



Bergey's Manual of
**Systematic
Bacteriology**



S E C O N D E D I T I O N

Volume Four

*The Bacteroidetes, Spirochaetes,
Tenericutes (Mollicutes), Acidobacteria,
Fibrobacteres, Fusobacteria,
Dictyoglomi, Gemmatimonadetes,
Lentisphaerae, Verrucomicrobia, Chlamydiae,
and Planctomycetes*

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Second Edition

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and Planctomycetes***

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WITH CONTRIBUTIONS FROM 129 COLLEAGUES

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*This volume is dedicated to our colleague
Karl-Heinz Schleifer,
who retired from the Board of Trustees of Bergey's Manual as this volume was in preparation.
We deeply appreciate his efforts as an editor, author and officer of the Trust. He has devoted many
years to helping the Trust meet its objectives.*

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Preface to volume 4 of the second edition of *Bergey's Manual*[®] of *Systematic Bacteriology*

Prokaryotic systematics has remained a vibrant and exciting field of study, one of challenges and opportunities, great discoveries and gradual advances. To honor the leaders of our field, the Trust presented the 2010 Bergey's Award in recognition of outstanding contributions to the taxonomy of prokaryotes to Antonio Ventosa.

We expect that this will be the last volume to be edited by Jim Staley and Noel Krieg, both of whom served on the Trust for many years and continued to be active after their retirements. Noel contributed to *Bergey's Manual of Determinative Bacteriology*, in both the 8th edition as an author and the 9th edition as an editor. Moreover, he also edited volume 1 of the 1st edition of *Bergey's Manual of Systematic Bacteriology*. This was a massive achievement for this volume included the "Gram-negatives" and comprised more than one-third of that edition. In the 2nd edition of *Bergey's Manual of Systematic Bacteriology*, Noel and Jim edited volume 2 along with Don Brenner. This three-part volume comprised the *Proteobacteria* and was also a major portion of the current edition. In the current volume, Noel edited the phylum *Bacteroidetes*, which is the largest phylum in this work. In addition to his passion for prokaryotic systematics, Noel is well known by his colleagues and students at Virginia Tech as a dedicated and passionate teacher.

Jim Staley's service to the Trust paralleled that of Noel's. Jim also contributed to *Bergey's Manual of Determinative Bacteriology*, in both the 8th edition as an author and the 9th edition as an editor. He edited volume 3 of the 1st edition of *Bergey's Manual of Systematic Bacteriology* along with Marvin Bryant and Norbert Pfennig and volume 2 of the 2nd edition. In the current volume, he edited the phyla *Acidobacteria*, *Chlamydiae*, *Dictyoglomi*, *Fibrobacteres*, *Fusobacteria*, and *Gemmatimonadetes*. More importantly, he coached and mentored the rest of us throughout the entire editorial process. Most recently, Jim has led the efforts of the Trust to form Bergey's International Society for Microbial Systematics (BISMIS), whose purpose is to

promote excellent research in microbial systematics as well as enhance global communication among taxonomists who study the *Bacteria* and *Archaea*. The society will also serve internationally as an advocate for research efforts on microbial systematics and diversity. We wish Jim the best in this new adventure.

Acknowledgements

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

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

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

The Trust also thanks its Springer colleagues, Editorial Director Andrea Macaluso and Production Manager Susan Westendorf. In addition, we thank Amina Ravi, our manager at our typesetters, SPi, for her work in the proofing and production of the book.

We thank our current copyeditors, proofreaders and other staff, including Susan Andrews, Joanne Auger, Francis Brenner, MaryAnn Brickner, Travis Dean, Robert Gutman, Judy Leventhal and Linda Sanders, without whose hard work and attention to detail the production of this volume would be impossible. Lastly, we thank the Department of Microbiology at the University of Georgia for its assistance and encouragement in thousands of ways.

William B. (Barny) Whitman

Contents

Preface to volume 4	ix
Contributors	xix
On using the <i>Manual</i>	xxv
Road map of volume 4 phyla	1
Taxonomic outline of volume 4	21
Phylum XIV. <i>Bacteroidetes</i> phyl. nov.	25
Class I. <i>Bacteroidia</i> class. nov.	25
Order I. <i>Bacteroidales</i> ord. nov.	25
Family I. <i>Bacteroidaceae</i>	25
Genus I. <i>Bacteroides</i>	27
Genus II. <i>Acetofilamentum</i>	41
Genus III. <i>Acetomicrobium</i>	42
Genus IV. <i>Acetothermus</i>	44
Genus V. <i>Anaerorhabdus</i>	45
Family II. <i>Marinilabiliaceae</i> fam. nov.	49
Genus I. <i>Marinilabilia</i>	49
Genus II. <i>Anaerophaga</i>	51
Genus III. <i>Alkaliflexus</i>	53
Family III. <i>Rikenellaceae</i> fam. nov.	54
Genus I. <i>Rikenella</i>	55
Genus II. <i>Alistipes</i>	56
Family IV. <i>Porphyromonadaceae</i> fam. nov.	61
Genus I. <i>Porphyromonas</i>	62
Genus II. <i>Barnesiella</i>	70
Genus III. <i>Dysgonomonas</i>	71
Genus IV. <i>Paludibacter</i>	76
Genus V. <i>Petrimonas</i>	77
Genus VI. <i>Proteiniphilum</i>	77
Genus VII. <i>Tannerella</i>	78
Family V. <i>Prevotellaceae</i> fam. nov.	85
Genus I. <i>Prevotella</i>	86
Genus II. <i>Xylanibacter</i>	102
Class II. <i>Flavobacteriia</i> class. nov.	105
Order I. <i>Flavobacteriales</i> ord. nov.	105
Family I. <i>Flavobacteriaceae</i>	106
Genus I. <i>Flavobacterium</i>	112
Genus II. <i>Aequorivita</i>	155
Genus III. <i>Algibacter</i>	157
Genus IV. <i>Aquimarina</i>	158
Genus V. <i>Arenibacter</i>	161
Genus VI. <i>Bergeyella</i>	165

Genus VII. <i>Bizionia</i>	166
Genus VIII. <i>Capnocytophaga</i>	168
Genus IX. <i>Cellulophaga</i>	176
Genus X. <i>Chryseobacterium</i>	180
Genus XI. <i>Cloacibacterium</i>	197
Genus XII. <i>Coenonia</i>	198
Genus XIII. <i>Costertonia</i>	199
Genus XIV. <i>Croceibacter</i>	199
Genus XV. <i>Dokdonia</i>	201
Genus XVI. <i>Donghaeana</i>	201
Genus XVII. <i>Elizabethkingia</i>	202
Genus XVIII. <i>Empedobacter</i>	210
Genus XIX. <i>Epilithonimonas</i>	212
Genus XX. <i>Flaviramulus</i>	213
Genus XXI. <i>Formosa</i>	214
Genus XXII. <i>Gaetbulibacter</i>	218
Genus XXIII. <i>Gelidibacter</i>	219
Genus XXIV. <i>Gillisia</i>	221
Genus XXV. <i>Gramella</i>	226
Genus XXVI. <i>Kaistella</i>	227
Genus XXVII. <i>Kordia</i>	228
Genus XXVIII. <i>Krokinobacter</i>	230
Genus XXIX. <i>Lacinutrix</i>	231
Genus XXX. <i>Leeuwenhoekiella</i>	232
Genus XXXI. <i>Lutibacter</i>	234
Genus XXXII. <i>Maribacter</i>	235
Genus XXXIII. <i>Mariniflexile</i>	238
Genus XXXIV. <i>Mesonia</i>	239
Genus XXXV. <i>Muricauda</i>	240
Genus XXXVI. <i>Myroides</i>	245
Genus XXXVII. <i>Nonlabens</i>	248
Genus XXXVIII. <i>Olleya</i>	249
Genus XXXIX. <i>Ornithobacterium</i>	250
Genus XL. <i>Persicivirga</i>	254
Genus XLI. <i>Polaribacter</i>	255
Genus XLII. <i>Psychroflexus</i>	258
Genus XLIII. <i>Psychroserpens</i>	261
Genus XLIV. <i>Riemerella</i>	262
Genus XLV. <i>Robiginitalea</i>	264
Genus XLVI. <i>Salegentibacter</i>	266
Genus XLVII. <i>Sandarakinotalea</i>	269
Genus XLVIII. <i>Sediminicola</i>	270
Genus XLIX. <i>Sejongia</i>	271
Genus L. <i>Stenothermobacter</i>	275
Genus LI. <i>Subsaxibacter</i>	275
Genus LII. <i>Subsaximicrobium</i>	277
Genus LIII. <i>Tenacibaculum</i>	279
Genus LIV. <i>Ulvibacter</i>	283
Genus LV. <i>Vitellibacter</i>	284
Genus LVI. <i>Wautersiella</i>	285
Genus LVII. <i>Weeksella</i>	286
Genus LVIII. <i>Winogradskyella</i>	288
Genus LIX. <i>Yeosuana</i>	291
Genus LX. <i>Zhouia</i>	292
Genus LXI. <i>Zobellia</i>	292

Family II. <i>Blattabacteriaceae</i> fam. nov.	315
Genus I. <i>Blattabacterium</i>	315
Family III. <i>Cryomorphaceae</i>	322
Genus I. <i>Cryomorpha</i>	323
Genus II. <i>Brumimicrobium</i>	323
Genus III. <i>Crocinitomix</i>	326
Genus IV. <i>Fluviicola</i>	327
Genus V. <i>Lishizhenia</i>	327
Genus VI. <i>Owenweeksia</i>	328
Class III. <i>Sphingobacteriia</i> class. nov.	330
Order I. <i>Sphingobacteriales</i> ord. nov.	330
Family I. <i>Sphingobacteriaceae</i>	331
Genus I. <i>Sphingobacterium</i>	331
Genus II. <i>Pedobacter</i>	339
Family II. <i>Chitinophagaceae</i> fam. nov.	351
Genus I. <i>Chitinophaga</i>	351
Genus II. <i>Terrimonas</i>	356
Family III. <i>Saprospiraceae</i> fam. nov.	358
Genus I. <i>Saprospira</i>	359
Genus II. <i>Aureispira</i>	361
Genus III. <i>Haliscomenobacter</i>	363
Genus IV. <i>Lewinella</i>	366
Class IV. <i>Cytophagia</i> class. nov.	370
Order I. <i>Cytophagales</i>	370
Family I. <i>Cytophagaceae</i>	371
Genus I. <i>Cytophaga</i>	371
Genus II. <i>Adhaeribacter</i>	375
Genus III. <i>Arcicella</i>	377
Genus IV. <i>Dyadobacter</i>	380
Genus V. <i>Effluviibacter</i>	387
Genus VI. <i>Emticicia</i>	388
Genus VII. <i>Flectobacillus</i>	389
Genus VIII. <i>Flexibacter</i>	392
Genus IX. <i>Hymenobacter</i>	397
Genus X. <i>Larkinella</i>	404
Genus XI. <i>Leadbetterella</i>	405
Genus XII. <i>Meniscus</i>	406
Genus XIII. <i>Microscilla</i>	408
Genus XIV. <i>Pontibacter</i>	410
Genus XV. <i>Runella</i>	412
Genus XVI. <i>Spirosoma</i>	415
Genus XVII. <i>Sporocytophaga</i>	418
Family II. <i>Cyclobacteriaceae</i> fam. nov.	423
Genus I. <i>Cyclobacterium</i>	423
Genus II. <i>Algoriphagus</i>	426
Genus III. <i>Aquiflexum</i>	433
Genus IV. <i>Belliella</i>	434
Genus V. <i>Echinicola</i>	437
Genus VI. <i>Rhodonellum</i>	440
Family III. <i>Flammeovirgaceae</i> fam. nov.	442
Genus I. <i>Flammeovirga</i>	442
Genus II. <i>Fabibacter</i>	447
Genus III. <i>Flexithrix</i>	448
Genus IV. <i>Persicobacter</i>	450
Genus V. <i>Reichenbachiella</i>	452

Genus VI. <i>Roseivirga</i>	453
Order II. <i>Incertae sedis</i>	457
Family I. <i>Rhodothermaceae</i> fam. nov.	457
Genus I. <i>Rhodothermus</i>	458
Genus II. <i>Salinibacter</i>	460
Order III. <i>Incertae sedis</i>	465
Genus I. <i>Thermonema</i>	465
Order IV. <i>Incertae sedis</i>	467
Genus I. <i>Toxothrix</i>	467
Phylum XV. <i>Spirochaetes</i> phyl. nov.	471
Class I. <i>Spirochaetia</i> class. nov.	471
Order I. <i>Spirochaetales</i>	471
Family I. <i>Spirochaetaceae</i>	473
Genus I. <i>Spirochaeta</i>	473
Genus II. <i>Borrelia</i>	484
Genus III. <i>Cristispira</i>	498
Genus IV. <i>Treponema</i>	501
Family II. <i>Brachyspiraceae</i>	531
Genus I. <i>Brachyspira</i>	531
Family III. <i>Brevinemataceae</i> fam. nov.	545
Genus I. <i>Brevinema</i>	545
Family IV. <i>Leptospiraceae</i>	546
Genus I. <i>Leptospira</i>	546
Genus II. <i>Leptonema</i>	556
Genus III. <i>Turneriella</i>	558
Hindgut spirochetes of termites and <i>Cryptocercus punctulatus</i>	563
Phylum XVI. <i>Tenericutes</i>	567
Class I. <i>Mollicutes</i>	568
Order I. <i>Mycoplasmatales</i>	574
Family I. <i>Mycoplasmataceae</i>	575
Genus I. <i>Mycoplasma</i>	575
Genus II. <i>Ureaplasma</i>	613
Family II. <i>Incertae sedis</i>	639
Genus I. <i>Eperythrozoon</i>	640
Genus II. <i>Haemobartonella</i>	642
Order II. <i>Entomoplasmatales</i>	644
Family I. <i>Entomoplasmataceae</i>	645
Genus I. <i>Entomoplasma</i>	646
Genus II. <i>Mesoplasma</i>	649
Family II. <i>Spiroplasmataceae</i>	654
Genus I. <i>Spiroplasma</i>	654
Order III. <i>Acholeplasmatales</i>	687
Family I. <i>Acholeplasmataceae</i>	687
Genus I. <i>Acholeplasma</i>	688
Family II. <i>Incertae sedis</i>	696
Genus I. " <i>Candidatus</i> Phytoplasma" gen. nov.	696
Order IV. <i>Anaeroplasmatales</i>	719
Family I. <i>Anaeroplasmataceae</i>	720
Genus I. <i>Anaeroplasma</i>	720
Genus II. <i>Asteroleplasma</i>	722

Phylum XVII. <i>Acidobacteria</i> phyl. nov.	725
Class I. <i>Acidobacteriia</i>	727
Order I. <i>Acidobacteriales</i>	727
Family I. <i>Acidobacteriaceae</i> fam. nov.	728
Genus I. <i>Acidobacterium</i>	728
Genus II. <i>Edaphobacter</i>	729
Genus III. <i>Terriglobus</i>	730
Class II. <i>Holophagae</i>	731
Order I. <i>Holophagales</i>	731
Family I. <i>Holophagaceae</i>	732
Genus I. <i>Holophaga</i>	732
Genus II. <i>Geothrix</i>	732
Order II. <i>Acanthopleuribacterales</i>	734
Family I. <i>Acanthopleuribacteraceae</i>	734
Genus I. <i>Acanthopleuribacter</i>	734
Phylum XVIII. " <i>Fibrobacteres</i> "	737
Class I. <i>Fibrobacteria</i> class. nov.	739
Order I. <i>Fibrobacterales</i> ord. nov.	739
Family I. <i>Fibrobacteraceae</i> fam. nov.	739
Genus I. <i>Fibrobacter</i>	740
Phylum XIX. " <i>Fusobacteria</i> "	747
Class I. <i>Fusobacteriia</i> class. nov.	747
Order I. <i>Fusobacteriales</i> ord. nov.	747
Family I. <i>Fusobacteriaceae</i> fam. nov.	748
Genus I. <i>Fusobacterium</i>	748
Genus II. <i>Cetobacterium</i>	758
Genus III. <i>Ilyobacter</i>	759
Genus IV. <i>Propionigenium</i>	761
Family II. <i>Leptotrichiaceae</i> fam. nov.	766
Genus I. <i>Leptotrichia</i>	766
Genus II. <i>Sebaldella</i>	769
Genus III. <i>Sneathia</i>	770
Genus IV. <i>Streptobacillus</i>	771
Phylum XX. <i>Dictyoglomi</i> phyl. nov.	775
Class I. <i>Dictyoglomia</i> class. nov.	776
Order I. <i>Dictyoglomales</i> ord. nov.	776
Family I. <i>Dictyoglomaceae</i> fam. nov.	776
Genus I. <i>Dictyoglomus</i>	776
Phylum XXI. <i>Gemmatimonadetes</i>	781
Class I. <i>Gemmatimonadetes</i>	781
Order I. <i>Gemmatimonadales</i>	781
Family I. <i>Gemmatimonadaceae</i>	782
Genus I. <i>Gemmatimonas</i>	782
Phylum XXII. <i>Lentisphaerae</i>	785
Class I. <i>Lentisphaeria</i> class. nov.	787
Order I. <i>Lentisphaerales</i>	788
Family I. <i>Lentisphaeraceae</i> fam. nov.	788
Genus I. <i>Lentisphaera</i>	788

Order II. <i>Victivallales</i>	791
Family I. <i>Victivallaceae</i> fam. nov.	791
Genus I. <i>Victivallis</i>	791
Phylum XXIII. <i>Verrucomicrobia</i> phyl. nov.	795
Class I. <i>Verrucomicrobiae</i>	799
Order I. <i>Verrucomicrobiales</i>	802
Family I. <i>Verrucomicrobiaceae</i>	803
Genus I. <i>Verrucomicrobium</i>	803
Genus II. <i>Prostheco bacter</i>	805
Family II. <i>Akkermansiaceae</i> fam. nov.	809
Genus I. <i>Akkermansia</i>	809
Family III. <i>Rubritaleaceae</i> fam. nov.	812
Genus I. <i>Rubritalea</i>	812
Class II. <i>Opitutae</i>	817
Order I. <i>Opitutaes</i>	820
Family I. <i>Opitutaceae</i>	820
Genus I. <i>Opitutus</i>	820
Genus II. <i>Alterococcus</i>	821
Order II. <i>Puniceicoccales</i>	823
Family I. <i>Puniceicoccaceae</i>	824
Genus I. <i>Puniceicoccus</i>	824
Genus II. <i>Cerasicoccus</i>	825
Genus III. <i>Coraliomargarita</i>	827
Genus IV. <i>Pelagicoccus</i>	829
Class III. <i>Spartobacteria</i> class. nov.	834
Order I. <i>Chthoniobacterales</i> ord. nov.	836
Family I. <i>Chthoniobacteraceae</i> fam. nov.	837
Genus I. <i>Chthoniobacter</i>	837
Genus II. " <i>Candidatus Xiphinematobacter</i> ".	838
Phylum XXIV. " <i>Chlamydiae</i> "	843
Class I. <i>Chlamydiia</i> class. nov.	844
Order I. <i>Chlamydiales</i>	844
Family I. <i>Chlamydiaceae</i>	845
Genus I. <i>Chlamydia</i>	846
Family II. " <i>Candidatus Clavichlamydiaceae</i> ".	865
Genus I. " <i>Candidatus Clavichlamydia</i> ".	865
Family III. <i>Criblamydiaceae</i>	867
Genus I. <i>Criblamydia</i>	867
Family IV. <i>Parachlamydiaceae</i>	867
Genus I. <i>Parachlamydia</i>	868
Genus II. <i>Neochlamydia</i>	869
Genus III. <i>Protochlamydia</i> gen. nov.	870
Family V. " <i>Candidatus Piscichlamydiaceae</i> ".	872
Genus I. " <i>Candidatus Piscichlamydia</i> ".	872
Family VI. <i>Rhabdochlamydiaceae</i> fam. nov.	873
Genus I. <i>Rhabdochlamydia</i> gen. nov.	873
Family VII. <i>Simkaniaceae</i>	874
Genus I. <i>Simkania</i>	875
Genus II. " <i>Candidatus Fritschea</i> ".	875
Family VIII. <i>Waddliaceae</i>	876
Genus I. <i>Waddlia</i>	877

Phylum XXV. " <i>Planctomycetes</i> "	879
Class I. <i>Planctomycetia</i> class. nov.	879
Order I. <i>Planctomycetales</i>	879
Family I. <i>Planctomycetaceae</i>	880
Genus I. <i>Planctomyces</i>	881
Genus II. <i>Blastopirellula</i>	895
Genus III. <i>Gemmata</i>	897
Genus IV. <i>Isosphaera</i>	900
Genus V. <i>Pirellula</i>	903
Genus VI. <i>Rhodopirellula</i>	906
Genus VII. <i>Schlesneria</i>	910
Genus VIII. <i>Singulisphaera</i>	913
Order II. " <i>Candidatus Brocadiales</i> " ord. nov.	918
Family I. " <i>Candidatus Brocadiaceae</i> " fam. nov.	918
Author index.	927
Index of scientific names of <i>Archaea</i> and <i>Bacteria</i>	931

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On using the *Manual*

NOEL R. KRIEG AND GEORGE M. GARRITY

Citation

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

Arrangement of the Manual

As in the previous volumes of this edition, the *Manual* is arranged in phylogenetic groups based upon the analyses of the 16S rRNA presented in the introductory chapter “Road map of the phyla *Bacteroidetes*, *Spirochaetes*, *Tenericutes* (*Mollicutes*), *Acidobacteria*, *Fibrobacteres*, *Fusobacteria*, *Dictyoglomi*, *Gemmatimonadetes*, *Lentisphaerae*, *Verrucomicrobia*, *Chlamydiae* and *Planctomycetes*”. These groups have been substantially modified since the publication of volume 1 in 2001, reflecting both the availability of more experimental data and a different method of analysis. Since volume 4 includes only the phylum *Firmicutes*, taxa are arranged by class, order, family, genus and species. Within each taxon, the nomenclatural type is presented first and indicated by a superscript T. Other taxa are presented in alphabetical order without consideration of degrees of relatedness.

Articles

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

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

b. Name of author(s). The person or persons who prepared the Bergey’s article are indicated. The address of each author can be found in the list of Contributors at the beginning of the *Manual*.

c. Synonyms. In some instances a list of some synonyms used in the past for the same genus is given. Other synonyms can be found in the *Index Bergeyana* or the *Supplement to the Index Bergeyana*.

d. Etymology of the name. Etymologies are provided as in previous editions, and many (but undoubtedly not all) errors have been corrected. It is often difficult, however, to determine why a particular name was chosen, or the nuance intended, if the details were not provided in the original publication. Those authors who propose new names are urged to consult a Greek and Latin authority before publishing in order to ensure grammatical correctness and also to ensure that the meaning of the name is as intended.

e. Salient features. This is a brief resume of the salient features of the taxon. The most important characteristics are given in **boldface**. The DNA G+C content is given.

f. Type species. The name of the type species of the genus is also indicated along with the defining publication(s).

g. Further descriptive information. This portion elaborates on the various features of the genus, particularly those features having significance for systematic bacteriology. The treatment serves to acquaint the reader with the overall biology of the organisms but is not meant to be a comprehensive review. The information is normally presented in the following sequence:

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

h. Enrichment and isolation. A few selected methods are presented, together with the pertinent media formulations.

i. Maintenance procedures. Methods used for maintenance of stock cultures and preservation of strains are given.

j. Procedures for testing special characters. This portion provides methodology for testing for unusual characteristics or performing tests of special importance.

k. Differentiation of the genus from other genera. Those characteristics that are especially useful for distinguishing the genus from similar or related organisms are indicated here, usually in a tabular form.

l. Taxonomic comments. This summarizes the available information related to taxonomic placement of the genus and indicates the justification for considering the genus a distinct taxon. Particular emphasis is given to the methods of molecular biology used to estimate the relatedness of the genus to other taxa, where such information is available. Taxonomic information regarding the arrangement and status of the various species within the genus follows. Where taxonomic controversy exists, the problems are delineated and the various alternative viewpoints are discussed.

m. Further reading. A list of selected references, usually of a general nature, is given to enable the reader to gain access to additional sources of information about the genus.

n. Differentiation of the species of the genus. Those characteristics that are important for distinguishing the various species within the genus are presented, usually with reference to a table summarizing the information.

o. List of species of the genus. The citation of each species is given, followed in some instances by a brief list of objective synonyms. The etymology of the specific epithet is indicated. Descriptive information for the species is usually presented in tabular form, but special information may be given in the text. Because of the emphasis on tabular data, the species descriptions are usually brief. The type strain of each species is indicated, together with the collection(s) in which it can be found. (Addresses of the various culture collections are given in the article in volume 1 entitled *Culture Collections: An Essential Resource for Microbiology*.) The 16S rRNA gene sequence used in phylogenetic analysis and placement of the species into the taxonomic framework is given, along with the GenBank (or other database) accession number. Additional comments may be provided to point the reader to other well-characterized strains of the species and any other known DNA sequences that may be relevant.

p. Species *incertae sedis*. The List of Species may be followed in some instances by a listing of additional species under the heading “Species *Incertae sedis*” or “Other organisms”, etc. The taxonomic placement or status of such species is questionable, and the reasons for the uncertainty are presented.

q. References. All references given in the article are listed alphabetically at the end of the family chapter.

Tables

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

+, 90% or more of the strains are positive

d, 11–89% of the strains are positive

–, 90% or more of the strains are negative

D, different reactions occur in different taxa (e.g., species of a genus or genera of a family)

v, strain instability (NOT equivalent to “d”)

w, weak reaction.

nd, not determined or no data.

nr, not reported.

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

Use of the *Manual* for determinative purposes

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

The index is useful for locating the articles on unfamiliar taxa or in discovering the current classification of a particular taxon. Every bacterial name mentioned in the *Manual* is listed in the index. In addition, an up-to-date outline of the taxonomic framework is provided in the introductory chapter “Road map of the phyla *Bacteroidetes*, *Spirochaetes*, *Tenericutes* (*Mollicutes*), *Acidobacteria*, *Fibrobacteres*, *Fusobacteria*, *Dictyoglomi*, *Gemmatimonadetes*, *Lentisphaerae*, *Verrucomicrobia*, *Chlamydiae* and *Planctomycetes*”.

Errors, comments, and suggestions

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

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Road map of the phyla *Bacteroidetes*, *Spirochaetes*, *Tenericutes* (*Mollicutes*), *Acidobacteria*, *Fibrobacteres*, *Fusobacteria*, *Dictyoglomi*, *Gemmatimonadetes*, *Lentisphaerae*, *Verrucomicrobia*, *Chlamydiae*, and *Planctomycetes*

WOLFGANG LUDWIG, JEAN EUZÉBY AND WILLIAM B. WHITMAN

This revised road map updates previous outlines of Garrity and Holt (2001) and Garrity et al. (2005) with the description of additional taxa and new phylogenetic analyses. While the outline/road map seeks to be complete for all taxa validated prior to July 1, 2006, some taxa described after that date are included.

The new phylogenetic trees are strict consensus trees based on various maximum-likelihood and maximum-parsimony analyses and corrected according to results obtained when applying alternative treeing methods. Multifurcations indicate that a common branching order was not significantly supported after applying alternative treeing approaches. Detailed branching orders are shown if supported by at least 50% of the “treeings” performed in addition to the maximum-likelihood approach.

Given that the focus is on the higher taxonomic ranks, rather restrictive variability filters were applied. Consequently, resolution power is lost for lower levels. Of special importance, relationships within genera lack the resolution that would be obtained with genus–family level analyses. Furthermore, the type strain tree, which is available online at www.bergeys.org, is an extract of comprehensive trees comprising some thousand sequences. Thus, trees for the specific groups in subsequent chapters, which are based upon smaller datasets and include the variable sequence positions, may differ with respect to detailed topology, especially at levels of closer relationships within and between genera. In the trees shown here, branch lengths – in first instance – indicate significance and only approximate estimated number of substitutions.

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

The taxonomic road map proposed in volume 1 and updated and emended in volume 2 was derived from phylogenetic and principal-component analyses of comprehensive datasets of small-subunit rRNA gene sequences. A similar approach is continued here. Since the introduction of comparative rRNA sequencing (Ludwig and Klenk, 2005; Ludwig and Schleifer, 2005), there has been a continuous debate concerning the justification and power of a single marker molecule for elucidating phylogeny and establishing taxonomy of organisms. Although generally well established in taxonomy, the polyphasic approach cannot currently be applied for sequence-based analyses due to the lack of adequate comprehensive datasets for alternative marker molecules. Even in the age of genomics, the datasets for non-rRNA markers are poor in comparison to more than 400,000 rRNA primary structures available in general and special databases (Cole et al., 2007; Pruesse et al., 2007). Nevertheless, the data provided by the full genome-sequencing projects allow the definition of a small set of genes representing the conserved core of prokaryotic genomes (Cicarelli et al., 2006; Ludwig and Schleifer, 2005). Furthermore, comparative analyses of the core gene sequences globally support the small-subunit rRNA derived view of prokaryotic evolution. Although the tree topologies reconstructed from alternative markers differ in detail, the major groups (and taxa) are verified or at least not disproved (Ludwig and Schleifer, 2005). Consequently, the structuring of this volume is based on updated and curated (<http://www.arb-silva.de>; Pruesse et al., 2007) databases of processed small-subunit rRNA primary structures.

Data analysis

The current release of the integrated small-subunit rRNA database of the SILVA project (Pruesse et al., 2007) provides the basis for these phylogenetic analyses. The tools of the ARB software package (Ludwig et al., 2004) were used for data evaluation, optimization, and phylogenetic inference. A subset of about 33,000 high-quality sequences from *Bacteria* was extracted from the current SILVA SSU Ref database. Among the criteria for restrictive quality analyses and data selection were coverage of at least positions 18–1509 (*Escherichia coli* 16S rRNA numbering), no ambiguities or missing sequence stretches, no chimeric primary structures, low deviation from overall and group-specific consensus and conservation profiles, and good agreement of tree topologies and branch length with processed sequence

data. Unfortunately, only some of the type strain sequences successfully passed this restrictive quality check. The alignment of the sequences of this subset, as well as all type strain sequences initially excluded given incompleteness or lower quality, was manually evaluated and optimized. Phylogenetic treeing was first based on the high-quality dataset and performed applying phylum specific position filters (50% positional identity). The partial or lower quality type strain sequences were subsequently added using a special ARB-tool allowing the optimal positioning of branches to the reference tree without admitting topology changes (Ludwig and Klenk, 2005). The consensus trees used for evaluating or modifying the taxonomic outline were based on maximum-likelihood analyses (RAXML, implemented in the ARB package; Stamatakis et al., 2005) and further evaluated by maximum-parsimony and distance matrix analyses with the respective ARB tools (Ludwig et al., 2004).

Taxonomic interpretation

The phylogenetic conclusions were used for evaluating and modifying the taxonomic outline of the phyla "*Bacteroidetes*", "*Spirochaetes*", *Tenericutes* (*Mollicutes*), "*Acidobacteria*", "*Fibrobacteres*", "*Fusobacteria*", "*Dictyoglomi*", *Gemmatimonadetes*, *Lentisphaerae*, "*Verrucomicrobia*", "*Chlamydiae*", and "*Planctomycetes*". These include all the phyla not described in earlier volumes with the exception of the *Actinobacteria*, which will be included in the fifth and last volume of this edition. There is no particular rationale for inclusion in this volume. Although some of the phyla may be related in a kingdom or superphylum (i.e., "*Chlamydiae*", *Lentisphaerae*, "*Planctomycetes*", and "*Verrucomicrobia*") (Griffiths and Gupta, 2007; Lee et al., 2009; Pilhofer et al., 2008; Wagner and Horn, 2006), most are unrelated to each other (Figure 1). Some are major pathogens of humans, other animals, and plants. Some are exotic and only described in the last decade.

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

Upon the recommendation of the Judicial Commission (De Vos et al., 2005), many of the names and classifications previously proposed by Cavalier-Smith (2002) are not used in this work. The classification used categories not covered by the Rules of the Code and priority and proposed types without standing in nomenclature. For these reasons, the following phylum (or

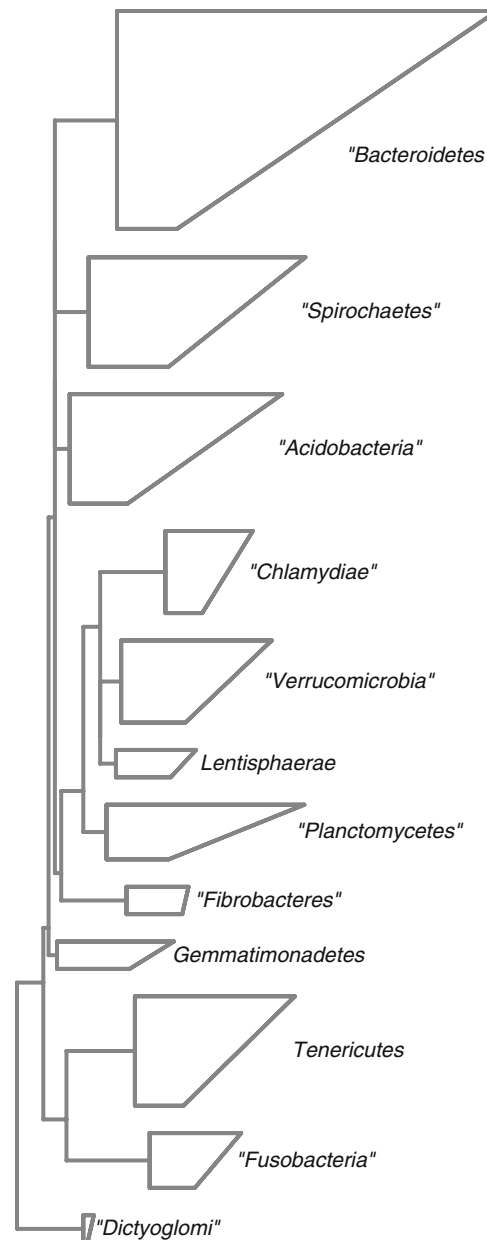


FIGURE 1. Phyla *Bacteroidetes*, *Spirochaetes*, *Tenericutes*, *Acidobacteria*, *Fibrobacteres*, *Fusobacteria*, *Dictyoglomi*, *Gemmatimonadetes*, *Lentisphaerae*, *Verrucomicrobia*, *Chlamydiae*, and *Planctomycetes*. While the phyla *Lentisphaerae*, *Verrucomicrobia*, *Chlamydiae*, and *Planctomycetes* may be specifically related to each other, the other phyla included in volume 4 are not related.

division) names are not used: *Planctobacteria*, *Sphingobacteria*, and *Spirochaetae*. Likewise, the following class names are not used: *Acidobacteria*, *Chlamydiae*, *Flavobacteria*, *Planctomycea*, and *Spirochaetes*. Lastly, priority for the order name *Acidobacteriales* is no longer attributed to Cavalier-Smith (2002).

Phylum "*Bacteroidetes*"

In previous classifications, the phylum "*Bacteroidetes*" was proposed to comprise three classes, "*Bacteroidia*", "*Flavobacteriia*", and "*Sphingobacteriia*" (Garrity et al., 2005). While the analyses performed here, which were based upon many more sequences and differ-

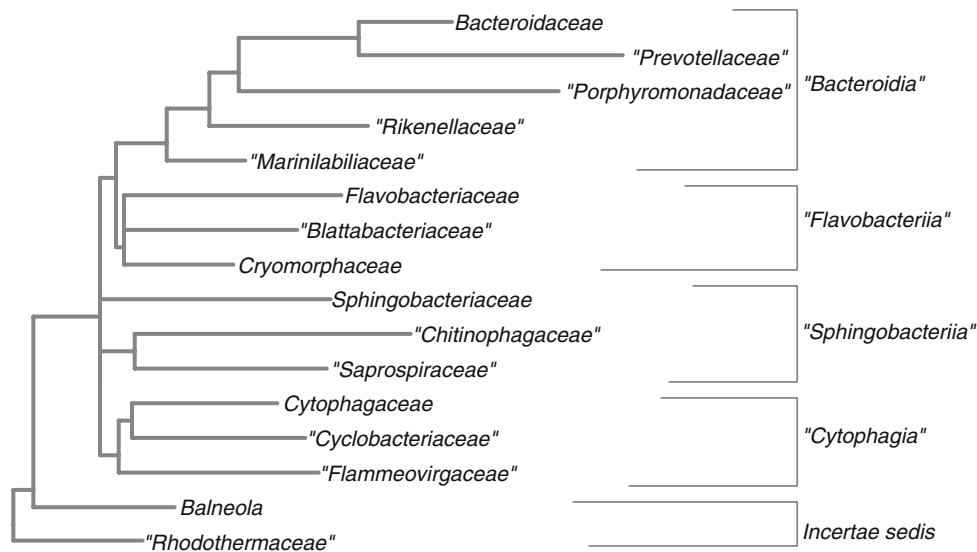


FIGURE 2. Overview of the phylum "Bacteroidetes". This phylum contains 15 families classified within four classes. Currently, the *incertae sedis* taxa *Balneola* and "Rhodothermaceae" are classified within the class "Cytophagia".

ent methods, generally support this conclusion, they also justify formation of a fourth class within this phylum, the "Cytophagia" (Figure 2). This new class comprises many genera previously classified within the "Flexibacteraceae", "Flammeovirgaceae", and "Crenotrichaceae" (see below). Thus, the phylum "Bacteroidetes" comprises at least four phylogenetic groups that are well delineated on the basis of their 16S rRNA gene sequences. In addition, two groups are affiliated with the phylum but could not be readily assigned to one of these classes. While additional evidence may warrant classification with one of the known or novel classes, these organisms were grouped within *Incertae sedis* of the "Cytophagia" for the present time (Figure 2).

Class "Bacteroidia" and order "Bacteroidales"

The class "Bacteroidia" contains five families, all classified within the order "Bacteroidales". These families include the four families proposed previously (Garrity et al., 2005), *Bacteroidaceae*, "Rikenellaceae", "Porphyromonadaceae", and "Prevotellaceae", as well as a new family proposed here, "Marinilabiliaceae" (Figure 3). In addition, on the basis of the dissimilarity of its 16S rRNA gene sequence to other members of the order, *Odoribacter* (*Bacteroides*) *splanchnicus* may represent an additional undescribed family or a member of the "Marinilabiliaceae". However, chemotaxonomic characteristics and analyses of the *fimA* gene imply a close relationship to the family "Porphyromonadaceae" (Hardham et al., 2008). Therefore, its reclassification is not proposed at this time. Lastly, the recently described marine organism, *Prolixibacter bellariivorans*, appears to represent a deep lineage in this class but whose affiliation with these families is ambiguous (Holmes et al., 2007).

Family *Bacteroidaceae*

In addition to the type genus, *Bacteroides*, this family comprises three monospecific genera, *Acetofilamentum*, *Acetothermus*, and *Anaerorhabdus*, and one genus, *Acetomicrobium*, comprising two species. Because complete 16S rRNA gene sequences are not available for representatives of these four genera, these assignments are tentative. Two genera previously assigned to

this family have also been reassigned. As recommended by Morotomi et al. (2007), *Megamonas* has been transferred to the *Firmicutes*. Based on its rRNA gene sequence, *Anaerophaga* has been transferred to the new family "Marinilabiliaceae".

The genus *Bacteroides* comprises at least six lineages or clades. The type species, *Bacteroides fragilis*, together with *Bacteroides acidifaciens*, *caccae*, *finogoldii*, *nordii*, *ovatus*, *salyersiae*, *thetaitotamicon*, and *xylanisolvans*, represent a cluster slightly separated from the other members of the genus. If supported by other evidence, each of the other lineages could be classified as new genera within this family. The other lineages are represented by *Bacteroides cellulolyticus* and *intestinalis*; *Bacteroides coprosus* and *propionifaciens*; *Bacteroides pyogenes*, *suis*, and *tectus*; *Bacteroides barnesiae*, *coprocola*, *coprophilus*, *dorei*, *helicogenes*, *massiliensis*, *plebeius*, *salanitronis*, *uniformis*, and *vulgatus*. The species *Bacteroides eggerthii*, *gallinarum*, and *stercoris* cannot clearly be assigned to one of the lineages.

In addition to these clades within the genus, the following validly published species are probably misclassified. *Bacteroides splanchnicus* was recently reclassified as *Odoribacter splanchnicus* (Hardham et al., 2008); this genus may represent a novel member of family "Porphyromonadaceae" (see above). *Bacteroides capillosus* and *cellulosolvans* are probably members of the phylum *Firmicutes*. In addition, rRNA gene sequences are not available for *Bacteroides capillus*, *forsythus*, *furcosus*, *polypragmatus*, and *salivovus*, so their assignment is uncertain.

Lastly, the family *Bacteroidaceae* appears to be paraphyletic, and the family "Prevotellaceae" falls within the radiation of *Bacteroides* clades. Because the members of the "Prevotellaceae" are generally closely related and the branch length to the *Bacteroidaceae* is fairly long, this conclusion is tentative. While these families were not combined at this time, this classification may warrant further investigation.

Family "Marinilabiliaceae"

This family represents a group of sister but not clearly monophyletic branches within the "Bacteroidales" and comprises three genera.