

BERGEY'S MANUAL® OF

**Systematic
Bacteriology**

Second Edition

Volume One

**The *Archaea* and the Deeply Branching and
Phototrophic *Bacteria***

Springer Science+Business Media, LLC

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

Volume One
**The *Archaea* and the Deeply Branching and
Phototrophic *Bacteria***

David R. Boone
Richard W. Castenholz
EDITORS, VOLUME ONE

George M. Garrity
EDITOR-IN-CHIEF

EDITORIAL BOARD
James T. Staley, Chairman, **David R. Boone**, Vice Chairman,
Don J. Brenner, **Richard W. Castenholz**, **George M. Garrity**, **Michael**
Goodfellow, **Noel R. Krieg**, **Fred A. Rainey**, **Karl-Heinz Schleifer**

WITH CONTRIBUTIONS FROM 105 COLLEAGUES



Springer

Library of Congress Cataloging-in-Publication Data

Bergey's manual of systematic bacteriology / David R. Boone, Richard W. Castenholz, editors, volume 1 ; George M. Garrity, editor-in-chief.—2nd ed.

p. cm.

Includes bibliographical references and index.

Contents: v. 1. The archaea and the deeply branching and phototrophic bacteria.

I. Bacteria—Classification. I. Title: Systematic bacteriology. II. Boone, David R. III. Castenholz, Richard W. IV. Garrity, George M.

QR81.B46 2001

579.3'01'2—dc21

2001020400

With 330 illustrations

The following proprietary names of products are used in this volume: Casamino[®] acids; Vector NTI[®]; XL10-Gold[®]; Gelrite[®]; Tryptone[®]; Phytigel[®]; bio-Trypcase[®]; Trypticase[®]; Oxoid[®] purified agar.

Printed on acid-free paper.

First edition published 1984–1989 by Bergey's Manual Trust and Williams & Wilkins, Baltimore.

© 2001 Springer Science+Business Media New York

Originally published by Bergey's Manual Trust in 2001

Softcover reprint of the hardcover 1st edition 2001

All rights reserved. This work may not be translated or copied in whole or in part without the written permission of the publisher Springer Science+Business Media, LLC

except for brief excerpts in connection with reviews or scholarly analysis. Use in connection with any form of information storage and retrieval, electronic adaptation, computer software, or by similar or dissimilar methodology now known or hereafter developed is forbidden.

The use of general descriptive names, trade names, trademarks, etc., in this publication, even if the former are not especially identified, is not to be taken as a sign that such names, as understood by the Trade Marks and Merchandise Marks Act, may accordingly be used freely by anyone.

While the advice and information in this book are believed to be true and accurate at the date of going to press, neither the authors nor the editors nor the publisher can accept any legal responsibility for any errors or omissions that may be made. The publisher makes no warranty, express or implied, with respect to the material contained herein.

Production coordinated by Impressions Book and Journal Services, Inc., and managed by Frederick Bartlett, Theresa Kornak, and Catherine Lyons; manufacturing supervised by Jacqui Ashri.

Typeset by Impressions Book and Journal Services, Inc., Madison, WI.

9 8 7 6 5 4 3 2 1

SPIN 10711344

ISBN 978-1-4419-3159-7 ISBN 978-0-387-21609-6 (eBook)

DOI 10.1007/978-0-387-21609-6

EDITORIAL BOARD AND TRUSTEES
OF BERGEY'S MANUAL TRUST

James T. Staley, *Chairman*
David R. Boone, *Vice Chairman*
Don J. Brenner
Richard W. Castenholz
George M. Garrity
Michael Goodfellow
Noel R. Krieg
Fred A. Rainey
Karl-Heinz Schleifer
John G. Holt, *Emeritus*
John Liston, *Emeritus*
James W. Moulder, *Emeritus*
R.G.E. Murray, *Emeritus*
Charles F. Niven, Jr., *Emeritus*
Norbert Pfennig, *Emeritus*
Peter H.A. Sneath, *Emeritus*
Joseph G. Tully, *Emeritus*
Stanley T. Williams, *Emeritus*

Preface to the Second Edition of *Bergey's Manual*[®] of *Systematic Bacteriology*

There is a long-standing tradition for the Editors of each successive edition of *Bergey's Manual* to open their respective volumes with the observation that the new edition is a departure from the earlier ones. We shall not waver from this tradition, as the very nature of our field compels us to make this pronouncement. Systematic bacteriology (or perhaps systematic procaryotic biology) is a dynamic field, driven by constant theoretical and methodological advances that will ultimately lead to a more perfect and useful classification scheme.

Since publication of the First Edition of the *Systematics Manual*, we have witnessed a major shift in how we view the relationships among *Bacteria* and *Archaea*. While the possibility of a universally applicable natural classification was evident as the First Edition was in preparation, it is only recently that the sequence databases became large enough, and the taxonomic coverage broad enough, to make such an arrangement feasible. We have relied heavily upon these data in organizing the contents of this edition of *Bergey's Manual of Systematic Bacteriology*, which will follow a phylogenetic framework based on analysis of the nucleotide sequence of the small ribosomal subunit RNA, rather than a phenotypic structure. This departs from the First Edition, as well as the Eighth and Ninth Editions of the *Determinative Manual*. While the rationale for presenting the content of this edition in such a manner should be evident to most readers, they should bear in mind that this edition, as have all preceding ones, represents a progress report rather than a final classification of procaryotes.

The Editors remind the readers that the *Systematics Manual* 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. Citation should refer to the author, the chapter title, and inclusive pages rather than to the Editors. 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 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. We would also like to recognize the special efforts of Drs. Hans Trüper and Brian Tindall for their assistance on

matters of nomenclature and etymology and Dr. Aharon Oren for his critical reading of large portions of the *Manual*.

We would like to express our thanks to the Department of Microbiology and Molecular Genetics at Michigan State University for housing our headquarters and editorial office and for providing a congenial and supportive environment for microbial systematics. We would also like to thank Connie Williams not only for her expert secretarial assistance, but also for unflagging dedication to the mission of Bergey's Manual Trust and Dr. Denise Searles for her editorial assistance and diligence in verifying countless pieces of critical information, along with Heather Everett, Alissa Wesche, and Mathew Winters for their assistance in fact-checking and compilation of the bibliography.

A project such as the *Systematics Manual* also requires the strong and continued support of a dedicated publisher, and we have been most fortunate in this regard. We would also like to express our gratitude to Springer-Verlag for supporting our efforts and for the development of the Bergey's Document Type Definition (DTD). We would especially like to thank our Executive Editor, Dr. Robert Badger, for his courage, patience, understanding, and support; Catherine Lyons for her expertise in designing and developing our DTD, and Terry Kornak and Fred Bartlett for their efforts during the pre-production and production phases. We would also like to acknowledge the support of ArborText, Inc., for providing us with state-of-the-art SGML development and editing tools at reduced cost. Lastly, I would like to express my personal thanks to my fellow trustees for providing me with the opportunity to participate in this effort, to Drs. David Boone and Richard Castenholz for their enormous efforts as volume editors and to my wife, Nancy, and daughter, Jane, for their patience, tolerance, and support.

Comments on this edition are welcomed and should be directed to Bergey's Manual Trust, Department of Microbiology and Molecular Genetics, Giltner Hall, Michigan State University, East Lansing, MI, USA 48824-1101. Email: garrity@pilot.msu.edu

George M. Garrity

Preface to the 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 au-

thorities 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. . .

Preface to the 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 (1911, 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.

Contents

Preface to the Second Edition of <i>Bergey's Manual</i> ® of Systematic Bacteriology	vii
Preface to the First Edition of <i>Bergey's Manual</i> ® of Systematic Bacteriology	ix
Preface to the First Edition of <i>Bergey's Manual</i> ® of Determinative Bacteriology	xi
Contributors	xix
The History of <i>Bergey's Manual</i>	1
On Using the <i>Manual</i>	15
Procaryotic Domains	21
Classification of Procaryotic Organisms and the Concept of Bacterial Speciation	27
Identification of Procaryotes	33
Numerical Taxonomy	39
Polyphasic Taxonomy	43
Overview: A Phylogenetic Backbone and Taxonomic Framework for Procaryotic Systematics	49
Nucleic Acid Probes and Their Application in Environmental Microbiology	67
Bacterial Nomenclature	83
Etymology in Nomenclature of Procaryotes	89
Microbial Ecology—New Directions, New Importance	101
Culture Collections: An Essential Resource for Microbiology	111
Intellectual Property of Procaryotes	115
The Road Map to the <i>Manual</i>	119
DOMAIN ARCHAEA	
PHYLUM AI	
Crenarchaeota	169
Class I. <i>Thermoprotei</i>	169
Order I. <i>Thermoproteales</i>	170
Family I. <i>Thermoproteaceae</i>	170
Genus I. <i>Thermoproteus</i>	171
Genus II. <i>Caldivirga</i>	173
Genus III. <i>Pyrobaculum</i>	174
Genus IV. <i>Thermocladium</i>	177
Family II. <i>Thermofilaceae</i>	178
Genus I. <i>Thermofilum</i>	178
Order II. <i>Desulfurococcales</i>	179
Family I. <i>Desulfurococcaceae</i>	180
Genus I. <i>Desulfurococcus</i>	181
Genus II. <i>Aeropyrum</i>	183
Genus III. <i>Ignicoccus</i>	184
Genus IV. <i>Staphylothermus</i>	186
Genus V. <i>Stetteria</i>	187
Genus VI. <i>Sulfophobococcus</i>	188

Genus VII. <i>Thermodiscus</i>	189
Genus VIII. <i>Thermosphaera</i>	190
Family II. <i>Pyrodictiaceae</i>	191
Genus I. <i>Pyrodictium</i>	192
Genus II. <i>Hyperthermus</i>	195
Genus III. <i>Pyrolobus</i>	196
Order III. <i>Sulfolobales</i>	198
Family I. <i>Sulfolobaceae</i>	198
Genus I. <i>Sulfolobus</i>	198
Genus II. <i>Acidianus</i>	202
Genus III. <i>Metallosphaera</i>	204
Genus IV. <i>Stygiolobus</i>	207
Genus V. <i>Sulfurisphaera</i>	208
Genus VI. <i>Sulfurococcus</i>	209
PHYLUM AII	
Euryarchaeota	211
Taxonomy of Methanogenic Archaea	211
Class I. <i>Methanobacteria</i>	213
Order Methanobacteriales	214
Family I. <i>Methanobacteriaceae</i>	214
Genus I. <i>Methanobacterium</i>	215
Genus II. <i>Methanobrevibacter</i>	218
Genus III. <i>Methanosphaera</i>	226
Genus IV. <i>Methanothermobacter</i>	230
Family II. <i>Methanothermaceae</i>	233
Genus I. <i>Methanothermus</i>	233
Class II. <i>Methanococci</i>	235
Order I. <i>Methanococcales</i>	236
Family I. <i>Methanococcaceae</i>	236
Genus I. <i>Methanococcus</i>	236
Genus II. <i>Methanothermococcus</i>	241
Family II. <i>Methanocaldococcaceae</i>	242
Genus I. <i>Methanocaldococcus</i>	243
Genus II. <i>Methanotorris</i>	245
Order II. <i>Methanomicrobiales</i>	246
Family I. <i>Methanomicrobiaceae</i>	247
Genus I. <i>Methanomicrobium</i>	247
Genus II. <i>Methanoculleus</i>	251
Genus III. <i>Methanofollis</i>	253
Genus IV. <i>Methanogenium</i>	256
Genus V. <i>Methanolacinia</i>	258
Genus VI. <i>Methanoplanus</i>	259
Family II. <i>Methanocorpusculaceae</i>	262
Genus I. <i>Methanocorpusculum</i>	262
Family III. <i>Methanospirillaceae</i>	264
Genus I. <i>Methanospirillum</i>	264
Genus Incertae Sedis I. <i>Methanocalculus</i>	267
Order III. <i>Methanosarcinales</i>	268
Family I. <i>Methanosarcinaceae</i>	268
Genus I. <i>Methanosarcina</i>	269
Genus II. <i>Methanococcoides</i>	276
Genus III. <i>Methanohalobium</i>	279
Genus IV. <i>Methanohalophilus</i>	281
Genus V. <i>Methanolobus</i>	283
Genus VI. <i>Methanosalsum</i>	287
Family II. <i>Methanosaetaceae</i>	289

Genus I. <i>Methanosaeta</i>	289
Class III. <i>Halobacteria</i>	294
Order I. <i>Halobacteriales</i>	294
Family I. <i>Halobacteriaceae</i>	299
Genus I. <i>Halobacterium</i>	301
Genus II. <i>Haloarcula</i>	305
Genus III. <i>Halobaculum</i>	309
Genus IV. <i>Halococcus</i>	311
Genus V. <i>Haloferax</i>	315
Genus VI. <i>Halogeometricum</i>	318
Genus VII. <i>Halorubrum</i>	320
Genus VIII. <i>Haloterrigena</i>	324
Genus IX. <i>Natrialba</i>	325
Genus X. <i>Natrinema</i>	327
Genus XI. <i>Natronobacterium</i>	329
Genus XII. <i>Natronococcus</i>	330
Genus XIII. <i>Natronomonas</i>	332
Genus XIV. <i>Natronorubrum</i>	333
Class IV. <i>Thermoplasmata</i>	335
Order I. <i>Thermoplasmatales</i>	335
Family I. <i>Thermoplasmataceae</i>	335
Genus I. <i>Thermoplasma</i>	335
Family II. <i>Picrophilaceae</i>	339
Genus I. <i>Picrophilus</i>	339
Class IV. <i>Thermococci</i>	341
Order I. <i>Thermococcales</i>	341
Family I. <i>Thermococcaceae</i>	341
Genus I. <i>Thermococcus</i>	342
Genus II. <i>Pyrococcus</i>	346
Class VI. <i>Archaeoglobi</i>	349
Order I. <i>Archaeoglobales</i>	349
Family I. <i>Archaeoglobaceae</i>	349
Genus I. <i>Archaeoglobus</i>	349
Genus II. <i>Ferroglobus</i>	352
Class VII. <i>Methanopyri</i>	353
Order I. <i>Methanopyrales</i>	353
Family I. <i>Methanopyraceae</i>	353
Genus I. <i>Methanopyrus</i>	354

DOMAIN *BACTERIA*

PHYLUM BI

Aquificae	359
Class I. <i>Aquificae</i>	359
Order I. <i>Aquificales</i>	359
Family I. <i>Aquificaceae</i>	360
Genus I. <i>Aquifex</i>	360
Genus II. <i>Calderobacterium</i>	362
Genus III. <i>Hydrogenobacter</i>	363
Genus IV. <i>Thermocrinis</i>	364
Genus Incertae Sedis I. <i>Desulfurobacterium</i>	366

PHYLUM BII

Thermotogae	369
Class I. <i>Thermotogae</i>	369
Order I. <i>Thermotogales</i>	369
Family I. <i>Thermotogaceae</i>	370
Genus I. <i>Thermotoga</i>	370

Genus II. <i>Fervidobacterium</i>	375
Genus III. <i>Geotoga</i>	377
Genus IV. <i>Petrotoga</i>	382
Genus V. <i>Thermosipho</i>	385
PHYLUM BIII	
Thermodesulfobacteria	389
Class I. <i>Thermodesulfobacteria</i>	389
Order I. <i>Thermodesulfobacteriales</i>	389
Family I. <i>Thermodesulfobacteriaceae</i>	390
Genus I. <i>Thermodesulfobacterium</i>	390
PHYLUM BIV	
“Deinococcus–Thermus”	395
Class I. <i>Deinococci</i>	395
Order I. <i>Deinococcales</i>	395
Family I. <i>Deinococcaceae</i>	395
Genus I. <i>Deinococcus</i>	396
Order II. <i>Thermales</i>	403
Family I. <i>Thermaceae</i>	403
Genus I. <i>Thermus</i>	404
Genus II. <i>Meiothermus</i>	414
PHYLUM BV	
Chrysiogenetes	421
Class I. <i>Chrysiogenetes</i>	421
Order I. <i>Chrysiogenales</i>	421
Family I. <i>Chrysiogenaceae</i>	421
Genus I. <i>Chrysiogenes</i>	422
PHYLUM BVI	
Chloroflexi	427
Class I. “ <i>Chloroflexi</i> ”	427
Order I. “ <i>Chloroflexales</i> ”	427
Family I. “ <i>Chloroflexaceae</i> ”	427
Filamentous Anoxygenic Phototrophic Bacteria	427
Genus I. <i>Chloroflexus</i>	429
Genus II. <i>Chloronema</i>	437
Genus III. <i>Heliothrix</i>	438
Genus IV. <i>Oscillochloris</i>	440
Order II. “ <i>Herpetosiphonales</i> ”	444
Family I. “ <i>Herpetosiphonaceae</i> ”	445
Genus I. <i>Herpetosiphon</i>	445
PHYLUM BVII	
Thermomicrobia	447
Class I. <i>Thermomicrobia</i>	447
Order I. <i>Thermomicrobiales</i>	447
Family I. <i>Thermomicrobiaceae</i>	447
Genus I. <i>Thermomicrobium</i>	448
PHYLUM BVIII	
Nitrospirae	451
Class I. “ <i>Nitrospira</i> ”	451
Order I. “ <i>Nitrospirales</i> ”	451
Family I. “ <i>Nitrospiraceae</i> ”	451
Genus I. <i>Nitrospira</i>	451
Genus II. <i>Leptospirillum</i>	453
Genus III. “ <i>Candidatus Magnetobacterium</i> ”	457
Genus IV. <i>Thermodesulfovibrio</i>	460

PHYLUM BIX

Deferribacteres	465
Class I. <i>Deferribacteres</i>	465
Order I. <i>Deferribacterales</i>	465
Family I. <i>Deferribacteraceae</i>	465
Genus I. <i>Deferribacter</i>	466
Genus II. <i>Flexistipes</i>	468
Genus III. <i>Geovibrio</i>	468
Genus Incertae Sedis I. <i>Synergistes</i>	470

PHYLUM BX

Cyanobacteria	473
Oxygenic Photosynthetic Bacteria	473
Oxygenic Photosynthetic Bacteria	474
General Characteristics of the Cyanobacteria	474
Phylogenetic Relationships Among the Cyanobacteria Based on	
16S rRNA Sequences	487
Subsection I.	493
Form-genus I. <i>Chamaesiphon</i>	495
Form-genus II. <i>Chroococcus</i>	496
Form-genus III. <i>Cyanobacterium</i>	497
Form-genus IV. <i>Cyanobium</i>	498
Form-genus V. <i>Cyanothece</i>	499
Form-genus VI. <i>Dactylococcopsis</i>	501
Form-genus VII. <i>Gloeobacter</i>	502
Form-genus VIII. <i>Gloeocapsa</i>	503
Form-genus IX. <i>Gloeotheca</i>	504
Form-genus X. <i>Microcystis</i>	505
Form-genus XI. <i>Prochlorococcus</i>	506
Form-genus XII. <i>Prochloron</i>	507
Form-genus XIII. <i>Synechococcus</i>	508
Form-genus XIV. <i>Synechocystis</i>	512
Subsection II.	514
Genera Reproducing by Multiple Fissions Only, or in Combination with	
Limited (1–3) Binary Fissions	520
Form-genus I. <i>Cyanocystis</i>	520
Form-genus II. <i>Dermocarpella</i>	520
Form-genus III. <i>Stanieria</i>	523
Form-genus IV. <i>Xenococcus</i>	524
Genera in Which Extensive Vegetative Binary Fission Precedes Multiple	
Fission	528
Form-genus I. <i>Chroococcidiopsis</i>	528
Form-genus II. <i>Myxosarcina</i>	531
Pleurocapsa-group	533
Subsection III.	539
Form-genus I. <i>Arthrospira</i>	542
Form-genus II. <i>Borzia</i>	543
Form-genus III. <i>Crinalium</i>	543
Form-genus IV. <i>Geitlerinema</i>	544
Form-genus V. <i>Leptolyngbya</i>	544
Form-genus VI. <i>Limnothrix</i>	546
Form-genus VII. <i>Lyngbya</i>	547
Form-genus VIII. <i>Microcoleus</i>	548
Form-genus IX. <i>Oscillatoria</i>	550
Form-genus X. <i>Planktothrix</i>	553
Form-genus XI. <i>Prochlorothrix</i>	554
Form-genus XII. <i>Pseudanabaena</i>	554

Form-genus XIII. <i>Spirulina</i>	557
Form-genus XIV. <i>Starria</i>	559
Form-genus XV. <i>Symploca</i>	559
Form-genus XVI. <i>Trichodesmium</i>	560
Form-genus XVII. <i>Tychonema</i>	561
Subsection IV.	562
Subsection IV.I	565
Form-genus I. <i>Anabaena</i>	566
Form-genus II. <i>Anabaenopsis</i>	568
Form-genus III. <i>Aphanizomenon</i>	569
Form-genus IV. <i>Cyanospira</i>	570
Form-genus V. <i>Cylindrospermopsis</i>	571
Form-genus VI. <i>Cylindrospermum</i>	572
Form-genus VII. <i>Nodularia</i>	574
Form-genus VIII. <i>Nostoc</i>	575
Form-genus IX. <i>Scytonema</i>	580
Subsection IV.II	582
Form-genus I. <i>Calothrix</i>	582
Form-genus II. <i>Rivularia</i>	586
Form-genus III. <i>Tolypothrix</i>	587
Subsection V.	589
Form-genus I. <i>Chlorogloeopsis</i>	591
Form-genus II. <i>Fischerella</i>	593
Form-genus III. <i>Geitleria</i>	595
Form-genus IV. <i>Iyengariella</i>	598
Form-genus V. <i>Nostochopsis</i>	598
Form-genus VI. <i>Stigonema</i>	599
PHYLUM BXI	
Chlorobi	601
Class I. " <i>Chlorobia</i> "	601
Subclass I.	601
Order I. " <i>Chlorobiales</i> "	601
Family I. " <i>Chlorobiaceae</i> "	601
Green Sulfur Bacteria	601
Genus I. <i>Chlorobium</i>	605
Genus II. <i>Ancalochloris</i>	610
Genus III. <i>Chloroherpeton</i>	612
Genus IV. <i>Pelodictyon</i>	614
Genus V. <i>Prosthecochloris</i>	617
Addendum to the Green Sulfur Bacteria: Phototrophic Green Sulfur Bacteria	
Living in Consortia with Other Microorganisms.	620
PHYLUM BXIII	
Firmicutes	625
Class I. " <i>Clostridia</i> "	625
Order I. " <i>Clostridiales</i> "	625
Family VI. " <i>Heliobacteriaceae</i> "	625
Genus I. <i>Heliobacterium</i>	626
Genus II. <i>Heliobacillus</i>	629
Genus III. <i>Heliophilum</i>	629
Genus IV. <i>Heliorestis</i>	630
The Anoxygenic Phototrophic Purple Bacteria	631
Bibliography	639
Index of Scientific Names of <i>Archaea</i> and <i>Bacteria</i>	703

Contributors

Milton J. Allison

USDA, Agricultural Research Service—Midwest Area, National Animal Disease Center, Ames, IA 50010-0070, USA

Rudolf Amann

Nachwuchsgruppe Molekulare Ökologie, Max Planck Institute für Marine Mikrobiologie, Celsiusstrasse 1, D28359 Bremen, Germany

Chad C. Baker

Oregon Graduate Institute, P.O. Box 91000, Portland, OR 97291-1000, USA

John R. Battista

Department of Microbiology, Louisiana State University, Baton Rouge, LA 70803-0001, USA

Eberhard Bock

Inst. für Allgemeine Botanik und Botanischer Garten, Universität Hamburg, Ohnhorststrasse 18, Hamburg D-22609, Germany

David R. Boone

Department of Environmental Biology, Portland State University, Portland, OR 97207-0751, USA

Don J. Brenner

Meningitis & Special Pathogens Branch Laboratory Section, Centers for Disease Control & Prevention, Atlanta, GA 30333, USA

Frank Caccavo, Jr.

Department of Microbiology, University of New Hampshire, Rudman Hall/Spaulding, 46 College Road, Durham, NH 03824, USA

Richard W. Castenholz

Department of Biology, University of Oregon, Eugene, OR 97403-1210, USA

Song C. Chong

Department of Environmental Biology, Portland State University, Portland, OR 97207-0751, USA

Milton S. da Costa

Centro de Neurociências, Departamento de Zoologia, Universidade de Coimbra, Apartado 3126, P-3004-517, Coimbra, Portugal

Mary Ellen Davey

Microbiology Department, Dartmouth Medical School, Room 202, Vail Bldg., North College Street, Hanover, NH 03755, USA

Paul De Vos

Department of Biochemistry, Physiology & Microbiology (WE 10V), K.L. Ledeganckstraat 35, B-9000, Gent, Belgium

Wolfgang Eder

Lehrstuhl für Mikrobiologie, Universität Regensburg, Universitätsstrasse 31, Regensburg 93053, Germany

James G. Ferry

Department of Biochemistry & Molecular Biology, The Pennsylvania State University, University Park, PA 16802-4500, USA

Jean-Louis Garcia

Laboratoire de Microbiologie, Université de Provence, OR-

STROM-ESIL-Case 925, 163, Avenue de Luminy, 13288 Marseille Cédex 9, France

George M. Garrity

Department of Microbiology and Molecular Genetics, Michigan State University, East Lansing, MI 48824-1101, USA

Jane Gibson

Section of Biochemistry, Molecular & Cell Biology, Division of Biological Sciences, Cornell University, Ithaca, NY 14853-0001, USA

Monique Gillis

Laboratorium voor Microbiologie en Microbiele Genetica (WE 10V), Rijksuniversiteit Gent, K.-L. Ledeganckstraat 35, B-9000 Gent, Belgium

Vladimir M. Gorlenko

Institute of Microbiology, Russian Academy of Sciences, Prospect 60-letiya, Otyabrya 7 k.2, Moscow 117811, Russia

William D. Grant

Microbiology & Immunology, Leicester University, University Road, Leicester LE1 9HN, England

Anthony C. Greene

School of Biomolecular and Biomedical Science, Academic 1 Building, Logan Campus, Griffith University, Meadowbrook, Queensland 4131, Australia

Doris Hafenbradl

10665 Sorrento Valley Road, San Diego, CA 92121, USA

E. Claude Hatchikian

IBSM-CNRS, Unité de Bioenergetique et Ingenierie des Proteines, 31, Chemin Joseph-Aiguier, 13402 Marseille Cedex 20, France

Michael Herdman

Physiologie Microbienne, Dept. B.M.G., CNRS-URA, 2172, Institut Pasteur, 28 Rue du Docteur Roux, F-75724 Paris Cedex 15, France

Lucien Hoffmann

Laboratoire d'Algologie, de Mycologie et de Systématique Expérimentale, Institut de Botanique, B. 22, Université de Liège, Sart Tilman, B-4000, Liège, Belgium

John G. Holt

Department of Microbiology and Molecular Genetics, Michigan State University, East Lansing, MI 48824-1101, USA

Gertrud Huber

Lehrstuhl für Mikrobiologie, Universität Regensburg, Universitätsstrasse 31, Regensburg, Germany

Harald Huber

Lehrstuhl für Mikrobiologie, Universität Regensburg, Universitätsstrasse 31, Regensburg, Germany

Robert Huber

Lehrstuhl für Mikrobiologie, Universität Regensburg, Universitätsstrasse 31, Regensburg, Germany

Yasuo Igarashi

Department of Biotechnology, University of Tokyo, 1-1-1 Yayoi, Bunkyo-ku, Tokyo 113-8657, Japan

Johannes F. Imhoff

Institut für Meereskunde, Universität Kiel, Abt. Marine Mikrobiologie, Düsternbrooker Weg 20, D-24105 Kiel, Germany

Masaharu Ishii

Department of Biotechnology, The University of Tokyo, 1-1-1 Yayoi, Bunkyo-ku, Tokyo 113-8657, Japan

Isabelle Iteanu

Physiologie Microbienne, Dept. B.M.G., CNRS-URA 2172, Institut Pasteur, 28 Rue du Docteur Roux, F-75724 Paris Cedex 15, France

Takashi Itoh

Japan Collection of Microorganisms, The Institute of Physical and Chemical Research, Riken, Hirosawa, Wako-shi, Saitama 351-0198, Japan

Christian Jeanthon

Université de Bretagne Occidentale, Institut Universitaire Européen de la Mer, 29680 Plouzané, France

D. Barrie Johnson

School of Biological Sciences, University of Wales, Bangor LL57 2UW, United Kingdom

Masahiro Kamekura

Noda Institute for Scientific Research, 399 Noda, Noda-shi, Chiba-ken 278, Japan

Toshiyuki Kawasumi

Department of Food and Nutrition, Faculty of Home Economics, Women's University, 2-8-1, Mejirodai, Bunkyo-ku, Tokyo, 112-8681, Japan

Olga I. Keppen

Department of Microbiology, Moscow State University, 119899 Moscow, Russia

Karel Kersters

Lab. voor Microbiologie, Rijksuniversiteit Gent, Vakgroep Biochemie, Fysiologie en Microbiologie, K.L. Ledeganckstraat 35, B-9000, Gent, Belgium

Jyoti Keswani

3157 Sylvan Circle, Morgantown, WV 26505, USA

Hans-Peter Klenk

VP Genomics, Epidauros Biotechnology Inc., Am Neuland 1, D-82347 Bernried, Germany

Tetsuo Kobayashi

Department of Applied Biological Sciences, Nagoya University, Lab. for Gene Regulation, School of Agricultural Sciences, Chikusa-ku, Nagoya-shi, Aichi 464-01, Japan

Yosuke Koga

Department of Chemistry, University of Occupational & Environmental Health, Fukuoka 807, Japan

Torsten Krafft

Am Grenzgraben 13, D-63067 Offenbach, Germany

Noel R. Krieg

Department of Biology, Virginia Polytechnic Institute & State University, Blacksburg, VA 24061-0406, USA

David P. Labeda

USDA, National Center for Agricultural Utilization Research, Microbial Properties Research, Peoria, IL 61604-3999, USA

Thomas A. Langworthy

Department of Microbiology, University of South Dakota School of Medicine, Vermillion, SD 57069-2390, USA

Stéphane L'Haridon

Université de Bretagne Occidentale, Institut Universitaire Européen de la Mer, 29680 Plouzané, France

Wolfgang Ludwig

Lehrstuhl für Mikrobiologie, Technische Universität München, Am Hochanger 4, Freising, D-85350, Germany

Barbara J. MacGregor

Civil Engineering Department, Northwestern University, Evanston, IL 60208, USA

Joan M. Macy

Department of Microbiology, LaTrobe University, Bundoora Victoria 3083, Australia

Michael T. Madigan

Department of Microbiology, Southern Illinois University, Mail Stop 6508, Carbondale, IL 62901-4399, USA

Robert A. Mah

Division of Environmental Health Science, UCLA School of Public Health, Los Angeles, CA 90024-1772, USA

James S. Maki

Department of Biology, WEHR Life Science Building, Marquette University, Milwaukee, WI 53201-1881, USA

Terry J. McGenity

Department of Biological Sciences, University of Essex, Main Campus, Wivenhoe Park, Colchester, Essex CO4 3SQ, United Kingdom

Roy D. Meredith

Ringoes Wertsville R, Hopewell, NJ 08525, USA

Terry L. Miller

Wadsworth Centre for Lab. & Research, New York State Department of Health, Albany, NY 12201-0509, USA

Rafael Montalvo-Rodriguez

University of Nebraska, Lincoln, NB, USA

R.G.E. Murray

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

Takashi Nakase

Japan Collection of Microorganisms, The Institute of Physical and Chemical Research, Riken, Wako-shi, Saitama 351-0198, Japan

M. Fernanda Nobre

Departamento de Zoologia, Universidade de Coimbra, Apartado 3126, P-3000 Coimbra, Portugal

Norimichi Nomura

Laboratory of Marine Microbiology, Division of Applied Bioscience, Graduate School of Agriculture, Kyoto University, Kyoto 606-8502, Japan

Bernard Ollivier

Laboratoire de Microbiologie des Anaérobies, Université de Provence, CESB-ESIL ORSTOM, Case 921, 163 Avenue de Liminy, Marseille 13288 Cedex 9, France

Aharon Oren

Division of Microbial and Molecular Ecology, The Institute of Life Science, and the Moshe Shilo Minerva Center for Marine Biogeochemistry, The Hebrew University of Jerusalem, Givat Ram, Jerusalem 91904, Israel

Jörg Overmann

Institute für Chemie und Biologie des Meeres (ICBM), Universität Oldenburg, Carl-von-Ossietzky-Strasse 9-11, Postfach 25 03, D-26111 Oldenburg, Germany

Bharat K.C. Patel

School of Biomolecular & Biomedical Sciences, Faculty of Science & Technology, Griffith University, Nathan Campus, Brisbane, Queensland 4111, Australia

Girishchandra B. Patel

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

Jerome J. Perry

3125 Eton Road, Raleigh, NC 27608-1113, USA

Norbert Pfennig

Primelweg 12, D-88662 Überlingen, Germany

Beverly K. Pierson

Department of Biological Sciences, University of Puget Sound, 1500 N. Warner, Jones Hall #007, Tacoma, WA 98416, USA

Fred A. Rainey

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

Anna-Louise Reysenbach

Department of Environmental Biology, Portland State University, Portland, OR 97207-0751, USA

Rosmarie Rippka

Physiologie Microbienne, Dept. B.M.G., CNRS-URA 2172, Institut Pasteur, 28 Rue du Docteur Roux, F-75724 Paris Cedex 15, France

James A. Romesser

Betz Dearborn, Inc. P.O. Box 4300, The Woodlands, TX 77380, USA

Yoshihiko Sako

Department of Applied Bioscience, Graduate School of Agriculture, Laboratory of Marine Microbiology, Kyoto University, Kyoto 606-8502, Japan

Priscilla C. Sanchez

Museum of Natural History, University of the Philippines, Los Baños, College, Laguna 4031, Philippines

Abigail A. Salyers

Department of Microbiology, University of Illinois-Urbana, Champaign, Urbana, IL 61801-3704, USA

Karl-Heinz Schleifer

Lehrstuhl für Mikrobiologie, Universität München, Am Hochanger 4, D-85350 Freising, Germany

Lindsay I. Sly

Centre for Bacterial Diversity and Identification, Department of Microbiology, University of Queensland, St. Lucia, Brisbane, Queensland 4072, Australia

Peter H.A. Sneath

Department of Microbiology & Immunology, School of Medicine, University of Leicester, P.O. Box 138, Leicester LE1 9HN, England

Kevin R. Sowers

Center for Marine Biotechnology, Maryland Biotechnology Institute, Baltimore, MD 21202, USA

Eva Spieck

Inst. für Allgemeine Botanik und Botanischer Garten, Universität Hamburg, Ohnhorststrasse 18, Hamburg D-22609, Germany

Stefan Spring

Deutsche Sammlung von Mikroorganismen und Zellkulturen, GmbH, Mascheroder Weg 1b, D-38124 Braunschweig, Germany

David A. Stahl

Department of Civil Engineering/Technology Institute, Northwestern University, Evanston, IL 60208-3109, USA

James T. Staley

Department of Microbiology, University of Washington, Seattle, WA 98195-0001, USA

Karl O. Stetter

Lehrstuhl für Mikrobiologie, Universität Regensburg, Universitätsstrasse 31, D-93053 Regensburg, Germany

Ken-ichiro Suzuki

Japan Collection of Microorganisms, The Institute of Physical and Chemical Research, Riken, Hirosawa, Wako-shi, Saitama 351-0198, Japan

Jean Swings

Laboratorium voor Microbiologie, Universiteit of Gent, Vakgroep WE 10V, Fysiologie en Microbiologie, K.L. Ledeganckstraat 35, B-9000, Gent, Belgium

Xinyu Tian

Institute of Microbiology, Academia Sinica, Beijing 100080, China

Brian J. Tindall

Deutsche Sammlung von Mikroorganismen und Zellkulturen, GmbH, Mascheroder Weg 1b, D-38124 Braunschweig, Germany

Hans G. Trüper

Institute für Mikrobiologie und Biotechnologie, Rheinsche Friedrich-Wilhelms-Universität, Mechenheimer Allee 168, W-53115 Bonn, Germany

Peter Vandamme

Lab. voor Microbiologie en Microbiele Genetica, Universiteit of Gent, Faculteit Wetenschappen, K.L. Ledeganckstraat 35, B-9000 Gent, Belgium

Antonio Ventosa

Departamento de Microbiología, Universidad de Sevilla y Parasitología, Facultad de Farmacia, Apdo. 874, 41080 Sevilla, Spain

Russell H. Vreeland

Department of Biology, West Chester University, West Chester, PA 19383, USA

John B. Waterbury

Woods Hole Oceanographic Institute, Woods Hole, MA 02543, USA

William B. Whitman

Department of Microbiology, University of Georgia, Athens, GA 30602-2605, USA

Annick Wilmotte

Labo d'Algologie, Mycologie et Systematique Experimentale, Department de Botanique, B-22, Université de Liège, B-4000 Liège, Belgium

Yi Xu

Institute of Microbiology, Academia Sinica, Beijing 100080, China

Gerhard Zellner

Institute of Hydrology, GSF-National Research Center for Environment & Climate, Home address: Fuchsbergstrasse 7, D-85386 Eching, Germany

Tatjana N. Zhilina

Institute of Microbiology, Russian Academy of Sciences, Prospect 60-letja Oktyabrya 7a, Moscow 117312, Russia

Peijin Zhou

Institute of Microbiology, Academia Sinica, Beijing 100080, China

Wolfram Zillig

Max-Planck-Institut für Biochemie, Am Klopferspitz 18a, D-82152 Martinsried, Germany

Stephen H. Zinder

Department of Microbiology, Cornell University, Ithaca, NY 14853-0001, USA