

# **CRC Handbook of Microbiology**

**2nd Edition**

## **Volume I Bacteria**

**EDITORS:**

**Allen I. Laskin, Ph.D.**

**Hubert A. Lechevalier, Ph.D.**

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Exxon Research and Engineering Company

**Hubert A. Lechevalier, Ph.D.**

Waksman Institute of Microbiology  
Rutgers University



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## PREFACE

The first edition of the CRC HANDBOOK OF MICROBIOLOGY consisted of four volumes. The first of these, entitled *Organismic Microbiology*, was published in 1973 and dealt with information dealing with the organisms themselves. The revised, enlarged material dealing with this subject could not be conveniently bound within a single cover. Thus, we decided to include only information on bacteria in the first volume of the second edition of this handbook. The second volume of this series will contain information dealing with fungi, algae, protozoa, and viruses.

We wish to thank all those who directly or indirectly have made constructive criticisms of the first edition of the HANDBOOK OF MICROBIOLOGY. We have tried to present information on bacteria in an order that could easily be related to that followed in the 8th edition of *Bergey's Manual of Determinative Bacteriology*. We opted not to follow the order suggested by one of our critics, John Sieburth, but we think that our readers will be able to profit from his ideas as presented in the Introduction to this volume. Completely new subjects covered in this second edition include a chapter on paleomicrobiology by A. Knoll and one on bacterial cytology by B. K. and Arati Ghosh.

We extend our thanks to the members of the Advisory Board and to all our authors, who have worked so unselfishly to make this second edition possible. We also wish to express our gratitude to Mrs. Lisbeth Hammer and to Mrs. Verna Lepping for their excellent editorial work.

A. I. Laskin  
H. A. Lechevalier  
New Jersey, 1977

## THE EDITORS

**Allen I. Laskin**, Head of Biosciences Research at Exxon Research and Engineering Company, Linden, N.J., received his B.S. degree in Biology from the City College of New York in 1950. His M.A. and Ph.D. degrees in Microbiology were obtained from the University of Texas in 1952 and 1955 respectively.

From 1955 to 1969 Dr. Laskin was at the Squibb Institute for Medical Research, first as Senior Research Microbiologist, then as Head of Microbial Biochemistry, and subsequently as Assistant Director of Microbiology. His research on microbial transformations of steroids led to several publications and more than twenty U.S. patents. Dr. Laskin then switched to molecular biology and studies on cell-free protein and cell wall synthesis, which led to work on the mode of action of tetracycline and several other antibiotics. In 1969 Dr. Laskin joined Exxon Research and Engineering Company to head the laboratory program concerned with single-cell protein. In 1971 he moved to his present position, heading the research on petroleum microbiology and enzymology.

Dr. Laskin is President-Elect of the Society for Industrial Microbiology, a Fellow of the American Academy of Microbiology, a Fellow of the New York Academy of Sciences, and recipient of the 1974 Selman A. Waksman Honorary Lectureship Award. At present he serves on the Panel on Microbial Degradation of Oil of the American Petroleum Institute and as Chairman of a subgroup for a National Academy of Sciences/National Research Council Panel on Underutilized Microbial Processes of Potential Value. Earlier Dr. Laskin was President of the Theobald Smith Society (New Jersey Branch, ASM) and National Councilor for many years. He was Vice-Chairman of the local committee for the 1965 ASM National Meeting and Chairman for the 1976 National Meeting. He also served as Chairman of the Environmental and General Applied Microbiology Division and of the Fermentation Division of ASM, as well as of the Microbiology Section of the New York Academy of Sciences.

Dr. Laskin is not only Co-Editor of the *CRC Handbook of Microbiology* and of *CRC Critical Reviews in Microbiology*, but also of a series entitled *Methods in Molecular Biology* as well as of the books *Extracellular Microbial Polysaccharides* and *The Problems of Drug-Resistant Bacteria*. In addition, he serves as Editor for a series of books on microbiology. Dr. Laskin has also authored and co-authored reviews on the mode of action of tetracycline and on single-cell protein, as well as organized and chaired numerous symposia, seminars, and conferences.

**Hubert A. Lechevalier**, Professor of Microbiology at Rutgers University, New Brunswick, N.J., received a Licence ès Sciences Naturelles (*summa cum laude*) in 1947 and his M.S. degree (*cum laude*) in 1948 from Laval University, Quebec City, Canada. He obtained his Ph.D. from Rutgers University in 1951.

Dr. Lechevalier remained at Rutgers University as Assistant Professor of Microbiology from 1951 to 1956, and subsequently as Associate Professor, before advancing to his present position in 1966. Within this period he also was an exchange scientist at the Academy of Sciences of the U.S.S.R. in Moscow, Visiting Investigator at the Czechoslovak Academy of Sciences in Prague, and Visiting Investigator at the Pasteur Institute, Section of Mycology, in Paris. His research during those years led to U.S. patents for neomycin and candicidin as well as to sixteen foreign patents.

A recipient of Fellowships from the National Research Council of Canada, from Rutgers University, and from the U.S. Public Health Service, Dr. Lechevalier was also awarded membership in Sigma Xi and is an Associate Member of the Société Française de Microbiologie. In 1976 he received the Lindbach Award for Distinguished Research.

In addition to his membership in the American Society for Microbiology, in the Canadian Society for Microbiologists, and in the Mycological Society of America, Dr. Lechevalier has served as a participant on the Editorial Boards of *Applied Microbiology* and of *Annales de Microbiologie*, on the Subcommittee on the Taxonomy of the Actinomycetes of the International Committee on Bacteriological Nomenclature, on the Subcommittee on Tastes and Odors of the American Water Works Association, and on the ASM Archives Committee. He also served as Chairman of the AMS Subcommittee on Actinomycetes, as a Trustee of the American Type Culture Collection, and as consultant to various industrial and legal firms.

Dr. Lechevalier is not only Co-Editor of the *CRC Handbook of Microbiology* and of *CRC Critical Reviews in Microbiology*, but has also collaborated on a number of books — *A Guide to the Actinomycetes and Their Antibiotics*, *Neomycin — Nature, Formation, Isolation, and Practical Application*, *Neomycin — Its Nature and Practical Application*, *Antibiotics of Actinomycetes*, *Three Centuries of Microbiology*, and *The Microbes*. He has also authored or co-authored numerous papers.

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## TABLE OF CONTENTS

|  |     |
|--|-----|
| <b>Introduction, Paleomicrobiology, Cytological Techniques</b> . . . . .     |     |
| How Can We Divide the Microbes? . . . . .                                    | 3   |
| Paleomicrobiology . . . . .  | 9   |
| Techniques to Study the Ultrastructure of Microorganisms . . . . .           | 31  |
| <br><b>The Bacteria</b> . . . . .  |     |
| Introduction to the Bacteria . . . . .                                       | 41  |
| Introduction to the Ultrastructure of Bacteria . . . . .                     | 43  |
| The Rhodospirillales (Phototrophic or Photosynthetic Bacteria) . . . . .     | 119 |
| The Myxobacterales [(Fruiting) Myxobacterales] . . . . .                     | 131 |
| Non-fruiting, Non-trichome-forming, Gram-negative Gliding Bacteria . . . . . | 145 |
| Trichome-forming Bacteria . . . . .  | 147 |
| Budding and Prosthecae Bacteria . . . . .                                    | 165 |
| Bacteria with Acellular Appendages . . . . .                                 | 189 |
| The Spirochaetales . . . . .   | 195 |
| Vibrios and Spirilla . . . . .   | 229 |
| Gram-negative Aerobic Rods and Cocci . . . . .                               | 237 |
| <i>Pseudomonas</i> . . . . .   | 247 |
| Gram-negative Facultatively Anaerobic Rods . . . . .                         | 259 |
| Enterobacteriaceae . . . . .   | 263 |
| Gram-negative Anaerobic Bacteria . . . . .                                   | 273 |
| Gram-negative Cocci and Coccobacilli . . . . .                               | 277 |
| Neisseriaceae . . . . .  | 279 |
| Non-motile, Non-sporulating, Gram-negative Anaerobic Cocci . . . . .         | 283 |
| Chemoautotrophic Bacteria . . . . .  | 285 |
| Methane-producing Bacteria: Anaerobic . . . . .                              | 301 |
| Anaerobic Non-motile Gram-positive Cocci . . . . .                           | 303 |
| Aerobic or Facultatively Anaerobic Gram-positive Cocci . . . . .             | 305 |
| <i>Staphylococcus</i> . . . . .  | 309 |
| <i>Streptococcus</i> . . . . .   | 313 |
| Endospore-forming Rods and Cocci . . . . .                                   | 317 |
| The Genus <i>Bacillus</i> . . . . .  | 319 |
| The Clostridia . . . . .   | 337 |
| Gram-positive Asporogenous Rod-shaped Bacteria . . . . .                     | 347 |
| The Coryneform Bacteria . . . . .  | 351 |
| The Actinomycetales . . . . .  | 361 |
| Introduction . . . . .   | 361 |
| Soil or Oxidative Actinomycetes . . . . .                                    | 363 |
| Parasitic or Fermentative Actinomycetes . . . . .                            | 373 |
| The Rickettsiales . . . . .  | 381 |
| The Chlamydiae . . . . .   | 397 |
| The Mollicutes (Mycoplasmas) . . . . .                                       | 405 |
| Mycoplasma and Ureaplasmas . . . . .   | 417 |
| Acholeplasmas, Spiroplasmas, Thermoplasmas, and Anaeroplasmas . . . . .      | 445 |
| <br><b>General Information</b> . . . . .                                     |     |
| Immunological and Immunochemical Classification of Microorganisms . . . . .  | 463 |
| Glossary . . . . .   | 519 |
| Microorganisms and Symbiosis . . . . .                                       | 551 |

|  |                |
|--|----------------|
| Classification of Etiologic Agents on the Basis of Hazard. . . . . | 559            |
| Regulations Concerning the Shipment of Pathogens . . . . .         | 567            |
| Rules for Nomenclature . . . . .                                   | 575            |
| Numerical Taxonomy. . . . .  | 579            |
| Important Culture Collections . . . . .                            | 597            |
| Literature Guide for Microbiology . . . . .                        | 621            |
| Foreign Alphabets . . . . .  | <b>648-650</b> |
| American Standard Abbreviations. . . . .                           | 651            |
| Temperature Conversion. . . . .                                    | 665            |
| Weights and Measures. . . . .                                      | 675            |
| Logarithms. . . . .  | 679            |
| <b>Indexes . . . . .</b>   |                |
| Taxonomic Index . . . . .  | 687            |
| Topical Index . . . . .  | 743            |

*Introduction*

*Paleomicrobiology*

*Cytological Techniques*



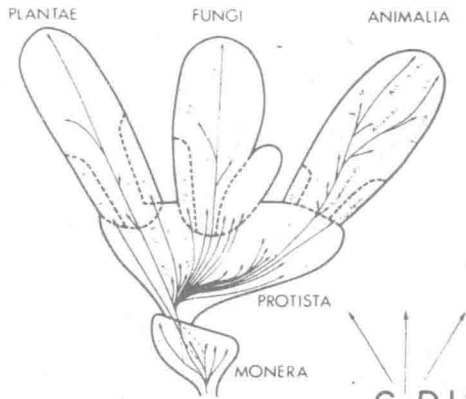
## HOW CAN WE DIVIDE THE MICROBES?

J. McN. Sieburth

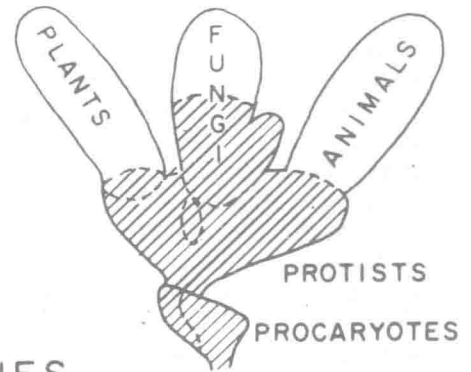
The importance of a reference book lies in the value of what it contains and on how it improves with each edition. Despite the patchwork nature of the first edition of Volume I of the *Handbook of Microbiology*, and despite the inadequate and redundant coverage of certain groups, it assembled under one cover much useful and previously scattered or unpublished information. It also seemed to me that the coverage of some multicellular groups was unnecessary. The book appeared while I was preparing a text on marine microorganisms, which discusses all the major groups of microorganisms studied by phycologists, bacteriologists, mycologists, and protozoologists.<sup>3</sup> In using Volume I as a guide to all the microbiological disciplines, some of its strengths and weaknesses became quite apparent. When I made my criticisms known to the Editors, they invited me to write an introduction to the organismic section of the second edition of the *Handbook*. The task of creating a head for a statue for which others will produce the body and appendages is a challenging and risky assignment. The purpose of this introduction is to show one way in which the entities studied by microbiologists can be organized to minimize redundancy, that is, by dividing them into pragmatic working groups according to their ultrastructure and feeding mode.

In a simpler time, naturalists like Ehrenberg<sup>1</sup> studied and described microorganisms in their environment without too much worry about what kind of microorganism each was. It is a joy to study Ehrenberg's plates and see microalgae, bacteria, and protozoa side by side as they occurred in his samples. As microbiologists in succeeding decades of the 19th century advanced to the culture of many microbial forms with different nutrient requirement and morphological properties, the division between plants and animals became obscure, and the microorganisms were separated into the kingdoms Monera and Protista. Only with the advent of transmission electron microscopy and techniques for thin-sectioning and staining were the tools provided to allow ultrastructural confirmation of the similarities and differences between what we now call prokaryotes and eukaryotes and the differences between the various trophic groups. When the absorptive mode of nutrition was taken into account by Whittaker,<sup>4</sup> the fungi fell into a group of their own, and the divergence of the three trophic modes and that between the three levels of cellular complexity (prokaryote, unicellular eukaryote, and multicellular eukaryote) became clear. The Five Kingdom concept is a pleasing way to show the relationships of the major groups of organisms. Figure 1 shows the now famous Whittaker Five Kingdom scheme and my attempts to divide the microorganisms (Figure 1B) on the basis of discipline (Figure 1C), ultrastructure (Figure 1D), and trophic modes (Figure 1E). When the microorganisms are divided into fiefs according to disciplines, there are too many territorial disputes. None is worse than deciding which protists fall within the province of the phycologist and which belong to the protozoologist. It seems absurd to find flagellates (both chloroplast-containing and chloroplast-lacking species) being claimed by both sides. To be sure, true mixotrophs — such as the marine dinoflagellate *Gyrodinium pavillardii*, containing functional chloroplasts while actively grazing on the holotrichous ciliate *Strombidium* — will continue to raise problems, as well the atrophy of the photosynthetic apparatus in photosynthetic euglenoids and its absence in apochlorotic diatoms. However, there are too many clear-cut photosynthetic flagellates (even called phytoflagellates by the protozoologists) to warrant pulling them away from the microalgae; conversely, the existence of one possible photosynthetic choanoflagellate is not enough to pull the whole group of these phagotrophic flagellates into the phytoflagellates. There will always be exceptions to general rules, since many bizarre forms resulting from offbeat experimental approaches to life persist.

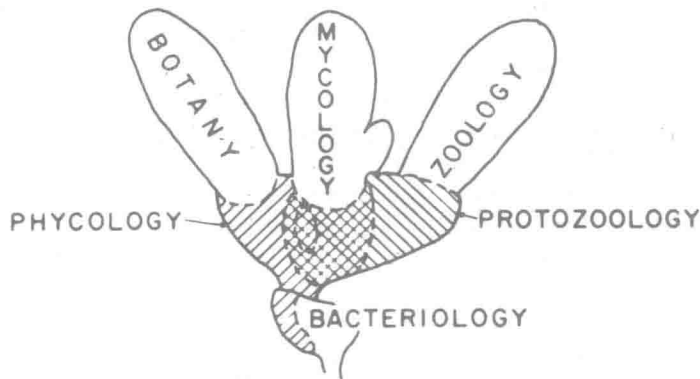
## A. WHITTAKER'S 5 Kingdoms



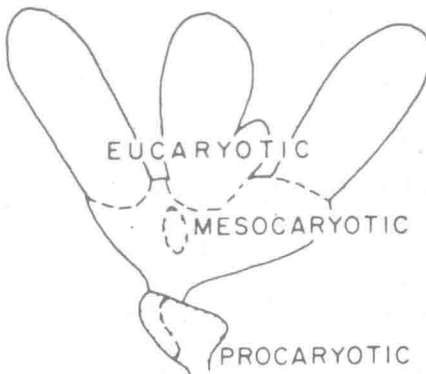
## B. MICROORGANISMS



## C. DISCIPLINES



## D. ULTRASTRUCTURE



## E. TROPHIC MODES

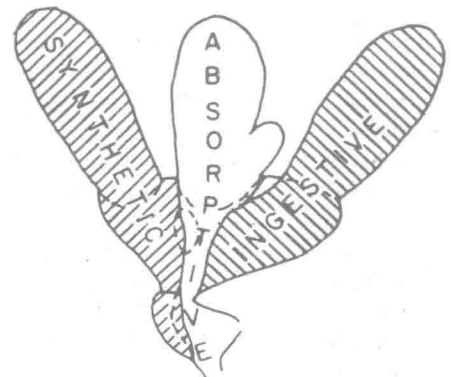


FIGURE 1. The division of the Five Kingdoms of Whittaker into microbial, disciplinary, ultrastructural, and trophic divisions. (Figure 1A taken from Whittaker, R. H., *Science*, 163, 150-160, 1969. Copyright 1969 by the American Association of Science.)

Microorganisms evolved together live together and depend upon each other, as well as on the higher forms of life, for their existence. The examination of natural populations, such as described in *Microbial Seascapes*,<sup>2</sup> shows the necessity of an interdisciplinary approach. The environmental and ecological problems of today require an interdisciplinary approach so that we will be able to jump the borders, knowing not only where we are, but also able to speak a common language. As I, a naive bacteriologist, tried to unravel what ultrastructural studies have done to the taxonomy of the phytoflagellates, tried to get a clearer idea of what the major groups of microscopic fungi are, and attempted to figure out which protozoa occur as free-living marine forms, I felt as though I were traveling through Europe without a road map or a phrase book. If this and other interdisciplinary texts on microorganisms are going to fulfill their function, they must be more than a compilation of uncoordinated summaries with overlapping and contradictory coverage. Of course, one has to make an arbitrary decision on how to divide the microorganisms in order to best minimize territorial disputes and serious overlaps. It would also help to speak a common and simple language. The use of jargon, such as the terms "lignicolous" or "xylophilous" for wood-digesting and wood-inhabiting microorganisms, is ridiculous.

Territorial disputes can be minimized by the simple philosophy of recognizing that, although mixotrophy occurs, most organisms have one dominant mode of nutrition. Therefore, primary division can be made according to this dominant nutritional mode, with further divisions according to ultrastructure. Although two ultrastructural kingdoms are usually recognized, a third kingdom, the Mesokaryota, has been proposed by Dodge<sup>5</sup> for dinoflagellates on the basis of their intermediate nuclear organization. Even including this dubious kingdom, division only by ultrastructure or only by trophic mode (Figures 1D and 1E) is insufficient to yield manageable groups. A division according to both criteria, however, results in seven convenient working groups, as shown in Table 1. The practicality of such a division is shown by further dividing the seven working groups into some 33 arbitrary vernacular groupings, as shown in Table 2, which covers the microorganisms considered in this volume and in Volume II. (For the convenience of the reader, volume and — where known — page numbers are given in parentheses for each grouping.) The size of each grouping varies greatly, but it puts the microbial realm into a manageable framework. I will not attempt here to show the reasoning behind the lumping and divisions that are made. This information will eventually be published.<sup>3</sup> Due to the multiple authorship of this *Handbook*, and due to the reluctance of the Editors to force the divorces, marriages, and rearrangements necessary to accomplish my suggested arrangement, the contents of the first two volumes of the second edition are presented in a different sequence than the one suggested.

These two volumes show many areas of improvement and updating over Volume I of the first edition. Their appeal is still the wide coverage of the forms studied by microbiologists. As with the microorganisms described, it will take succeeding generations to select the qualities that are needed for survival.

Table 1  
DIVISION OF THE MICROBIOLOGISTS' REALM INTO  
WORKING GROUPS ACCORDING TO FEEDING AND  
ULTRASTRUCTURE TYPES

| Feeding type      | Ultrastructural type |            |         |
|-------------------|----------------------|------------|---------|
|                   | Prokaryotes          | Eukaryotes | Virions |
| Chemolithotrophic | +                    |            |         |
| Phototrophic      | +                    | +          |         |
| Osmotrophic       | +                    | +          |         |
| Phagotrophic      |                      | +          |         |
| Ribosomotrophic   |                      |            | +       |



Table 2  
SUGGESTED DIVISION OF THE SEVEN WORKING GROUPS  
OF MICROORGANISMS INTO VERNACULAR SUBGROUPS

- I. CHEMOLITHOTROPHIC PROKARYOTES
  - A. Bacteria oxidizing ammonia and nitrite (Vol. I, pp. 288, 293–296)
  - B. Bacteria oxidizing sulfur and sulfur compounds (Vol. I, pp. 286, 288, 290–292)
- II. PHOTOTROPHIC PROKARYOTES
  - A. Cyanophytes (Vol. II)
  - B. Rhodospirilla (Vol. I, pp. 119–130)
- III. PHOTOTROPHIC EUKARYOTES
  - A. Diatoms (Vol. II)
  - B. Dinoflagellates (Vol. II)
  - C. Haptophytes (Vol. II)
  - D. Prasinophytes (Vol. II)
  - E. Chrysophytes (Vol. II)
  - F. Cryptophytes (Vol. II)
  - G. Euglenophytes (Vol. II)
  - H. Chlorophytes (Vol. II)
  - I. Xanthophytes (Vol. II)
  - J. Eustigmatophytes (Vol. II)
  - K. Rhapidophytes (Vol. II)
  - L. Rhodophytes (Vol. II)
- IV. OSMOTROPHIC PROKARYOTES
  - A. Aerobic/facultative, nondistinctive, Gram-negative:
    1. Azotobacteria (Vol. I, p. 239)
    2. Rhizobias (Vol. I, p. 240)
    3. Halobacters (Vol. I, p. 242)
    4. Enterobacters (Vol. I, pp. 259, 263–272)
    5. Vibrios (Vol. I, pp. 229–234)
    6. Neisserias (Vol. I, pp. 277, 279–282)
    7. Pseudomonads (Vol. I, pp. 237, 247–258)
  - B. Aerobic/facultative, distinctive, Gram-negative:
    1. Gliding bacteria (Vol. I, p. 145)
    2. Sheathed bacteria (Vol. I, pp. 147–151)
    3. Prosthecae bacteria (Vol. I, pp. 173–185)
    4. Spirals and curved bacteria (Vol. I, pp. 237, 240, 241)
    5. Methyamonads
  - C. Aerobic/facultative, Gram-positive:
    1. Cocci (Vol. I, pp. 305–307)
    2. Endospore-forming bacteria (Vol. I, pp. 317, 318)
    3. Asporogenous bacteria (Vol. I, pp. 347–350)
    4. Actinomycetes (Vol. I, pp. 361–380)
  - D. Obligately anaerobic:
    1. Clostridia (Vol. I, pp. 337–345)
    2. Spirochetes (Vol. I, pp. 195–227)
    3. Gram-negative rods (Vol. I, pp. 259, 260, 262, 273–275)
    4. Gram-negative cocci (Vol. I, p. 261)
    5. Methanogenic bacteria (Vol. I, p. 301)
    6. Sulfate-reducing bacteria (Vol. I, pp. 229, 337)
  - E. Mycoplasmas (Vol. I, pp. 405–459)
  - F. Rickettsias (Vol. I, pp. 381–395)
  - G. Chlamydias (Vol. I, pp. 397–404)
- V. OSMOTROPHIC EUKARYOTES
  - A. Filamentous fungi:
    1. Ascomycetous (Vol. II)
    2. Basidiomycetous (Vol. II)
    3. Deuteromycetous (Vol. II)
  - B. Yeasts:
    1. Ascomycetous (Vol. II)
    2. Basidiomycetous (Vol. II)
    3. Deuteromycetous (Vol. II)
  - C. Zygomycetes (Vol. II)