

BERGEY'S MANUAL OF
**Systematic
Bacteriology**
Volume 1

NOEL R. KRIEG

EDITOR, VOLUME 1

JOHN G. HOLT

EDITOR-IN-CHIEF

EDITORIAL BOARD

**R. G. E. Murray, Chairman, Don J. Brenner
Marvin P. Bryant, John G. Holt, Noel R. Krieg
James W. Moulder, Norbert Pfennig
Peter H. A. Sneath, James T. Staley**

WITH CONTRIBUTIONS FROM
124 COLLEAGUES



WILLIAMS & WILKINS
Baltimore/London



Editor: Barbara Tansill
Associate Editor: Carol-Lynn Brown
Copy Editor: Carol S. Nolley
Design: Joanne Janowiak
Illustration Planning: Lorraine Wrozek
Production: Raymond E. Reter

Copyright © 1984
Williams & Wilkins
428 East Preston Street
Baltimore, MD 21202, U.S.A.

All rights reserved. This book is protected by copyright. No part of this book may be reproduced in any form or by any means, including photocopying, or utilized by any information storage and retrieval system without written permission from the copyright owner.

Made in the United States of America

Library of Congress Cataloging in Publication Data

Main entry under title:

Bergey's manual of systematic bacteriology.

Based on: Bergey's manual of determinative bacteriology.

Includes index.

1. Bacteriology—Classification. I. Bergey, D. H. (David Hendricks), 1860-1937. II. Holt, John G. III. Krieg, Noel R. IV. Bergey's manual of determinative bacteriology, [DNLM: 1. Bacteriology—Terminology. 2. Bacteria—Classification. QW 4 B832m] QR81.B46 1983 589.9'0012 82-21760
ISBN 0-683-04108-8 (v. 1)

Composed and printed in the United States of America

Contributors

Linda Baumann

Department of Bacteriology, University of California,
Davis, California 95616 USA

Paul Baumann

Department of Bacteriology, University of California,
Davis, California 95616 USA

Jan-Hendrik Becking

Institute for Atomic Sciences in Agriculture,
6 Keyenbergseweg, Postbus 48, Wageningen,
The Netherlands

Herve Bercovier

Department of Clinical Microbiology, The Hebrew University,
Hadassah Medical School, P.O. Box 1172, Jerusalem, Israel

Ernst L. Biberstein

Department of Veterinary Medicine, University of California,
Davis, California 95616 USA

Reneé Borral

Department of Microbiology, Louisiana State University,
Baton Rouge, Louisiana 70803 USA

Kjell Bøvre

Kaptein W. Wilhelmsen og Frues Bakteriologiske Institutt,
University of Oslo, Rikshospitalet, Universitetet I Oslo, Oslo
1, Norway

J. F. Bradbury

Commonwealth Mycological Institute, Ferry Lane, Kew,
Surrey TW9 3AF, England

Don J. Brenner

Molecular Biology Laboratory, Biotechnology Branch,
Division of Bacterial Diseases, Center for Infectious Diseases,
Centers for Disease Control, 1600 Clifton Road, N.E.,
Atlanta, Georgia 30333 USA

John A. Breznak

Department of Microbiology and Public Health, Michigan
State University, East Lansing, Michigan 48824 USA

W. J. Brinley-Morgan

Central Veterinary Laboratory, New Haw, Weybridge, Surrey
KT15 3NB, England

Thomas D. Brock

Department of Bacteriology, 1550 Linden Drive, University of
Wisconsin, Madison, Wisconsin 53706 USA

George H. Brownell

Department of Cell and Molecular Biology, Medical College of
Georgia, Augusta, Georgia 30902 USA

Marvin P. Bryant

Department of Dairy Science, University of Illinois,
Urbana, Illinois 61801 USA

Jeffrey C. Burnham

Department of Microbiology, Medical College of Ohio, C.S.
#10008, Toledo, Ohio 43699 USA

E. Canale-Parola

Department of Microbiology, University of Massachusetts,
Amherst, Massachusetts 01003 USA

G. R. Carter

Division of Pathobiology and Public Practice, Virginia-
Maryland Regional College of Veterinary Medicine, Virginia
Polytechnic Institute and State University, Blacksburg,
Virginia 24062 USA

Kwang-Poo Chang

The Rockefeller University, 1230 York Avenue, New York,
New York 10021 USA

Samuel F. Conti

A217 Graduate Research Center, University of
Massachusetts, Amherst, Massachusetts 01003 USA

M. J. Corbel

Central Veterinary Laboratory, New Haw, Weybridge, Surrey
KT15 3NB, England

Gregory A. Dasch

Rickettsial Diseases Branch, Mail Stop 32, Naval Medical
Research Institute, Bethesda, Maryland 20814 USA

Jozef De Ley

Laboratorium voor Microbiologie, K. L. Ledeganckstraat 35,
9000 Gent, Belgium

Robert S. Dickey

Department of Plant Pathology, Cornell University, Ithaca,
New York 14853 USA

Robert B. Dienst

Department of Cell and Molecular Biology, Medical College of
Georgia, Augusta, Georgia 30902 USA

Johanna Döbereiner

EMBRAPA-SNLCS-PFN, Km 47, 23460 Seropédica,
Rio de Janeiro, Brazil

Henry T. Eigelsbach

Western Maryland College, Westminster, Maryland 21157
USA

S. Faine

Department of Microbiology, Monash University, Clayton,
Victoria 3168, Australia

John J. Farmer, III

Enteric Bacteriology Section, Center for Infectious Diseases,
Centers for Disease Control, Atlanta, Georgia 30333 USA

James C. Feeley

Field Investigations Laboratory Section, Respiratory and
Special Pathogens Branch, Centers for Disease Control,
Atlanta, Georgia 30333 USA

E. A. Freundt

FAO/WHO Collaborating Centre for Animal Mycoplasmas,
Institute of Medical Microbiology, Bartholin Building,
University of Aarhus, DK-8000 Aarhus C., Denmark

A. L. Furniss

Public Health Laboratory, Preston Hall Hospital, Maidstone,
Kent ME20 7NH, England

Michel J. Gauthier

Institut National de la Santé et de la Recherche Médicale,
Unité n°40, 1, Avenue Jean Lorrain, 06300 Nice, France

Monique Gillis

Laboratorium voor Microbiologie, K.L. Ledeganckstraat 35,
9000 Gent, Belgium

Y. Goodman

Department of Medical Bacteriology, Medical Sciences
Building, University of Alberta, Edmonton, Alberta, Canada

Francis Gossele

Laboratorium voor Microbiologie, K.L. Ledeganckstraat 35,
9000 Gent, Belgium

Rainer Gothe

Institut für Parasitologie, Rudolf-Buchheim-Strasse 2, D-6300
Giessen, Federal Republic of Germany

R. Nigel Gourlay

ARC Institute for Research on Animal Diseases, Compton,
near Newbury, Berkshire RG16 0NN, England

J. R. Greenwood

Orange County Public Health Laboratory, 1729 W. 17th St.,
Santa Ana, California 92706, USA

Francine Grimont

Entérobactéries, Institut Pasteur, 28, Rue du Docteur Roux,
75724 Paris Cedex 15, France

Patrick A. D. Grimont

Entérobactéries, Institut Pasteur, 28, Rue du Docteur Roux,
75724 Paris Cedex 15, France

Roger J. Gross

Division of Enteric Pathogens, Central Public Health
Laboratory, Colindale Avenue, London NW9 5HT, England

Thomas P. Hatch

Department of Microbiology & Immunology, University of
Tennessee, Center for Health Sciences, Memphis,
Tennessee 38163 USA

Robert B. Hespell

Department of Dairy Science, University of Illinois, Urbana,
Illinois 61801 USA

Peter Hirsch

Institut für Allgemeine Mikrobiologie, Olshausenstrasse 40/60
Biologiezentrum, 2300 Kiel 1, Federal Republic of Germany

Tor Hofstad

Department of Microbiology and Immunology, The Gade
Institute, University of Bergen, N-5000 Bergen, Norway

Lillian V. Holdeman

Department of Anaerobic Microbiology, Virginia Polytechnic
Institute and State University, Blacksburg, Virginia 24061
USA

Barry Holmes

National Collection of Type Cultures, Central Public Health
Laboratory, Colindale Avenue, London NW9 5HT, England

John G. Holt

Department of Microbiology, 205 Sciences I, Iowa State
University, Ames, Iowa 50011 USA

David L. Huxsoll

Military Disease Hazards, Department of the Army, U.S.
Army Medical Research and Development Command, Ft.
Detrick, Frederick, Maryland 21701 USA

Roar L. Irgens

Department of Biology, Southwest Missouri State University,
Springfield, Missouri 65802 USA

F. L. Jackson

Department of Medical Bacteriology, Medical Sciences
Building, University of Alberta, Edmonton, Alberta, Canada

John L. Johnson

Department of Anaerobic Microbiology, Virginia Polytechnic
Institute and State University, Blacksburg, Virginia 24061
USA

Russell C. Johnson

Department of Microbiology, University of Minnesota
Medical School, 1060 Mayo Memorial, Box 196, Minneapolis,
Minnesota 55455 USA

Dorothy Jones

Department of Microbiology, School of Medicine and School
of Biological Sciences, University of Leicester, University
Road, Leicester LE1 7RH, England

D. Carlyle Jordan

Department of Microbiology, College of Biological Science,
University of Guelph, Guelph, Ontario N1G 2W1, Canada

Elliot Juni

Department of Microbiology and Immunology, University of
Michigan Medical School, Ann Arbor, Michigan 48109 USA

Roger W. Kelley

Department of Anaerobic Microbiology, Virginia Polytechnic
Institute and State University, Blacksburg, Virginia 24061
USA

Richard T. Kelly

Department of Pathology, Baptist Memorial Hospital,
Memphis, Tennessee 38146 USA

Karel Kersters

Laboratorium voor Microbiologie, K. L. Ledeganckstraat 35,
9000 Gent, Belgium

Mogens Kilian

Department of Oral Biology, The Royal Dental College,
Vennelyst Boulevard, DK-8000 Aarhus C., Denmark

Dieter H. Knösel

Institut für Angewandte Botanik, Universität Hamburg,
Marseiller Str. 7, D-2000 Hamburg, 36 Federal Republic of
Germany

Miloslav Kocur

Czechoslovak Collection of Microorganisms, J. E. Purkyně
University, 662 43 Brno, Czechoslovakia

A. E. Konopka

Department of Biological Science, Lilly Hall of Life Sciences,
Purdue University, West Lafayette, Indiana 47906 USA

Julius P. Kreier

Department of Microbiology, Ohio State University, 484 West
12th Avenue, Columbus, Ohio 43210 USA

Noel R. Krieg

Department of Biology, Virginia Polytechnic Institute and
State University, Blacksburg, Virginia 24061 USA

Cho-chou Kuo

Department of Pathobiology SC-38, School of Public Health
and Community Medicine, University of Washington, Seattle,
Washington 98195 USA

Thomas A. Langworthy

Department of Microbiology, School of Medicine, University
of South Dakota, Vermillion, South Dakota 57069 USA

Stephen Lapage

27 Salisbury Road, Fordingsbridge Hants SP6 1EH, England

John M. Larkin

Department of Microbiology, Louisiana State University,
Baton Rouge, Louisiana 70803 USA

Helge Larsen

Department of Biochemistry, Norwegian Institute of
Technology, University of Trondheim, N-7034 Trondheim-
NTH, Norway

John V. Lee

Environmental Microbiology and Safety Reference
Laboratory, CAMR, PHLS, Porton Down, Salisbury,
Wiltshire SP4 0JG, England

Sun Y. Lee

Research and Development Department, Adolph Coors
Company, Golden, Colorado 80401 USA

R. A. Lelliott

Ministry of Agriculture, Fisheries and Food, ADAS
Harpden Laboratory, Hatching Green, Harpenden, Herts
AL5 2BD, England

L. Le Minor

Entérobactéries, Institut Pasteur, 28, Rue du Docteur Roux,
75724 Paris Cedex 15, France

Walter Mannheim

Department of Bacteriology, Hygiene-Institut und Medizin-
Untersuchungsamt der Universität Marburg, 3550
Marburg/Lahn, Marburg, Federal Republic of Germany

Randolph E. McCoy

University of Florida, Institute of Food and Agricultural
Sciences, Agricultural Research and Education Center, 3205
S. W. College Avenue, Fort Lauderdale, Florida 33314 USA

Virginia G. McGann

U.S. Army Medical Research Institute of Infectious Diseases,
Frederick, Maryland 21701 USA

Thomas A. McMeekin

Department of Agricultural Science, University of Tasmania,
Box 252C, G.P.O., Hobart, Tasmania 7001, Australia

Alma C. McWhorter

Enteric Bacteriology Section, Center for Infectious Diseases,
Centers for Disease Control, Atlanta, Georgia 30333 USA

Henri H. Mollaret

Institut Pasteur, 28 Rue du Docteur Roux, 75724 Paris Cedex
15, France

W. E. C. Moore

Department of Anaerobic Microbiology, Virginia Polytechnic
Institute and State University, Blacksburg, Virginia 24061
USA

James W. Moulder

Department of Microbiology, Cummings Life Science Center,
University of Chicago, 920 East 58th Street, Chicago, Illinois
60637

R. G. E. Murray

Department of Microbiology and Immunology, University of
Western Ontario, London, Ontario N6A 5C1, Canada

Reinier Mutters

Department of Bacteriology, Medizinisches Zentrum für
Hygiene und Med. Mikrobiologie, Pilgrimstein 2, D-3550
Marburg, Federal Republic of Germany

Peter B. New

Department of Microbiology, University of Sydney, New
South Wales 2006, Australia

Frits Ørskov

International Escherichia and Klebsiella Centre, Statens
Seruminstitut, Artager Boulevard 80, DK-2300 Copenhagen
S, Denmark

Ida Ørskov

International Escherichia and Klebsiella Centre, Statens
Seruminstitut, Artager Boulevard 80, DK-2300 Copenhagen
S, Denmark

Robert J. Owen

National Collection of Type Cultures, Central Public Health
Laboratory, Colindale Avenue, London NW9, 5HT, England

Norberto J. Palleroni

Chemical Research Department, Hoffman-LaRoche, Nutley,
New Jersey 07110 USA

G. B. Patel

Division of Biological Sciences, National Research Council of
Canada, Ottawa, Ontario K1A 0R6, Canada

John L. Penner

Department of Medical Microbiology, University of Toronto,
Banting Institute, 100 College Street, Toronto, Ontario M5G
1L5, Canada

Jerome J. Perry

Department of Microbiology, North Carolina State
University, Raleigh, North Carolina 27650 USA

Norbert Pfennig

Faculty of Biology, University of Konstanz, P.O.B. 5560,
D-775 Konstanz, Federal Republic of Germany

J. E. Phillips

Department of Veterinary Pathology, Royal (Dick) School of
Veterinary Studies, Edinburgh EH9 1QH, Scotland

M. J. Pickett

Department of Microbiology, University of California, Los
Angeles, California 90024 USA

Margaret Pittman

Guest Worker, Office of Biologics, National Center for Drugs
and Biologics, Food and Drug Administration, 8800 Rockville
Pike, Bethesda, Maryland 20205 USA

Michel Popoff

Entérobactéries, Institut Pasteur, 28, Rue du Docteur Roux,
75724 Paris Cedex 15, France

John R. Postgate

ARC Unit of Nitrogen Fixation, University of Sussex,
Brighton BN1 9RQ, England

John R. Preer, Jr.

Department of Biology, Indiana University, Bloomington,
Indiana 47405 USA

Louise B. Preer

Department of Biology, Indiana University, Bloomington,
Indiana 47405 USA

Rudolf A. Prins

Research Institute for Nature Management, P.O. Box 46,
3956 ZR Leersum, The Netherlands

Shmuel Razin

Department of Membrane and Ultrastructure Research, The
Hebrew University—Hadassah Medical School, P.O.B. 1172,
Jerusalem 91010, Israel

C. Richard

Entérobactéries, Institut Pasteur, 28, Rue du Docteur Roux,
75724 Paris Cedex 15, France

Miodrag Ristic

College of Veterinary Medicine, University of Illinois,
Urbana, Illinois 61801 USA

Isadore M. Robinson

National Animal Disease Center, Agricultural Research Service, U.S. Department of Agriculture, Ames, Iowa 50010 USA

Morrison Rogosa

National Institutes of Health, Building 31, Room 3B04, Bethesda, Maryland 20014 USA

Bernard Rowe

Division of Enteric Pathogens, Central Public Health Laboratory, Colindale Avenue, London NW9 5HT, England

Riichi Sakazaki

Enterobacteriology Laboratories, National Institute of Health, 10-35 Kamiosaki-2-chome, Shinagawa-ku, Tokyo, Japan

Norman Savage

Department of Biology, Pan American University, Edinburg, Texas 78539 USA

Julius Schachter

Department of Laboratory Medicine, University of California, San Francisco, San Francisco, California 94143 USA

Hans G. Schlegel

Institut für Mikrobiologie der Universität Göttingen, 3400 Göttingen, Grisebachstrasse 8, Federal Republic of Germany

Ralph H. W. Schubert

Zentrum der Hygiene, Abt. für Allgemeine und Umwelthygiene, 6000 Frankfurt/Main, den, Paul-Ehrlich Strasse 40, Federal Republic of Germany

Robert M. Smibert

Department of Anaerobic Microbiology, Virginia Polytechnic Institute and State University, Blacksburg, Virginia 24061 USA

Paul F. Smith

Department of Microbiology, School of Medicine, University of South Dakota, Vermillion, South Dakota 57069 USA

Peter H. A. Sneath

Department of Microbiology, School of Medicine and School of Biological Sciences, University of Leicester, University Road, Leicester LE1 7RH, England

Jeremy J. S. Snell

Division of Microbiological Reagents and Quality Control, Central Public Health Laboratory, 175 Colindale Avenue, London NW9 5HT, England

Sigmund S. Socransky

Forsyth Dental Center, 140 The Fenway, Boston, Massachusetts 02115 USA

James T. Staley

Department of Microbiology and Immunology, University of Washington, Seattle, Washington 98195 USA

Johannes Storz

Department of Veterinary Microbiology and Parasitology, School of Veterinary Medicine, Louisiana State University, Baton Rouge, Louisiana 70803 USA

Jean Swings

Laboratorium voor Microbiologie, K.L. Ledeganckstraat 35, 9000 Gent, Belgium

Anne C. R. Tanner

Forsyth Dental Center, 140 The Fenway, Boston, Massachusetts 02115 USA

David Taylor-Robinson

Clinical Research Centre, Watford Road, Harrow, Middlesex HA1 3UJ, England

Yao-Tseng Tchan

Department of Microbiology, University of Sydney, New South Wales 2006, Australia

Joseph G. Tully

Mycoplasma Section, Laboratory of Molecular Microbiology, National Institute of Allergy and Infectious Diseases, Building 550, Frederick Cancer Research Facility, Frederick, Maryland 21701 USA

Richard F. Unz

Department of Civil Engineering, 212 Sackett Building, The Pennsylvania State University, University Park, Pennsylvania 16802 USA

Neylan A. Vedros

Department of Biomedical and Environmental Health Sciences, School of Public Health, University of California, Berkeley, California 94720 USA

Russell H. Vreeland

Department of Biological Sciences, University of New Orleans, Lakefront, New Orleans, Louisiana 70148

Robert E. Weaver

Respiratory and Special Pathogens Branch, Division of Bacterial Diseases, Center for Infectious Diseases, Centers for Disease Control, Atlanta, Georgia 30333 USA

Emilio Weiss

Naval Medical Research Institute, Bethesda, Maryland 20014, USA

Robert F. Whitcomb

Building 465, U.S. Department of Agriculture, BARCE, Beltsville, Maryland 20705 USA

Roger Whittenbury

Department of Biological Sciences, University of Warwick, Coventry CV4 7AL, England

Friedrich Widdel

Faculty of Biology, University of Konstanz, P.O. Box 5560, D-775 Konstanz, Federal Republic of Germany

Jürgen K. W. Wiegel

Department of Microbiology, University of Georgia, Athens, Georgia 30602

Advisory Committee Members

The Board of Trustees is grateful to all who served on the Advisory Committees and assisted materially in the preparation of this edition of the *Manual*. Chairmen of committees are indicated by an asterisk.

1. *The Spirochetes*: E. Canale-Parola*
2. *Motile and Nonmotile Helical and Curved Bacteria*: J. C. Burnham, J. Döbereiner, R. Irgens, N. R. Krieg,* J. M. Larkin, S. C. Rittenberg, M. Shilo, J. T. Staley, Y. Terasaki
3. *Gram-Negative Aerobic Rods and Cocci*: W. J. Brinley-Morgan, J. De Ley, D. W. Dye,* H. Larsen, J. M. Vincent, R. Whittenbury
4. *Enterobacteriaceae*: D. J. Brenner,* J. J. Farmer III, W. Frederiksen, L. Le Minor, R. Sakazaki
5. *Vibrionaceae and other Gram-Negative Facultatively Anaerobic Rods*: P. Baumann, D. J. Brenner,* J. J. Farmer, W. Frederiksen, J. M. Shewan
6. *Gram-Negative Anaerobic Bacteria*: M. P. Bryant,* S. Finegold, L. V. Holdeman, J. L. Johnson, W. E. C. Moore, N. Pfennig,* R. M. Smibert, F. Widdel
7. *Gram-Negative Cocci and Coccobacilli*: K. Bøvre,* B. W. Catlin
8. *Gram-Negative Anaerobic Cocci*: M. Rogosa*
9. *The Rickettsias and Chlamydias*: J. M. Moulder*
 Subcommittee on Rickettsias: K. P. Chang, M. Ristic,* E. Weiss
 Subcommittee on Chlamydias: T. Hatch, C.-c. Kuo, J. Schachter,* J. Storz
10. *The Mycoplasmas*: E. A. Freundt,* S. Razin, J. G. Tully, R. F. Whitcomb
11. *Endosymbionts*: G. A. Dasch, K. P. Chang, E. Weiss*

In addition, the Board extends special thanks to G. R. Carter, E. Juni, and N. A. Vedros for their invaluable help.

Preface to First Edition of Bergey's Manual of Systematic Bacteriology

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.

The invited authors were provided with instructions and exemplary chapters in June 1980 and, although the intended deadline for receipt of manuscripts was March 1981, all contributions were assembled in January 1982 for the final preparations. The *Manual* was forwarded to the publisher in June 1982.

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 with certain pathogens, 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 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 Editor.

To all contributors, the sincere thanks of the Trust is due; the Editor is 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 Department of Biology of the Virginia Polytechnic Institute and State University 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 continued support. A grant (LM-03707) from the National Library of Medicine, National Institutes of Health to assist in the preparation of this and the next volume of the *Manual* is gratefully acknowledged.

A number of individuals deserve special mention and thanks for their help. Professor Thomas O. McAdoo 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 Editor in the Blacksburg office were R. Martin Roop II, Don D. Lee, Eileen C. Falk and Michael W. Friedman and their help is sincerely appreciated. In the Ames office we were ably assisted by Gretchen Colletti and Diane Triggs during the early period of preparation and by Cynthia Pease during the major portion of the editing process. Mrs. Pease has been responsible for the construction of the List of References and her willingness to handle the cumbersome details of text editing on a big computer is gratefully acknowledged.

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

Preface to First Edition of Bergey's Manual of Determinative Bacteriology

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 student, 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*
FRANCIS C. HARRISON
ROBERT S. BREED
BERNARD W. HAMMER
FRANK M. HUNTOON
Committee on Manual.

August, 1923.



Archives of the ASM

DAVID HENDRICKS BERGEY

1860-1937

Bergey set up the Trust on January 2, 1936

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 for 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 The Williams & Wilkins Company 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.

David H. Bergey	Noel R. Krieg
Robert S. Breed	Hans Lautrop
Don J. Brenner	John Liston
Marvin P. Bryant	Stephen P. Lapage
R. E. Buchanan	James W. Moulder
Harold J. Conn	E. G. D. Murray
Samuel T. Cowan	R. G. E. Murray
Geoffrey Edsall	Charles F. Niven, Jr.
Norman E. Gibbons	Norbert Pfennig
Bernard W. Hammer	Arnold W. Ravin
Francis C. Harrison	Nathan R. Smith
A. Parker Hitchens	P. H. A. Sneath
John G. Holt	James T. Staley
Frank M. Huntoon	Roger Y. Stanier

On Using the Manual

Noel R. Krieg

ARRANGEMENT OF THE MANUAL

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 relatedness to one another. Such a general classification scheme would lead 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 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 *Gardnerella*. The organisms of this genus have had a checkered taxonomic history and it is still not entirely clear whether they should be placed in Volume 1 with Gram-negative bacteria or in Volume 2 with Gram-positive bacteria.
- (b) The genus *Butyrivibrio*. Although the cells stain Gram-negative the ultrastructure of the cell wall is of the Gram-positive type. It is not clear whether the genus should be placed in Volume 1 or Volume 2.
- (c) The genus *Xanthobacter*. The cells stain Gram-positive or Gram-variable, yet the cell wall structure and composition, as well as nucleic acid hybridization data, indicate that the organisms are of the Gram-negative type.
- (d) The genus *Chromobacterium*. Although 80% of the strains attack glucose fermentatively and grow well anaerobically, the remainder attack glucose oxidatively and grow slowly under anaerobic conditions. It is consequently difficult to assign the organisms definitively to either Section 5 (Facultatively Anaerobic Gram-

Negative Rods) or Section 4 (Gram-Negative Aerobic Rods and Cocci). Nucleic acid hybridization studies indicate a relationship to certain genera of aerobic rods.

- (e) The genus *Zymomonas*. Although the organisms are facultatively anaerobic (a few obligately anaerobic), they are related genetically, phenotypically and ecologically to the acetic acid bacteria, which are aerobic. Moreover, the occurrence of the Entner-Doudoroff pathway is typical of aerobic bacteria.
- (f) The genus *Thermoplasma*. The lack of a cell wall makes this genus compatible with Section 10 (The Mycoplasmas); however, studies of the ribosomal RNA, as well as various phenotypic characteristics, indicate that the genus is related to the archaeobacteria, covered in Volume 3 of the *Manual*.
- (g) The genera *Halobacterium* and *Halococcus*. Although these extreme halophiles are compatible with Section 4 (Gram-Negative Aerobic Rods and Cocci), nucleic acid studies and certain phenotypic characteristics indicate the genus is related to the archaeobacteria, covered in Volume 3.

As an interim solution to some of these problems, some taxa are described not only in Volume 1 but in an appropriate subsequent volume as well.

SECTIONS VS. TAXONOMIC NAMES

Each section bears a vernacular name, but sometimes it also bears the name of a taxon. For example, Section 10 (The Mycoplasmas) is

the Division Tenericutes, Class Mollicutes; Section 1 (The Spirochetes) is the order Spirochetetales; and Section 8 (Anaerobic Gram-Negative

Cocci) is the family *Veillonellaceae*. Some sections may contain more than one order (e.g. Section 9) or family (e.g. Section 5), and some may contain no taxa whatever above the level of genus (e.g. Section 7). 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?).

Some families recognized in the *Manual* represent groups of related genera (e.g. the family *Enterobacteriaceae*). Others, however, are merely families based on practical convenience rather than any known degree of relatedness (e.g. the family *Methylococcaceae*).

In sections containing one or more families, there may be an appendix entitled "Other Organisms." While these genera belong to a particular section, they have not been accepted into any of the recognized families

and cannot themselves be grouped into families on the information presently available. For example, Section 5 (Facultatively Anaerobic Gram-Negative Rods) consists of the families *Enterobacteriaceae*, *Vibrionaceae*, and *Pasteurellaceae* and concludes with an appended list of seven additional genera that do not belong to any family (*Zymomonas*, *Chromobacterium*, *Cardiobacterium*, *Calymmatobacterium*, *Gardnerella*, *Eikenella*, and *Streptobacillus*).

Certain sections of the *Manual* may conclude with descriptions of organisms which, for various reasons, have not yet been assigned to a genus. For example, Section 1 concludes with an article on Hindgut Spirochetes of Termites and *Cryptocercus punctulatus*, i.e. a group of spirochetes which have not been cultured. Section 11 (Endosymbionts) deals mainly with unclassified endosymbionts of insects and other organisms. The purpose of including such unclassified organisms in the *Manual* is to stimulate research on their taxonomy.

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 presented in a definite 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.
- (k) *Taxonomic Comments*. This summarizes the available information about the taxonomic placement of the genus and indicates the justification for considering the 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 the 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 The Williams & Wilkins Co., 428 East Preston St., Baltimore, Md. 21202, U.S.A.

Contents

Contributors	vii
Advisory Committee Members	xi
Preface to First Edition of Bergey's Manual of Systematic Bacteriology	xiii
Preface to First Edition of Bergey's Manual of Determinative Bacteriology	xv
History of the Manual	xvii
On Using the Manual	xix
Bacterial Classification	
I. Classification of Procaryotic Organisms: An Overview	1
II. Numerical Taxonomy	5
III. Nucleic Acids in Bacterial Classification	8
IV. Genetic Methods	12
V. Serology and Chemotaxonomy	15
Bacterial Nomenclature	19
Identification of Bacteria	24
Reference Collections of Bacteria—The Need and Requirement for Type Strains	27
List of Culture Collections	29
The Higher Taxa, or a Place for Everything?	31
KINGDOM PROCARYOTAE	35
Division I. Gracilicutes	35
Division II. Firmicutes	36
Division III. Tenericutes	36
Division IV. Mendosicutes	36
SECTION 1.	
The Spirochetes	38
Order I. <i>Spirochaetales</i>	38
Family I. <i>Spirochaetaceae</i>	39
Genus I. <i>Spirochaeta</i>	39
Genus II. <i>Cristispira</i>	46
Genus III. <i>Treponema</i>	49
Genus IV. <i>Borrelia</i>	57
Family II. <i>Leptospiraceae</i>	62
Genus I. <i>Leptospira</i>	62
Other Organisms	
Hindgut Spirochetes of Termites and <i>Cryptocercus punctulatus</i>	67