrangement of the Manual

As in the previous volumes of this edition, the *Manual* is arranged in phylogenetic groups based upon the analyses of the 16S rRNA presented in the introductory chapter "Revised road map to the phylum *Firmicutes*". These groups have been substantially modified since the publication of volume 1 in 2001, reflecting both the availability of more experimental data and a different method of analysis. Since volume 3 includes only the phylum *Firmicutes*, taxa are arranged by class, order, family, genus and species. Within each taxon, the nomenclatural type is presented first and indicated by a superscript T. Other taxa are presented in alphabetical order without consideration of degrees of relatedness.

Articles

Each article dealing with a bacterial genus is presented wherever possible in a definite sequence as follows:

a. Name of the genus. Accepted names are in boldface, followed by "defining publication(s)", i.e. the authority for the name, the year of the original description, and the page on which the taxon was named and described. The superscript AL indicates that the name was included on the Approved Lists of Bacterial Names, published in January 1980. The superscript VP indicates that the name, although not on the Approved Lists of Bacterial Names, was subsequently validly published in the International Journal of Systematic and Evolutionary Microbiology (or the International Journal of Systematic Bacteriology). Names given within quotation marks have no standing in nomenclature; as of the date of preparation of the Manual they had not been validly published in the International Journal of Systematic and Evolutionary Microbiology, although they may have been "effectively published" elsewhere. Names followed by the term "nov." are newly proposed but will not be validly published until they appear in a Validation List in the *Interna*tional Journal of Systematic and Evolutionary Microbiology. Their proposal in the Manual constitutes only "effective publication", not valid publication.

- **b. Name of author(s).** The person or persons who prepared the Bergey's article are indicated. The address of each author can be found in the list of Contributors at the beginning of the *Manual*.
- **c. Synonyms.** In some instances a list of some synonyms used in the past for the same genus is given. Other synonyms can be found in the *Index Bergeyana* or the *Supplement to the Index Bergeyana*.
- **d. Etymology of the name.** Etymologies are provided as in previous editions, and many (but undoubtedly not all) errors have been corrected. It is often difficult, however, to determine why a particular name was chosen, or the nuance intended, if the details were not provided in the original publication. Those authors who propose new names are urged to consult a Greek and Latin authority before publishing in order to ensure grammatical correctness and also to ensure that the meaning of the name is as intended.
- **e. Salient features.** This is a brief resume of the salient features of the taxon. The most important characteristics are given in **boldface**. The DNA G+C content is given.
- **f. Type species.** The name of the type species of the genus is also indicated along with the defining publication(s).
- **g. Further descriptive information.** This portion elaborates on the various features of the genus, particularly those features having significance for systematic bacteriology. The treatment serves to acquaint the reader with the overall biology of the organisms but is not meant to be a comprehensive review. The information is normally presented in the following sequence:

Colonial morphology and pigmentation Growth conditions and nutrition Physiology and metabolism Genetics, plasmids, and bacteriophages Phylogenetic treatment Antigenic structure Pathogenicity Ecology

- **h. Enrichment and isolation.** A few selected methods are presented, together with the pertinent media formulations.
- **i. Maintenance procedures.** Methods used for maintenance of stock cultures and preservation of strains are given.
- **j. Procedures for testing special characters.** This portion provides methodology for testing for unusual characteristics or performing tests of special importance.

- **k. Differentiation of the genus from other genera.** Those characteristics that are especially useful for distinguishing the genus from similar or related organisms are indicated here, usually in a tabular form.
- **1. Taxonomic comments.** This summarizes the available information related to taxonomic placement of the genus and indicates the justification for considering the genus a distinct taxon. Particular emphasis is given to the methods of molecular biology used to estimate the relatedness of the genus to other taxa, where such information is available. Taxonomic information regarding the arrangement and status of the various species within the genus follows. Where taxonomic controversy exists, the problems are delineated and the various alternative viewpoints are discussed.
- **m. Further reading.** A list of selected references, usually of a general nature, is given to enable the reader to gain access to additional sources of information about the genus.
- **n. Differentiation of the species of the genus.** Those characteristics that are important for distinguishing the various species within the genus are presented, usually with reference to a table summarizing the information.
- o. List of species of the genus. The citation of each species is given, followed in some instances by a brief list of objective synonyms. The etymology of the specific epithet is indicated. Descriptive information for the species is usually presented in tabular form, but special information may be given in the text. Because of the emphasis on tabular data, the species descriptions are usually brief. The type strain of each species is indicated, together with the collection(s) in which it can be found. (Addresses of the various culture collections are given in the article in Volume 1 entitled Culture Collections: An Essential Resource for Microbiology.) The 16S rRNA gene sequence used in phylogenetic analysis and placement of the species into the taxonomic framework is given, along with the GenBank (or other database) accession number. Additional comments may be provided to point the reader to other well-characterized strains of the species and any other known DNA sequences that may be relevant.
- **p. Species** *incertae sedis.* The List of Species may be followed in some instances by a listing of additional species under the heading "Species *Incertae Sedis*" or "Other organisms". The taxonomic placement or status of such species is questionable, and the reasons for the uncertainty are presented.
- **q. References.** All references given in the article are listed alphabetically at the end of the family chapter.

Tables

In each article dealing with a genus, there are generally three kinds of table: (a) those that differentiate the genus from similar or related genera, (b) those that differentiate the species within the genus, and (c) those that provide additional information about the species (such information not being particularly useful for differentiation). The meanings of symbols are as follows:

- +: 90% or more of the strains are positive
- d: 11-89% of the strains are positive
- -: 90% or more of the strains are negative
- D: different reactions occur in different taxa (e.g., species of a genus or genera of a family)
 - v: strain instability (NOT equivalent to "d")

w: weak reaction.

ND, not determined or no data.

These symbols, and exceptions to their use, as well as the meaning of additional symbols, are given in footnotes to the tables.

Use of the Manual for determinative purposes

Many chapters have keys or tables for differentiation of the various taxa contained therein. For identification of species, it is important to read both the generic and species descriptions because characteristics listed in the generic descriptions are not usually repeated in the species descriptions.

The index is useful for locating the articles on unfamiliar taxa or in discovering the current classification of a particular taxon. Every bacterial name mentioned in the *Manual* is listed in the index. In addition, an up-to-date outline of the taxonomic framework is provided in the introductory chapter "Revised road map to the phylum *Firmicutes*".

Errors, comments, suggestions

As in previous volumes, the editors and authors earnestly solicit the assistance of all microbiologists in the correction of possible errors in *Bergey's Manual of Systematic Bacteriology*. Comments on the presentation will also be welcomed as well as suggestions for future editions. Correspondence should be addressed to:

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Revised road map to the phylum Firmicutes

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Starting with the Second Edition of Bergey's Manual of Systematic Bacteriology, the arrangement of content follows a phylogenetic framework or "road map" based largely on analyses of the nucleotide sequences of the ribosomal small-subunit RNA rather than on phenotypic data (Garrity et al., 2005). Implicit in the use of the road map are the convictions that prokaryotes have a phylogeny and that phylogeny matters. However, the reader should be aware that phylogenies, like other experimentally derived hypotheses, are not static but may change whenever new data and/or improved methods of analysis become available (Ludwig and Klenk, 2005). Thus, the large increases in data since the publication of the taxonomic outlines in the preceding volumes have led to a re-evaluation of the road map. Not surprisingly, the taxonomic hierarchy has been modified or newly interpreted for a number of taxonomic units of the Firmicutes. These changes are described in the following paragraphs.

The taxonomic road map proposed in Volume 1 and updated and emended in Volume 2 was derived from phylogenetic and principal-component analyses of comprehensive datasets of smallsubunit rRNA sequences. A similar approach is continued here. Since the introduction of comparative rRNA sequencing (Ludwig and Klenk, 2005; Ludwig and Schleifer, 2005), there has been a continuous debate concerning the justification and power of a single marker molecule for elucidating and establishing the phylogeny and taxonomy of organisms, respectively. Although generally well established in taxonomy, the polyphasic approach cannot be currently applied for sequence-based analyses due to the lack of adequate comprehensive datasets for alternative marker molecules. Even in the age of genomics, the datasets for non-rRNA markers are poor in comparison to more than 300,000 rRNA primary structures available in general and special databases (Cole et al., 2007; Pruesse et al., 2007). Nevertheless, the data provided by the full genome sequencing projects allow defining a small set of genes representing the conserved core of prokaryotic genomes (Cicarelli et al., 2006; Ludwig and Schleifer, 2005). Furthermore, comparative analyses of the core gene sequences globally support the small-subunit rRNA derived view of prokaryotic evolution. Although the tree topologies reconstructed from alternative markers differ in detail, the major groups (and taxa) are verified or at least not disproved (Ludwig and Schleifer, 2005). Consequently, the structuring of this volume is based on updated and curated (http://www.arb-silva.de; Ludwig et al., 2004) databases of processed small-subunit rRNA primary structures.

Data analysis

The current release of the integrated small-subunit rRNA database of the SILVA project (Pruesse et al., 2007) provided the basis for these phylogenetic analyses of the *Firmicutes*. The tools of the ARB software package (Ludwig et al., 2004) were used for data evaluation, optimization and phylogenetic inference. The alignment of sequences comprising at least 1000 monomers was manually evaluated and optimized for all representatives of the phylum. Phylogenetic treeing was performed with all of the approximately 14,000 sequences from Firmicutes which contain at least 1400 nucleotides and an additional 1000 sequences from representatives of the other phyla and domains. For recognizing and avoiding the influences of chimeric sequences, all calculations were performed twice, once including and once excluding environmental clone data. The datasets also varied with respect to the inclusion of highly variable sequence positions, which were eliminated in some analyses (Ludwig and Klenk, 2005). The consensus tree used for evaluating or modifying the taxonomic outline was based on maximum-likelihood analyses (RAXML, implemented in the ARB package; Stamatakis et al., 2005) and further evaluated by maximum-parsimony and distance matrix analyses with the respective ARB tools (Ludwig et al., 2004). In the case that type strains were only represented by partial sequences (less than 1400 nucleotides), the respective data were inserted by a special ARB-tool allowing the optimal positioning of branches to the reference tree without admitting topology changes.

Taxonomic interpretation

The phylogenetic conclusions were used for evaluating and modifying the taxonomic outline of the Firmicutes. In order to ensure applicability and promote acceptance, the proposed modifications were made following a conservative procedure. The overall organization follows the type 'taxon' principle as applied in the previous volumes. Taxa defined in the outline of the preceding volumes were only unified, dissected or transferred in the cases of strong phylogenetic support. This approach is justified by the well-known low significance of local tree topologies (also called "range of unsharpness" around the nodes; Ludwig and Klenk, 2005). Thus, many of the cases of paraphyletic taxa found were maintained in the current road map if the respective (sub)-clusters rooted closely together, even if they were separated by intervening clusters representing other taxa. While reorganization of these taxa may be warranted, it was not performed in the absence of confirmatory evidence. The names of validly published but phylogenetically misplaced type strains are also generally maintained. These strains are mentioned in the context of the respective phylogenetic groups. In case of paraphyly, all concerned species or higher taxa are assigned to the respective (sub)-groups. New higher taxonomic ranks are only proposed if species or genera — previously assigned to different higher taxonomic units — are significantly unified in a monophyletic branch.

The taxonomic backbone of the Firmicutes

In the current treatment, the phylum *Firmicutes* contains three classes, "*Bacilli*", "*Clostridia*" and "*Erysipelotrichia*". This organization is similar to that of Garrity et al. (2005). However, the *Mollicutes*

were removed from the phylum given the general low support by alternative markers (Ludwig and Schleifer, 2005) and its unique phenotypic properties, in particular the lack of rigid cell walls (see Emended description of *Firmicutes*, this volume). The family *Erysipelotrichaceae*, which includes wall-forming Gram-positive organisms previously classified with the *Mollicutes*, was retained in the *Firmicutes* as a novel class, "*Erysipelotrichia*", and order, "*Erysipelotrichales*".

While the bipartition of the classes "Clostridia" and "Bacilli" is corroborated by the new analyses, some of the taxa previously assigned to the "Clostridia" tend to root outside the Firmicutes and may represent separate phyla. These include taxa previously classified within the "Thermoanaerobacterales" and

Syntrophomonadaceae (Garrity et al., 2005), which may contain a number of phylogenetic clades that are distinct at the phylum level. However, given the absence of corroboration by other phylogenetic markers for many of these assignments and a clear consensus on the definition of a phylum, these taxa were retained within the *Firmicutes* for the present.

Class "Bacilli"

Compared to Garrity et al. (2005), only minor restructuring of the "Bacilli" is indicated by this new analysis of the rRNA data. The separation into two orders, Bacillales and "Lactobacillales", is well supported (Figure 1). However, a number of paralogous

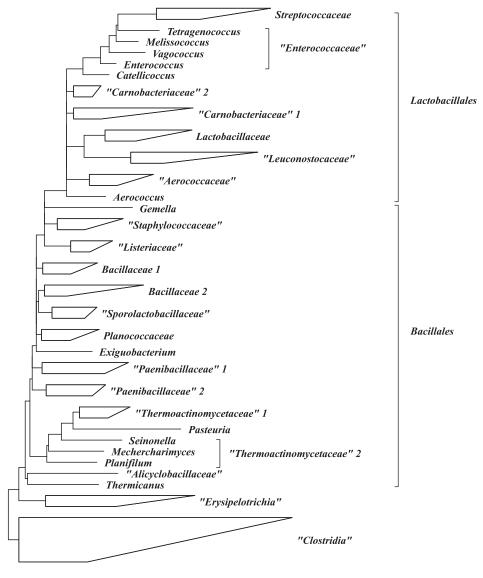


FIGURE 1. Consensus dendrogram reflecting the phylogenetic relationships of the classes "Bacilli" and "Erysipelotrichia" within the Firmicutes. The tree is based on maximum-likelihood analyses of a dataset comprising about 5000 almost full-length high-quality 16S rRNA sequences from representatives of the Firmicutes and another 1000 representing the major lines of decent of the three domains Bacteria, Archaea, and Eucarya. The topology was evaluated by distance matrix and maximum-parsimony analyses of the dataset. In addition, maximum-parsimony analyses of all currently available almost complete small-subunit rRNA sequences (137,400 of Arb-SILVA release 92, Prüsse et al., 2007) were performed. Only alignment positions invariant in at least 50% of the included primary structures from Firmicutes were included for tree reconstruction. Multifurcations indicate that a common relative branching order was not significantly supported applying alternative treeing methods. The (horizontal) branch lengths indicate the significance of the respective node separation.

groups are found within the "Bacilli", some of which have been reclassified.

Order Bacillales

The definition and taxonomic organization of the order *Bacillales* is as outlined in the previous volumes (Figure 2). Of the ten families proposed in Garrity et al. (2005), eight are retained. Upon transfer of the type genus *Caryophanon* to the *Planococcaceae*, the family *Caryophanaceae* was removed. Although the family *Caryophanaceae* Peskoff 1939^{AL} has priority over *Planococcaceae* Krassilnikov 1949^{AL}, the former is confusing because it is a misnomer, meaning 'that which has a conspicuous nucleus', and was based upon misinterpretation of staining results (Trentini, 1986). Similarly, upon transfer of the type genus *Turicibacter*

to the family "Erysipelotrichaceae", the family "Turicibacteraceae" was removed. In addition, the genus Pasteuria was transferred out of the family "Alicyclobacillaceae" to the family Pasteuriaceae. As described below, a number of genera were also moved to families incertae sedis in recognition of the ambiguity of their phylogeny and taxonomic assignments.

Family Bacillaceae

The 16S rRNA-based phylogenetic analyses indicate that the family *Bacillaceae* is paraphyletic and composed of species misassigned to the genus *Bacillus* as well as genera misassigned to the family (Figure 2). Reclassification of some taxa is proposed to correct some of these problems. However, the complete reorganization of this old and well-abused taxon is outside the scope of this work.

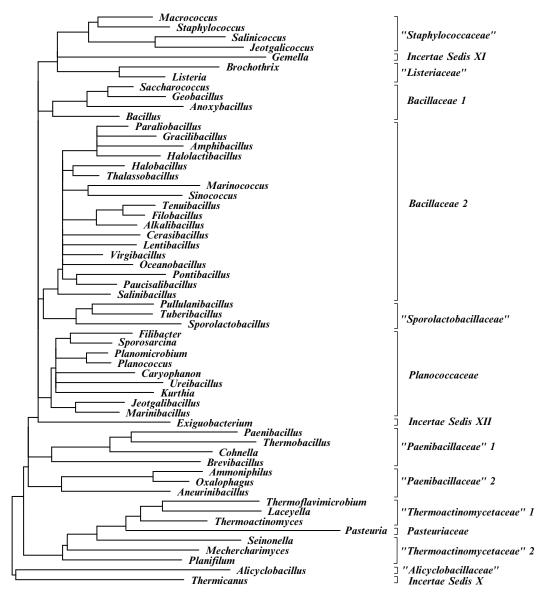


FIGURE 2. Consensus dendrogram reflecting the phylogenetic relationships of the order *Bacillales* within the class "*Bacilli*". Analyses were performed as described for Figure 1.

Genus Bacillus

The majority of the *Bacillus* species with validly published names are phylogenetically grouped into subclusters within this genus. However, some validly named species of *Bacillus* are not phylogenetically related to the type species, *B. subtilis*, and are more closely related to other genera. The phylogenetic subclusters within the genus *Bacillus* are:

- a: Bacillus subtilis, amyloliquefaciens, atrophaeus, mojavensis, licheniformis, sonorensis, vallismortis, including the very likely misclassified Paenibacillus popilliae.
 - b: Bacillus farraginis, fordii, fortis, lentus, galactosidilyticus
- c: Bacillus asahii, bataviensis, benzoevorans, circulans, cohnii, firmus, flexus, fumarioli, infernus, jeotgali, luciferensis, megaterium, methanolicus, niacini, novalis, psychrosaccharolyticus, simplex, soli, vireti
- d: Bacillus anthracis, cereus, mycoides, thuringiensis, weihenstephanensis
 - e: Bacillus aquimaris, marisflavi
- f: Bacillus badius, coagulans, thermoamylovorans, acidicola, oleronius, sporothermodurans
- g: Bacillus alcalophilus, arsenicoselenatis, clausii, gibsonii, halodurans, horikoshii, krulwichiae, okhensis, okuhidensis, pseudoalcaliphilus, pseudofirmus
 - h: Bacillus arsenicus, barnaricus, gelatini, decolorationis,
 - i: Bacillus carboniphilus, endophyticus, smithii,
 - j: Bacillus pallidus,
 - k: Bacillus funiculus, panaciterrae

The *Bacillus* cluster contains three additional groups of related genera: *Anoxybacillus*, *Geobacillus*, and *Saccharococcus*.

In addition to these taxa, which compose the family Bacillaceae sensu stricto, other phylogenetic groups have been assigned to this family (Garrity et al., 2005). Although the largest group appears to warrant elevation to a novel family, it is retained within the Bacillaceae in the present outline. This cluster comprises the genera Alkalibacillus (new; Jeon et al., 2005), Amphibacillus, Cerasibacillus (new; Nakamura et el., 2004), Filobacillus, Gracilibacillus, Halobacillus (new; Spring et al., 1996), Halolactibacillus (new; Ishikawa et al., 2005), Lentibacillus, Oceanobacillus, Paraliobacillus, Paucisalibacillus (new; Nunes et al., 2006); not described in the current volume), Pontibacillus, Salibacillus (not described in the current volume), Tenuibacillus, Thalassobacillus (new; Garcia et al., 2005), and Virgibacillus. The type strains of other species are positioned phylogenetically among the members of this lineage and merit taxonomical emendation: Bacillus halophilus and Bacillus thermocloacae, Sinococcus, and Marinococcus. For this reason, Marinococcus was transferred from the Sporolactobacillaceae in the current outline.

In addition, the genera *Ureibacillus, Marinibacillus, Jeotgalibacillus*, and *Exiguobacterium* were previously assigned to the *Bacillaceae* (Garrity et al., 2005). *Ureibacillus* falls within the clade represented by *Planococcaceae*, and it was reassigned to that family. *Marinibacillus* and *Jeotgalibacillus* are closely related to each other as well as to *Bacillus aminovorans*. This group is distantly related to the *Planococcaceae*, and they are also assigned to that family. Lastly, *Exiguobacterium* is not closely related to any of the described families, and it is assigned to a Family XII *Incertae Sedis* in the current road map.

Bacillus schlegelii and Bacillus solfatarae represent their own deeply branching lineage of the "Bacilli" and warrant reclassification.

Family "Alicyclobacillaceae"

Only the type genus Alicyclobacillus is retained in this family, and two genera previously classified with the Alicyclobacillaceae have been reclassified (Garrity et al., 2005). According to the new 16S rRNA sequence analyses, Sulfobacillus represents a deep branch of the "Clostridia", and it is now placed within Family XVII Incertae Sedis of the Clostridiales. Pasteuria, which was also previously classified within this family, is an obligate parasite of invertebrates. While it can be cultivated within the body of its prey, it has not been cultured axenically. Because of the substantial phenotypic differences and low 16S rRNA sequence similarity with Alicyclobacillus, it is now classified within its own family, Pasteuriaceae (see below). Lastly, Alicyclobacillus possesses a moderate relationship to Bacillus tusciae, which could be reclassified to this family.

Family "Listeriaceae"

The monophyletic family "Listeriaceae" combines the genera Listeria and Brochothrix as in the previous outline.

Family "Paenibacillaceae"

The members of the family "Paenibacillaceae" are distributed between two phylogenetic clusters. Paenibacillus, Brevibacillus, Cohnella (new; Kämpfer et al., 2006) and Thermobacillus share a common origin and represent the first group. Some validly named Bacillus species are found among the Paenibacillus species: Bacillus chitinolyticus, edaphicus, ehimensis, and mucilaginosus. The second group comprises the genera Aneurinibacillus, Ammoniphilus, and Oxalophagus. Although not clearly monophyletic, these two clusters are often associated together in several types of analyses. Thus, in the absence of clear evidence for a separation, the second cluster is retained within the family. In contrast, Thermicanus, which was classified within this family by Garrity et al. (2005), appears to represent a novel lineage of the Bacilli. In recognition of its ambiguous status, it was reclassified within Family X Incertae Sedis.

Family Pasteuriaceae

This family contains *Pasteuria*, an obligate parasite of invertebrates which has not yet been cultivated outside of its host. Although this genus was previously classified within the "*Alicyclobacillaceae*", the current analyses suggest that it is more closely associated with the "*Thermoactinomycetaceae*". In spite of the similarities in morphology and rRNA sequences between *Pasteuria* and *Thermoactinomycetes*, these genera were not combined into a single family for two reasons. First, in the absence of an axenic culture of *Pasteuria*, additional phenotypic and genotypic evidence for combining these organisms into a single family are not available. Second, the obligately pathogenic nature of *Pasteuria* was judged to be distinctive enough to warrant a unique classification in the absence of evidence to the contrary.

Family Planococcaceae

The family *Planococcaceae* is a clearly monophyletic unit that contains the genera *Planococcus*, *Filibacter*, *Kurthia*, *Planomicrobium*, and *Sporosarcina* as well as three genera transferred from the *Bacillaceae* (*Jeotgalibacillus*, *Marinibacillus*, and *Ureibacillus*) and *Caryophanon*. *Caryophanon* is the only genus of the *Caryophanaceae* in