

BERGEY'S MANUAL® OF
**Systematic
Bacteriology**
Second Edition

Volume Five
The *Actinobacteria*, Part A and B

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Systematic Bacteriology

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Volume Five

The *Actinobacteria*, Part A and B

**Michael Goodfellow, Peter Kämpfer, Hans-Jürgen Busse,
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and William B. Whitman**

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*This volume is dedicated to our colleagues
Michael Goodfellow and Peter H.A. Sneath.*

*Michael retired from the Board of Trustees of Bergey's Manual during preparation of this volume.
His tremendous efforts as an editor, author and officer of the Trust are truly appreciated.*

*Our late eminent colleague Peter H.A. Sneath (1923–2011) was a Trustee (1978–1994)
and Chairman of the Trust (1990–1994).*

*He also served as an editor of previous editions of The Manual and made many
other remarkable contributions to the systematics of prokaryotes.*

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Preface to volume 5 of the second edition of *Bergey's Manual*[®] of *Systematic Bacteriology*

Prokaryotic systematics remains a vibrant and exciting field of study, one of challenges and opportunities, great discoveries and gradual advances. To honor one of the leaders of our field, the Trust presented the Bergey Award in recognition of outstanding contributions to the taxonomy of prokaryotes to Antonio Ventosa in 2010. The Bergey Medal, in recognition of life-long contributions to the field of systematic bacteriology, was also awarded to Michael Goodfellow, Zhiheng Liu, Ji-Sheng Ruan, and James Tiedje in 2011.

Volume 5 will be the last volume to be edited by Michael Goodfellow, who served on the Trust for many years and has continued to be active during his retirement. Mike contributed to volumes 2 and 4 of the first edition of *Bergey's Manual of Systematic Bacteriology* and has made an enormous contribution to the present volume as an author, editor, and mentor. As a leader in actinobacterial research for many decades, he is also directly responsible for much of the wealth of information about this fascinating group of microorganisms described in the current volume. Mike served as the Vice-Chairman of the Trust for many years and Chairman for the last 3 years. During his tenure, the Trust underwent important transitions for the future beyond the second edition. Adept at saying the most difficult things in the nicest way and a master of the telling omission, he was the right person at the right time.

Acknowledgements

The Trust is indebted to all of the contributors and reviewers, without whom this work would not be possible. The Editors are grateful for the time and effort that each has expended on behalf of the entire scientific community. We also thank the authors for their good grace in accepting comments, criticisms, and editing of their manuscripts.

The Trust recognizes its enormous debt to Dr Aidan Parte, whose enthusiasm and professionalism have made this *Manual* possible. The completion of the second edition is due in great measure to his dedication, good judgment, and hard work. His vision for excellent science has made the *Manual* more than it would have been.

We also recognize the special efforts of Dr Jean Euzéby in checking and correcting where necessary the nomenclature and etymology of every described taxon in this volume.

The Trust also thanks its Springer colleagues, especially Editorial Director Andrea Macaluso and Production Manager Susan Westendorf, for all of their efforts. As this will be the last volume of the *Manual* published in collaboration with Springer, the Trust also wishes to acknowledge the tremendous support and understanding that Springer has demonstrated over the last 13 years in helping us to publish this comprehensive synthesis of the systematics of prokaryotes.

In addition, we thank Amina Ravi, our manager at our typesetters, SPi, for her work in the proofing and production of this and the previous two volumes.

We thank our current copyeditors, proofreaders and other staff, including Susan Andrews, Joanne Auger, Hannah Berle, Robert Gutman, Judy Leventhal, Linda Sanders, Tyler Sgro, Dana Schneider, and Mohammed Waqar, without whose hard work and attention to detail the production of this volume would have been impossible. Lastly, we thank Dale Boyer and the other members of the Department of Microbiology at the University of Georgia for their unfailing support of this endeavor.

William B. (Barney) 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 “Road map of the phylum *Actinobacteria*”. This phylum has 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 5 includes only the phylum *Actinobacteria*, taxa are arranged by class, order, family, genus and species. Within each taxon, the nomenclatural type is presented first. 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 *International 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.

l. 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 I 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”, etc. 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.
- nr, not reported.

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 “Road map of the phylum *Actinobacteria*”.

Errors, comments, and 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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