

BERGEY'S MANUAL® OF
Systematic
Bacteriology
Volume 2

PETER H. A. SNEATH
NICHOLAS S. MAIR
M. ELISABETH SHARPE
JOHN G. HOLT

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Bacteriology**
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In addition, the Board extends special thanks to S. T. Williams for his invaluable help.

Preface to First Edition of Bergey's Manual® of Systematic Bacteriology, Volume 2

Many microbiologists advised the Trust that a new edition of the *Manual* was urgently needed. Of great concern to us was the steadily increasing time interval between editions; this interval reached a maximum of 17 years between the seventh and eighth editions. To be useful the *Manual* must reflect relatively recent information; a new edition is soon dated or obsolete in parts because of the nearly exponential rate at which new information accumulates. A new approach to publication was needed, and from this conviction came our plan to publish the *Manual* as a sequence of four subvolumes concerned with systematic bacteriology as it applies to taxonomy. The four subvolumes are divided roughly as follows: (a) the Gram-negatives of general, medical or industrial importance; (b) the Gram-positives other than actinomycetes; (c) the archaeobacteria, cyanobacteria and remaining Gram-negatives; and (d) the actinomycetes. The Trust believed that more attention and care could be given to preparation of the various descriptions within each subvolume, and also that each subvolume could be prepared, published, and revised as the area demanded, more rapidly than could be the case if the *Manual* were to remain as a single, comprehensive volume as in the past. Moreover, microbiologists would have the option of purchasing only that particular subvolume containing the organisms in which they were interested.

The Trust also believed that the scope of the *Manual* needed to be expanded to include more information of importance for systematic bacteriology and bring together information dealing with ecology, enrichment and isolation, descriptions of species and their determinative characters, maintenance and preservation, all focused on the illumination of bacterial taxonomy. To reflect this change in scope, the title of the *Manual* was changed and the primary publication becomes *Bergey's Manual® of Systematic Bacteriology*. This contains not only determinative material such as diagnostic keys and tables useful for identification, but also all of the detailed descriptive information and taxonomic comments. Upon completion of each subvolume, the purely determinative information will be assembled for eventual incorporation into a much smaller publication which will continue the original name of the *Manual*, *Bergey's Manual® of Determinative Bacteriology*, which will be a similar but improved version of the present *Shorter Bergey's Manual®*

So, in the end there will be two publications, one systematic and one determinative in character.

An important task of the Trust was to decide which genera should be covered in the first and subsequent subvolumes. We were assisted in this decision by the recommendations of our Advisory Committees, composed of prominent taxonomic authorities to whom we are most grateful. Authors were chosen on the basis of constant surveillance of the literature of bacterial systematics and by recommendations from our Advisory Committees.

The activation of the 1976 Code had introduced some novel problems. We decided to include not only those genera that had been published in the Approved Lists of Bacterial Names in January 1980 or that had been subsequently validly published, but also certain genera whose names had no current standing in nomenclature. We also decided to include descriptions of certain organisms which had no formal taxonomic nomenclature, such as the endosymbionts of insects. Our goal was to omit no important group of cultivated bacteria and also to stimulate taxonomic research on "neglected" groups and on some groups of undoubted bacteria that have not yet been cultivated and subjected to conventional studies.

Some readers will note the consistent use of the stem -var instead of -type in words such as biovar, serovar and pathovar. This is in keeping with the recommendations of the Bacteriological Code and was done against the wishes of some of the authors.

We have deleted much of the synonymy of scientific names which was contained in past editions. The adoption of the new starting date of January 1, 1980 and publication of the Approved Lists of Bacterial Names has made mention of past synonymy obsolete. We have included synonyms of a name only if they have been published since the new starting date, or if they were also on the Approved Lists and, in rare cases, if the mention of an old name would help readers associate the organism with a clinical problem. If the reader is interested in tracing the history of a name we suggest he or she consult past editions of the *Manual* or the *Index to Bergeyana* and its *Supplement*. In citations of names we have used the abbreviation AL to denote the inclusion of the name on the Approved Lists of Bacterial Names and VP to show the name has been validly published.

In the matter of citation of the *Manual* in the scientific literature, we again stress the fact that the *Manual* is a collection of authored chapters and the citation should refer to the author, the chapter title and its inclusive pages, not the Editors.

To all contributors, the sincere thanks of the Trust is due; the Editors are especially grateful for the good grace with which the authors accepted comments, criticisms and editing of their manuscripts. It is only because of the voluntary and dedicated efforts of these authors that the *Manual* can continue to serve the science of bacteriology on an international basis.

A number of institutions and individuals deserve special acknowledgment from the Trust for their help in bringing about the publication of this volume. We are grateful to the University of Leicester for providing space, facilities and, above all, tolerance for the diverted time taken by the Editor during the preparation of the book. The Department of Microbiology at Iowa State University of Science and Technology continues to provide a welcome home for the main editorial offices and archives of the Trust and we acknowledge their contin-

ued support. A grant (LM-05707) from the National Library of Medicine, National Institutes of Health to assist in the preparation of this and the first volume of the *Manual* is gratefully acknowledged.

A number of individuals deserve special mention and thanks for their help. Professor Thomas O. MacAdoo of the Department of Foreign Languages and Literatures at the Virginia Polytechnic Institute and State University has given invaluable advice on the etymology and correctness of scientific names. Those assisting the Editors in the Leicester office were Dorothy Jones, Grace Redfern, Wynn Rutt, Brenda Jones and Pauline Carr, and their help is sincerely appreciated. In the Ames office, we were ably assisted by Cynthia Pease who had the major responsibility for keying and sorting the list of references and index and Susan Blakely who assisted in keying the list of references.

Comments on this edition of the *Manual* will be welcomed and should be addressed to the Bergey's Manual® Trust, c/o Williams & Wilkins, 428 E. Preston St., Baltimore, Md. 21202, U.S.A.

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Preface to First Edition of Bergey's Manual[®] of Determinative Bacteriology

2A

The elaborate system of classification of the bacteria into families, tribes and genera by a Committee on Characterization and Classification of the Society of American Bacteriologists (1917, 1920) has made it very desirable to be able to place in the hands of students a more detailed key for the identification of species than any that is available at present. The valuable book on "Determinative Bacteriology" by Professor F. D. Chester, published in 1901, is now of very little assistance to the students, and all previous classifications are of still less value, especially as earlier systems of classification were based entirely on morphologic characters.

It is hoped that this manual will serve to stimulate efforts to perfect the classification of bacteria, especially by emphasizing the valuable features as well as the weaker points in the new system which the Committee of the Society of American Bacteriologists has promulgated. The Committee does not regard the classification of species offered here as in any sense final, but merely a progress report leading to more satisfactory classification in the future.

The Committee desires to express its appreciation and thanks to those members of the society who gave valuable aid in the compilation of material and the classification of certain species . . .

The assistance of all bacteriologists is earnestly solicited in the correction of possible errors in the text; in the collection of descriptions of all bacteria that may have been omitted from the text; in supplying more detailed descriptions of such organisms as are described incompletely; and in furnishing complete descriptions of new organisms that may be discovered, or in directing the attention of the Committee to publications of such newly described bacteria.

DAVID H. BERGEY, *Chairman*
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Committee on Manual

August, 1923.



Archives of the ASM

DAVID HENDRICKS BERGEY
1860-1937

Bergey set up the Trust on January 2, 1936

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History of the Manual

The first edition of *Bergey's Manual*[®] of *Determinative Bacteriology* was initiated by action of the Society of American Bacteriologists (now called the American Society of Microbiology) by appointment of an Editorial Board consisting of David H. Bergey, Chairman, Francis C. Harrison, Robert S. Breed, Bernard W. Hammer, and Frank M. Huntoon. This Board, under auspices of the Society of American Bacteriologists who, then as now, published the *Journal of Bacteriology* as a service to science, brought the first edition of the *Manual* into print in 1923. The Board, with some changes in membership and Dr. David Bergey as Chairman, published a second edition of the *Manual* in 1925 and a third edition in 1930.

In 1934, during preparation of the fourth edition, Dr. Bergey requested that the Society of American Bacteriologists make available the royalties paid to the Treasurer of the Society from the sale of the earlier editions to defray the expense of preparing the fourth edition for publication. The Society made such provision, but the use of the Society's fiscal machinery proved cumbersome, both to the Society and the Editorial Board. Subsequently, it was agreed by the Society and Dr. Bergey that the Society would transfer to Dr. Bergey all of its rights, title, and interest in the *Manual* and that Dr. Bergey would, in turn, create an educational trust to which all rights would be transferred.

Dr. Bergey was then the nominal owner of the *Manual* and he executed a Trust Indenture on January 2, 1936 designating David H. Bergey, Robert S. Breed, and E. G. D. Murray as the initial trustees, and transferring to the Trustees and their successors the ownership of the *Manual*, its copyrights, and the right to receive the income arising from its publication. The Trust is a nonprofit organization and its income is used solely for the purpose of preparing, editing, and publishing revisions and successive editions of the *Manual* and any supplementary publications, as well as providing for any research that may be necessary or desirable in such activities.

Since the creation of the Trust, the Trustees have published, successively, the fourth, fifth, sixth, seventh, and eighth editions of the *Manual* (dated 1934, 1939, 1948, 1957, and 1974, respectively). In 1977 the Trust published an abbreviated version of the eighth edition, called *The Shorter Bergey's Manual*[®] of *Determinative Bacteriology*; this contained the outline classification of the bacteria, the descriptions of all genera and higher taxa, all of the keys and tables for the diagnosis of

species, all of the illustrations, and two of the introductory chapters; however, it did not contain the detailed species descriptions, most of the taxonomic comments, the etymology of names, and references to authors.

Other ventures in producing books to assist those engaged in bacteriology and bacterial taxonomy in particular include the *Index Bergeyana* (1966), a *Supplement to Index Bergeyana* (1981), and a planned future volume bringing the lists of published names up to date. The Trust is presently publishing the first edition of *Bergey's Manual*[®] of *Systematic Bacteriology*, which has a much broader scope than the previous publications and is intended to act as the amplified source for revision of the determinative *Manual*.

Through the years the *Manual* has become a widely used international reference work for bacterial taxonomy. Similarly, the Bergey's Manual Trust has become international in its composition, in the location of its meetings and in the breadth of its consultations. In addition to its publication activities, the Trust attempts to foster and support various aspects of taxonomic research. One of the ways in which it does this is by recognizing those individuals who have made outstanding contributions to bacterial taxonomy, through its periodic presentation of the Bergey Award, an effort jointly supported by funds from the Trust and Williams & Wilkins who have been involved in the production of the *Manual* from its beginning.

The following individuals have served as members of the Editorial Board and Board of Trustees.

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On Using the Manual

Peter H. A. Sneath

ARRANGEMENT OF THE MANUAL

The present section is largely based on that by N. R. Krieg prepared for Volume 1. One important goal of the *Manual* is to assist in the identification of bacteria, but another goal, equally important, is to indicate the relationships that exist between the various kinds of bacteria. The methods of molecular biology have now made it possible to envision the eventual development of a comprehensive classification of bacteria based on their phylogenetic relatedness to one another. Such a general classification scheme would lead, hopefully, to more unifying concepts of bacterial taxa, to greater stability and predictability, to the development of more reliable identification schemes, and to an understanding of how bacteria have evolved.

Such a general scheme, however, cannot yet be perceived fully. The relatedness within and between some bacterial groups has been intensively studied, but for other groups very little work has been done. Moreover, the relatedness studies that have been done often have involved the use of one or another method without confirmation by other methods. Studies have been done at differing levels of resolution,

and the interpretation of the data may not yet be entirely clear. Still another major difficulty is the conflict between "practical" classification vs. strange groupings that may be indicated by molecular biology methods. This is because some of the phenotypic characteristics traditionally used in bacterial classification (e.g. cell shape, flagellar arrangement, fermentative vs. respiratory types of metabolism, etc.) do not always correlate well with groups established on the basis of relatedness. This conflict will, one hopes, eventually be relieved by the finding of nontraditional, easily determined, phenotypic characteristics that do correlate well with relatedness groups, but much work needs to be done in this regard.

Such considerations have forced the present edition of the *Manual* to adhere largely to traditional characteristics in arranging bacterial taxa. It should be understood, however, that reassessments of these groupings will soon need to be made on a broad, comprehensive scale. The present classification, although of considerable practical value, must be regarded as only an interim arrangement.

THE SECTIONS

The *Manual* is presented as various "sections" based on a few readily determined criteria. Each section bears a vernacular name. All accepted genera have been placed in what seems the most appropriate section, although allocation of certain genera has presented difficulties, as indicated by the following examples:

- (a) The genus *Oscillospira* remains poorly studied, and the account given is that from the 8th edition of *Bergey's Manual*[®] of *Determinative Bacteriology*. It is only tentatively placed in Section 13, because it is still uncertain whether it produces true endospores.
- (b) The genus *Gardnerella*. It is not entirely clear whether this genus should be placed with Gram-negative or with Gram-positive bacteria. It has been reprinted from Volume 1 and is placed for convenience in Section 15.
- (c) The genera *Lachnospira* and *Butyrivibrio* stain Gram-negative under usual conditions, but whether or not they possess cell walls of the Gram-negative type is not clear. They are, therefore, reprinted from Volume 1 and are placed in Section 15.
- (d) The practical distinction between organisms of Sections 14 and 15 rests largely on the more regular shape of the cells of those in

Section 14. The reader is advised, therefore, to consult both sections when considering an organism that may belong to either of them. The placement of some of these genera is in considerable doubt.

- (c) The organisms of Sections 16 and 17 share a tendency to produce branching filaments, particularly in early phases of growth. This is less marked in the mycobacteria (Section 16) than the others, but the mycobacteria are acid-fast (as are some organisms in Section 17).
- (f) The genera *Corynebacterium* (Section 15), *Mycobacterium* (Section 16), *Nocardia* and *Rhodococcus* (Section 17) share many chemotaxonomic properties, which could justify their placement in one grouping. However, for determinative purposes they have been arranged as noted above.

As an interim solution to some of these problems, some taxa are described not only in Volume 2 but in an appropriate subsequent volume as well.

SECTIONS VS. TAXONOMIC NAMES

Each section bears a vernacular name, but may also bear the name of a taxon. Thus, Section 16 (The Mycobacteria) is the family *Mycobacteriaceae*. As indicated previously, no attempt has been made to provide a complete formal hierarchy of higher taxa throughout the

Manual, and the vernacular names of the sections form the primary basis for the organization of the *Manual*; however, a suggested hierarchy for higher taxa has been proposed in one of the introductory articles (see The Higher Taxa, or a Place for Everything).

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 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 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 Bacteriology, although they had been "effectively published" elsewhere. Names followed by the term "gen. nov." are newly proposed but will not be validly published until they appear in the International Journal of Systematic Bacteriology; 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 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 is given of synonyms which have been used in the past for the same genus. The synonymy may not always be complete, and usually is not given at all, as the Editorial Board believes that the earlier synonyms have been covered adequately in the *Index Bergeyana* or the *Supplement to the Index Bergeyana*.
- (d) *Etymology of the Genus 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 name means what it is intended to mean. An excellent authority to communicate with in this regard is Dr. Thomas O. MacAdoo, Department of Foreign Languages, Virginia Polytechnic Institute and State University, Blacksburg, Virginia U.S.A. 24061.
- (e) *Capsule Description.* This is a brief resume of the salient features of the genus. The most important characteristics are given in **boldface**. The name of the type species of the genus is also indicated.
- (f) *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 represented in sequence, as follows:
Morphological characteristics

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

- (g) *Enrichment and Isolation.* A few selected methods are presented, together with the pertinent media formulations.
- (h) *Maintenance Procedures.* Methods used for maintenance of stock cultures and preservation of strains are given.
- (i) *Procedures for Testing Special Characters.* This portion provides methodology for testing for unusual characteristics or performing tests of special importance.
- (j) *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.
Taxonomic Comment. This summarizes the available information about the taxonomic placement of the genus and indicates the justification for considering genus to be a distinct taxon. Particular emphasis is given to the methods of molecular biology for estimating the relatedness 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.
- (l) *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.
- (m) *Differentiation of the Species of the Genus.* Those characteristics that are important for distinguishing from one another the various species within the genus are presented, usually with reference to a table summarizing the information.
- (n) *List of the 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 in which it can be found. (Addresses of the various culture collections are given in the chapter List of Culture Collections.)
- (o) *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." The taxonomic placement or status of such species is questionable and the reasons for the uncertainty are presented.
- (p) *Literature Cited.* All references given in the article are listed alphabetically at the end of the volume rather than at the end of each article.

TABLES

In each article dealing with a genus, there are generally three kinds of tables: (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. Unless otherwise indicated, 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 (species of a genus or genera of a family).
- v strain instability (NOT equivalent to "d").

Exceptions to use of these symbols, as well as the meaning of additional symbols, are clearly indicated in footnotes to the tables.

USE OF THE MANUAL FOR DETERMINATIVE PURPOSES

Entry into the *Manual* is best achieved by studying the titles of the various sections, as listed in the Contents. These titles provide an elementary, but by no means perfect, key to the various kinds of bacteria. Each section has keys or tables for differentiation of the various taxa contained therein. Suggestions on identification may be found in the article *Identification of Bacteria*. 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 in locating the names of unfamiliar taxa or in discovering what has been done with a particular taxon. Every bacterial name mentioned in the *Manual* is listed in the index.

ERRORS, COMMENTS, SUGGESTIONS

As indicated in the Preface to the first edition of *Bergey's Manual*[®] of *Determinative Bacteriology*, the assistance of all bacteriologists is earnestly solicited in the correction of possible errors in the text. Comments on the presentation will also be welcomed, as well as

suggestions for future editions. Correspondence should be addressed to the Bergey's Manual[®] Board of Trustees c/o Williams & Wilkins, 428 East Preston St., Baltimore, Md. 21202, U.S.A.

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