BERGEY'S MANUAL® OF

Systematic Bacteriology

Second Edition

Volume Two

The *Proteobacteria*

Part A

Introductory Essays

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Introductory Essays

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TO COME

This volume is dedicated to our colleagues, David R. Boone, Don J. Brenner, Richard W. Castenholz, and Noel R. Krieg, who retired from the Board of Trustees of Bergey's Manual Trust as this edition was in preparation. We deeply appreciate their efforts as editors and authors; they have devoted their time and many years in helping the Trust meet its objectives.

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Preface to Volume Two of the Second Edition of *Bergey's Manual® of Systematic Bacteriology*

There is a long-standing tradition for the Editors of *Bergey's Manual* to open their respective editions with the observation that the new edition is a departure from the earlier ones. As this volume goes to press, however, we recognize a need to deviate from this practice, by offering a separate preface to each volume within this edition. In part, this departure is necessary because the size and complexity of this edition far exceeded our expectations, as has the amount of time that has elapsed between publication of the first volume of this edition and this volume.

Earlier, we noted that 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. Clearly, the pace has been accelerating as evidenced in the super-linear rate at which new taxa are being described. Much of the increase can be attributed to rapid advances in sequencing technology, which has brought about 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 in 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 thank Drs. Hans Trüper, Brian Tindall, and Jean Euzéby for their assistance on matters of nomenclature and etymology.

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 Drs. Julia Bell and Denise Searles for their expert editorial assistance and diligence in verifying countless pieces of critical information and to Dr. Timothy G. Lilburn for constructing many of the phylogenetic trees used in this volume. We also extend our thanks to Alissa Wesche, Matt Chval and Kristen Johnson for their assistance in 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. William Curtis for his courage, patience, understanding, and support; Catherine Lyons for her expertise in designing and developing our DTD, and Jeri Lambert and Leslie Grossberg of Impressions Book and Journal Services 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. Don Brenner, Noel Krieg, and James Staley for their enormous efforts as volume editors and to my wife, Nancy, and daughter, Jane, for their continued 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, 6162 Biomedical and Physical Sciences Building, Michigan State University, East Lansing, MI, USA 48824-4320. Email: garrity@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 authorities to whom we are most grateful. Authors were chosen on the basis of constant surveillance of the literature of bacterial systematics and by recommendations from our Advisory Committees.

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

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

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

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

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

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

A number of institutions and individuals deserve special acknowledgment from the Trust for their help in bringing about the publication of this volume. We are grateful to the Department of Biology of the Virginia Polytechnic Institute and State University for providing space, facilities and, above all, tolerance for the diverted time taken by the Editor during the preparation of the book. The Department of Microbiology at Iowa State University of Science and Technology continues to provide a welcome home for the main editorial offices and archives of the Trust and we acknowledge their continued support. A grant (LM-03707) from the National Library of Medicine, National Institutes of Health to assist in the preparation of this and the next volume of the *Manual* is gratefully acknowledged.

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

John G. Holt

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.

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Committee on Manual.
August, 1923.

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The History of *Bergey's Manual*

R.G.E. Murray and John G. Holt

Introduction

Bergey's Manual of Determinative Bacteriology has been the major provider of an outline of bacterial systematics since it was initiated in 1923 and has provided a resource ever since to workers at the bench who need to identify bacterial isolates and recognize new species. It originated in the Society of American Bacteriologists (SAB) but it has since become a truly international enterprise directed by an independent Trust which was founded in 1936. It has gone through nine editions and has generated, as a more comprehensive resource, a unique compendium on bacterial systematics, *Bergey's Manual of Systematic Bacteriology* (Holt et al., 1984–1989), which now enters its second edition.

A number of dedicated bacteriologists (Table 1) have formed, guided the development of, and edited, each edition of *Bergey's Manual*. Many of these individuals have been well known for activity in their national societies and devotion to encouraging worldwide cooperation in bacteriology and particularly bacterial taxonomy. Some of them worked tirelessly on the international stage towards an effective consensus in taxonomy and common approaches to classification. This led to the formation in 1930 of an International Association of Microbiological Societies (IAMS) holding regular Congresses. The regulation of bacterial taxonomy became possible within IAMS through an International Committee on Systematic Bacteriology (ICSB), thus recognizing the need for international discussions of the problems involved in bacterial systematics. Eventually, the need for a Code of Nomenclature of Bacteria was recognized and was published in 1948 (Buchanan et al., 1948), and a Judicial Commission (JC) was formed by ICSB to adjudicate conflicts with the Rules. Despite these efforts, an enormous number of synonyms and illegitimate names had accumulated by the 1970s and were an evident and major problem for the Editor/Trustees of *Bergey's Manual* and for all bacteriologists (Buchanan et al., 1966; Gibbons et al., 1981). A mechanism for recognizing useful, and abandoning useless, names was accomplished by the ICSB and the JC largely due to the insistent arguments of V.B.D. Skerman. Lists were made based on the names included in the Eighth edition of *Bergey's Manual of Determinative Bacteriology* (Buchanan and Gibbons, 1974), because they had been selected by expert committees and individual author/experts, together with the recommendations of sub-committees of ICSB. The results were (1) the published Approved Lists of Bacterial Names (Skerman et al., 1980); (2) a new starting date for bacterial names of January 1, 1980 to replace those of May 1, 1753; (3) freeing of names not on the Approved Lists for use in the future; and (4) definition in the Bacteriological Code (1976 revision; Lapage et al., 1975) of the valid and invalid publication of names. It is now evident that the care and thought of contributors to *Bergey's Manual* over the years played a major part in stimulating an orderly nomenclature for taxonomic purposes, in the development of a useful classification of bacteria often used as a basal reference, and in providing a continuing compendium of descriptions of known bacteria.

The *Manual* started as a somewhat idiosyncratic assembly of species and their descriptions following the interests and prejudices of the editor/authors of the early editions. Following the formation of the Bergey's Manual Trust in 1936 and the international discussions of the ICSB at Microbiological Congresses, the new editions became more and more the result of a consensus developed by advisory committees and specialist authors for each part or chapter of the volumes. This did not happen all at once; it developed out of practice and trials, and it is still developing as the basic sciences affecting taxonomy bring in new knowledge and new understanding of taxa and their relationships.

Antecedents of *Bergey's Manual*

Classification of named species of bacteria did not arise quickly or easily (Buchanan, 1948). The Linnaean approach to naming life forms was adopted in the earliest of systems, such as Müller's use of *Vibrio* and *Monas* (Müller, 1773, 1786), for genera of what we would now consider bacteria. There were few observations, and there was insufficient discrimination in the characters available during most of the nineteenth century to allow any system, even the influential attempts by Ehrenberg (1838) and Cohn (1872, 1875), to provide more than a few names that still survive (e.g. *Spirillum*, *Spirochaeta*, and *Bacillus*). Most descriptions could rest only on shape, behavior, and habitat since microscopy was the major tool.

Müller's work was the beginning of the descriptive phase of bacteriology, which is still going on today because we now realize that the majority of bacteria in nature have not been grown or characterized. Early observations such as Müller's were made by cryptogamic botanists studying natural habitats, usually aquatic, and who usually gave Linnaean binomials to the objects they described microscopically. The mycologist H.F. Link (1809) described the first bacterium that we still recognize today, which he named *Polyangium vitellinum* and is now placed with the fruiting myxobacteria. Bizio (1823) attempted to explain the occurrence of red pigment formation on starchy foods such as polenta as the result of microbial growth and named the organism he found there *Serratia marcescens*, a name now associated with the prodigiosin-producing Gram-negative rod. Perhaps one of the most significant observers of infusoria in the early nineteenth

TABLE 1. Members of the Board of Trustees

David H. Bergey	1923–1937
David R. Boone	1994–
Robert S. Breed	1923–1957 (Chairman 1937–1956)
Don J. Brenner	1979–2001
Marvin P. Bryant	1975–1986
R.E. Buchanan	1951–1973 (Chairman 1957–1973)
Richard W. Castenholz	1991–2001
Harold J. Conn	1948–1965
Samuel T. Cowan	late 1950s–1974
Paul De Vos	2002–
Geoffrey Edsall	late 1950s–1965
George M. Garrity	1997–
Norman E. Gibbons	1965–1976
Michael Goodfellow	1999–
Bernard W. Hammer	1923–1934
Francis C. Harrison	1923–1934
A. Parker Hitchens	1939–1950
John G. Holt	1973–2000
Frank M. Huntoon	1923–1934
Noel R. Krieg	1976–1991, 1996–2002
Stephen P. Lapage	1975–1978
Hans Lautrop	1974–1979
John Liston	1965–1976 (Chairman 1973–1976)
A.G. Lochhead	late 1950s–1960
James W. Moulder	1980–1989
E.G.D. Murray	1934–1964
R.G.E. Murray	1964–1990 (Chairman 1976–1990)
Charles F. Niven, Jr.	Late 1950s–1975
Norbert Pfennig	1978–1991
Arnold W. Ravin	1962–1980
Fred A. Rainey	1999–
Karl-Heinz Schleifer	1989–
Nathan R. Smith	1950–1964
Peter H.A. Sneath	1978–1994 (Chairman 1990–1994)
James T. Staley	1976– (Chairman 2000–)
Roger Y. Stanier	1965–1975
Joseph G. Tully	1991–1996
Jan Ursing	1991–1997
Stanley T. Williams	1989–2000 (Chairman 1994–2000)

century was C.G. Ehrenberg, who described many genera of algae and protozoa and, coincidentally, some bacteria (Ehrenberg, 1838). He named genera such as *Spirochaeta* and *Spirillum*, still recognized today, and *Bacterium*, which became a catch-all for rod-shaped cells, and was made *nomen rejiciendum* in 1947.

Logical classifications were attempted throughout the nineteenth century and that of Ferdinand Cohn (1872, 1875), with his attempts to classify the known bacteria, was most influential. In his 1872 paper Cohn recognized six genera of bacteria (*Micrococcus*, *Bacterium*, *Bacillus*, *Vibrio*, *Spirillum*, and *Spirochaeta*) and later (1875) expanded the classification to include the cyanobacteria while adding more bacterial genera (*Sarcina*, *Ascococcus*, *Leptothrix*, *Beggiatoa*, *Cladothrix*, *Crenothrix*, *Streptococcus* [not those recognized today], and *Streptothrix*). Buchanan (1925) suggested that Cohn's 1875 classification could be the starting date for bacterial nomenclature instead of Linnaeus' *Species Plantarum* of 1753 and discussed various ideas for the proper starting date for bacterial nomenclature, anticipating by a quarter of a century the actual change in starting date proposed in the revised Bacteriological Code (Lapage et al., 1975). The realization that cultivation was possible, and the development of pure culture techniques, extended enormously the capability to recognize and describe species by adding their growth characteristics and effects on growth media. The vague possibilities of pleomorphism gave way to a concept of fixity of species. All this was aided by the human preoccupation with health, the seriousness of infectious diseases, and the growing awareness of the association of particular kinds of bacteria with particular diseases. The result was a rapid increase in the number of taxonomic descriptions and the recognition that similar but not identical species of bacteria were to be found both associated with higher life forms and more generally distributed in nature.

Between 1885 and 1910 there were repeated attempts at classification and arrangements based on perceived similarities, mostly morphological. There were genuine attempts to bring order out of chaos, and a preliminary publication often stimulated subsequent and repeated additions and revisions, but all these authors neglected the determinative requirements of bacteriology. Some notable examples were Zopf (1885), Flügge (1886), Schroeter (1886), and Trevisan (1887, 1889). Migula produced his first outline in 1890 and new versions in 1894, 1895, 1897, and 1900; others followed, notably Fischer (1895), and importantly, because of a degree of nomenclatural regularity, Lehmann and Neumann published their atlas in 1896. The latter was probably the most successful of the systems and was used in successive editions until 1930, especially in Europe. All these were important in their time. However, a major influence in the subsequent development of *Bergey's Manual* in the environment of the Society of American Bacteriologists (SAB) was the work of F.D. Chester, who produced reports in 1897 and 1898 of bacteria of interest in agriculture, to be followed in 1901 by his *Manual of Determinative Bacteriology*. Chester had recognized that the lack of an organized assembly of descriptions and a scheme of classification made the identification of isolates as known species and the recognition of new species an insurmountable task. Another classification provided by Orla-Jensen (1909, 1919) was influential because it represented an interpretation of "natural relationships", reflecting a more physiological approach to description based on his own studies of the lactic acid bacteria encountered in dairy bacteriology. He delimited genera and species on the basis of characteristics such as metabolic byproducts, fermentation of various sugars, and temperature ranges for growth, in addition to morphology. Most classifications to that time reflected the idiosyncrasies of the authors and their areas of experience. What was yet to come was the ordering of assemblies of all known bacteria, arranged with properties documented to facilitate determination and presenting continuing trials of hierarchical arrangements; it was in that format that *Bergey's Manual* started.

Steps Leading to the First Edition of the *Manual*

Bergey's Manual of Determinative Bacteriology arose from the interest and efforts of a group of colleagues in the Society of American Bacteriologists, who were fully aware of previous attempts to systematize the information available on bacterial species and who recognized that the determination of bacterial identity was difficult and required extensive experience. A committee was formed with C.-E.A. Winslow as chairman and J. Broadhurst, R.E. Buchanan, C. Krumweide Jr., L.A. Rogers, and G.H. Smith as members. Their discussions at the meetings of the SAB and their reports, which were published in the Journal of Bacteriology (Winslow et al., 1917, 1920), were signposts for future efforts in systematics. There were two "starters" for a *Manual*: R.E. Buchanan (Fig. 1a), a rising star in the bacteriological firmament, and President of the SAB in 1918, working at Iowa State College, and D.H. Bergey (Fig. 1b), a senior and respected bacteriologist and President of the SAB for 1915, working at the University of Pennsylvania.

Between 1916 and 1918 Buchanan wrote ten papers entitled "Studies on the nomenclature and classification of the bacteria"

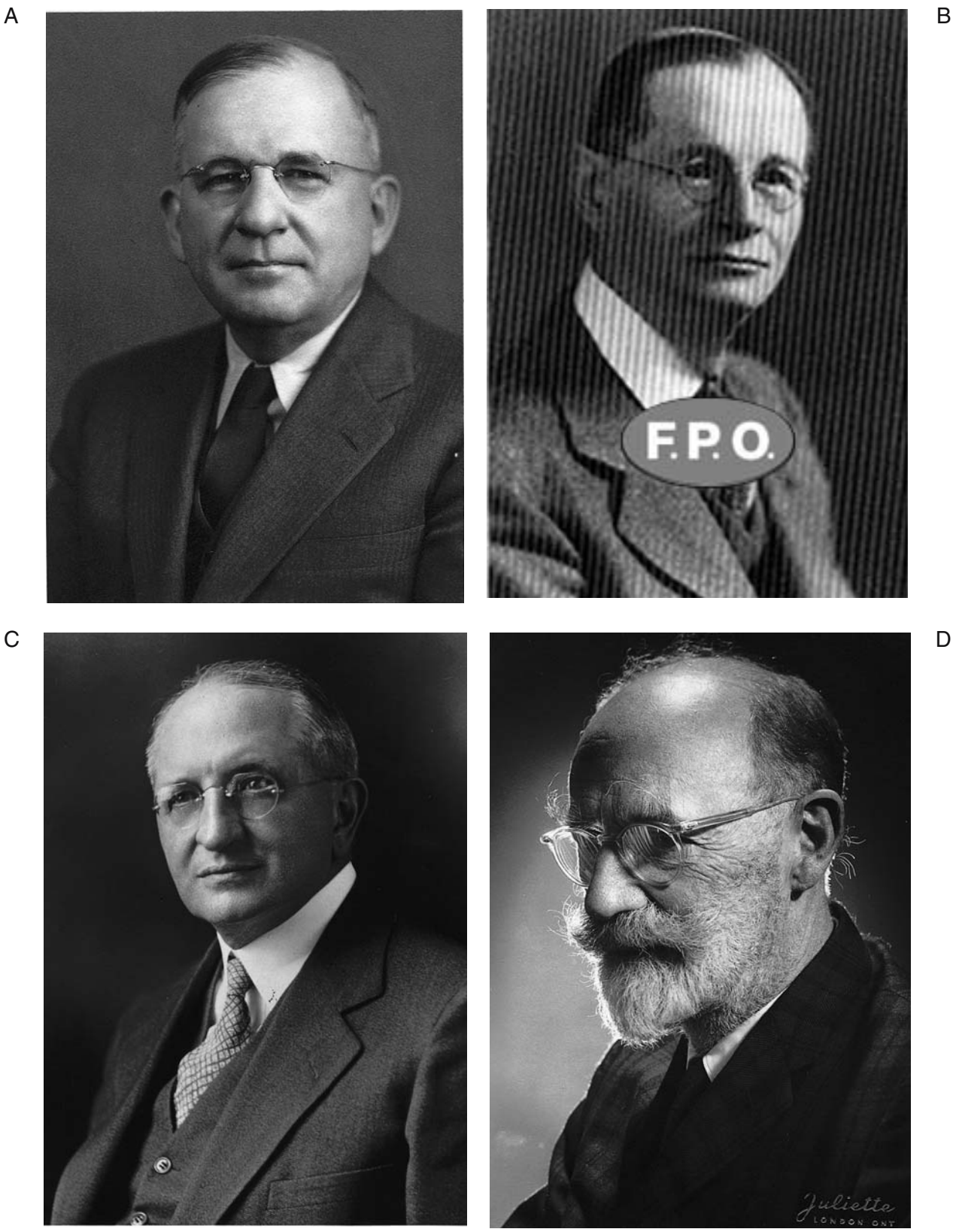

FIGURE 1. *A*, Robert Earle Buchanan, 1883–1973; *B*, David Henricks Bergey, 1860–1937; *C*, Robert Stanley Breed, 1877–1956; *D*, Everitt G.D. Murray, 1890–1964. (Fig. 1C courtesy of American Society for Microbiology Archives Collection.)

(Buchanan, 1916; 1917a, b, c; 1918a, b, c, d, e, f) which provided substance for the Winslow Committee (Buchanan was a member), and was intended to be the basis of a systematic treatise. These papers were revolutionary, in the sense that they included all the bacteria (except the cyanobacteria) that were described at that time. Buchanan included, and named the higher groupings of, bacteria such as the actinomycetes, myxobacteria, phototrophs, and chemolithotrophs, along with the other bacteria included in the classifications of the day. This classification had a logical and aesthetic appeal that helped launch the systematic efforts that followed. No doubt Buchanan was driven by dissatisfaction with sloppy and confusing nomenclature as well as inadequate descriptions of "accepted" bacteria (indeed, much of his later work on *Bergey's Manual* and the *Index Bergeyana* reflected his preoccupation with names and illegitimacy, and had much to do with getting a bacteriological code of nomenclature started.) He must have known of Bergey's book and, perhaps because of increasing academic responsibilities, publication of his concepts in his *General Systematic Bacteriology* was delayed until 1925 (Buchanan, 1925). The book did not try to duplicate *Bergey's Manual*, but rather presented a history of bacterial classification and nomenclature, followed by a discussion of the history of all the bacterial genera and higher ranks, listed alphabetically.

R.E. Buchanan was the key player in the renewal of concern for a sensible (not necessarily "natural") classification of bacteria, with a well-regulated nomenclature, working continuously and firmly to those ends from 1916 to the end of his life. He was a man of his times developing his own priorities and prejudices, yet he recognized in the end that new science was needed for a significant phylogeny to develop. Furthermore, he was more influential in gaining support for the initiation and progress of the first few editions of *Bergey's Manual* under the slightly reluctant aegis of the SAB than is obvious in the *Manual's* pages and prefaces. He also played a dominant role in international efforts (representing the SAB) concerning the regulation and codification of classification and nomenclature. As a member of the "Winslow Committee" of the SAB directed to report on the classification of bacteria, he furnished much of the basis for discussion through his series of papers in the Journal of Bacteriology. He provided voluminous detailed suggestions for the revision of Dr. Winslow's drafts for their reports to the SAB (1917 and 1920). He was also in a powerful position to influence decisions, being elected President of SAB for 1918–1919 when critical discussions were taking place.

The Winslow Committee was engaged in protecting ("conserving") the generic names for well-established species by listing them as *genera conservanda*, together with type species for discussion at the 1918 SAB meeting. The intention was to provide a basis for recommendations for formal action at the next International Botanical Congress, since they were working under the general rules of the Botanical Code. They went further by classifying the genera within higher taxa and providing a key to assist recognition. They intended seeking formal approval of the whole report by the SAB. At this stage, R.S. Breed (Fig. 1c) wrote many letters of objection to having any society ratify the concepts involved in contriving a classification, because it would suggest that it is "official", and he attempted unsuccessfully to gain a postponement of the report's presentation. This polemical correspondence with Committee members, including Buchanan, ended in Breed's withdrawing his name from the report despite his evident interest in a workable classification and a more stable nomenclature. Winslow read the report to the SAB meeting on December 29, 1919. Although it emphasized that its listings were not to be considered as a standard or official classification, it did ask "that the names be accepted as definite and approved genera". The report was then published in the *Journal of Bacteriology*. The Committee was discharged and a new Committee on Taxonomy was appointed with R.E. Buchanan as Chairman. In 1920 Breed was added as a member of the new committee, with the responsibility of making the representations at the Botanical Congress because of his membership on the Botanical Code Revision Committee.

It was at this time and in this climate of opinion that Dr. David Bergey decided to put his own studies of bacteria together with the current views on their classification. To do this required more than one person and he assembled a like-minded group to form a Committee of the SAB for the production of a *Manual of Determinative Bacteriology* (F.C. Harrison, R.S. Breed, B.W. Hammer, and F.M. Huntoon). There is no direct evidence that Buchanan was ever asked to participate or, equally, that he raised any formal objections; it seems more likely that there could have been none of the formal encouragement to go ahead evident in 1921 and 1922 without his support. Indeed he seems to have thought it a good enterprise (Preface in his 1925 book). However, he did find it difficult to work with Breed (letter of January 8, 1951 to J.R. Porter) and in expressing this stated "I have ... always refused to become a member of the Editorial Board of the *Manual*". One wonders if his experiences with Breed between 1918 and 1951 ("Scarcely a month passes in which we do not have some disagreement ... but he has a good many excellent qualities") had kept him at arm's length but not out of touch with what was going on with the *Manual*.

The Winslow Committee had put before the SAB the possibility of a major compilation on bacterial systematics. No doubt Buchanan was in a position, as a Past President, to reinforce the value of that project in principle and David Bergey, likewise a Past President, must have been aware of all the discussions. At the time of the last report (Winslow et al., 1920) Bergey must have started on his book, because R.S. Breed reported to the 1922 SAB Council meeting that the work was approaching completion. A more formal proposal was made to the same Council meeting that Bergey's book be published under the aegis of the Society. The SAB agreed to this with the proviso that it go to a substantial publishing house and, following a discussion of the disposition of royalties, *Bergey's Manual of Determinative Bacteriology* was published in 1923 by the Williams & Wilkins Co., Baltimore (Bergey et al., 1923). It was a group effort from the start, with the authors listed as D.H. Bergey, F.C. Harrison, R.S. Breed, B.W. Hammer, and F.M. Huntoon, and there was an acknowledgment of the assistance of six other colleagues on special groups.

One can imagine that Buchanan was upset by this turn of events, for which the only evidence is his sending Bergey a long list of errors he found in the published book (personal communication). However, he was quite generous in his preface to his 1925 book, with his assessment of *Bergey's Manual* as a step towards reducing chaos and confusion in the classification, phylogeny, and naming of bacteria. He writes: "The most hopeful sign of importance in this respect probably has been the work of the committee on taxonomy of bacteria of the Society of American Bacteriologists under the chairmanship of Dr. Winslow and of the more recent work of a committee on classification of bacteria under the chairmanship of Dr. Bergey.... It is to be expected that, as a result of their work, eventually a practical system of nomenclature which will be satisfactory and applicable to all fields of bacteriology will be evolved" (Buchanan, 1925). Furthermore, he emphasized the differences between practical

(medical) and academic attitudes towards individual species and the requirements of a classification. He was then, as later, concerned that bacterial nomenclature was not regulated by an appropriate Code. He writes: "It seems to be self-evident that until the bacteriologists can agree upon a code and follow it consistently, there is little hope or remedy for our present chaos". So it is not surprising that he contributed a section to the Fourth Edition (Bergey et al., 1934) discussing the International Botanical Code as a basis for a bacteriological code with modifications to make it more appropriate.

The committee that organized the First Edition stated that they did not regard their classification of species "as in any case final, but merely a progress report leading to more satisfactory classifications in the future". Clearly there was some feeling in the UK and Europe that this classification was an imposition on the part of the SAB*. As a counter, the Third Edition (Bergey et al., 1930) included a box opposite the title page which declares that it is *"Published at the direction of the Society"* which "disclaims any responsibility for the system of classification followed"; and states further that it "has not been formally approved by the Society and is in no sense official or standard" (italics are in the original). This shows that there had been, as indicated by the article by I.C. Hall in 1927 (Hall, 1927), some degree of contention among members of the SAB with the decisions of the Committee.

Hall's objections to the presentations of the Committee of the SAB on characterization and classification of bacterial types starts with the final report (Winslow et al., 1920) being "presented only to a small minority of the members of the Society who happened to return from lunch in time to attend a business session of the twenty-first annual meeting, which was held in Boston more than four months before the publication of the report". He regrets lack of opportunity for scientific consideration and "practically no discussion because only a few knew what was coming". He evidently objected to physiological criteria and believed that morphology should define genera, families, and orders; furthermore he disputed the validity of habitat and believed that serological characterization was futile. He was prepared to use cultural and physiological properties as criteria for species. He sought "unambiguous criteria". He quotes others who disagreed with the *Bergey's Manual* approach including W.W.C. Topley, who also expressed his distaste in his famous textbook ("Topley and Wilson") that was published in 1929.

Bergey's Manual was launched and successful enough for the publisher to encourage further editions with corrections and additions in 1925 and 1930, for which Bergey had the support of the same four co-authors. There were problems ahead. By 1930 Bergey was aging and becoming somewhat frail so that he was concerned about the *Manual*'s governance and future. He turned to Breed to an increasing degree for the overall editing and as a major contributor, but also to fight for financial support and for a degree of independence. The agreement co-signed by Bergey and Breed with the Society in 1922 had recommended that royalties " . . . be accumulated in a separate fund to be used to stimulate further work in this field" and Bergey himself felt that he had "donated" this fund to the Society for that purpose.

*As can be gathered from skeptical sentiments in the famous textbook by W.W.C Topley and G.S. Wilson, *Principles of Bacteriology and Immunity*, 1st ed. (1929), Edward Arnold Ltd., London, and continued in large part to the Fifth Edition (1964) but not thereafter.

The Struggle for Financial and Editorial Independence

Breed's correspondence after 1930 with the powerful Secretary-Treasurers of the SAB (J.M. Sherman 1923–1934; I.L. Baldwin 1935–1942) seeking funds to assist the business of producing new editions became increasingly sharp and argumentative because this assistance was almost uniformly refused. The royalties were small and the publisher did not pay any until the costs were covered; the result was that the Society felt they were exposed to risk with a property that they considered not likely to go on much longer. Sherman, in particular, strongly objected to Breed's rhetoric and proprietary attitude, yet he reluctantly agreed in 1933 to cede $900 (half the accumulated royalties) for Fourth Edition purposes. The Society felt that the funds were theirs (the contract was between the Society and Williams & Wilkins) and there might be others deserving of support from the fund. A request for funds by A.T. Henrici in 1935 brought the whole matter of ownership back into contention and into Baldwin's more diplomatic hands. At the same time Breed was asking for $1000 (essentially the remainder of royalties plus interest) and decisions had to be made during a flurry of correspondence with a repetitive *non placet obligato* from Sherman. There was also a *Bergey's Manual* Committee (Winslow, Buchanan and Breed) reporting to the Council in support of a mechanism for funding the *Manual*. In the end, and agreeably to all parties for different reasons, it was decided between Sherman and Baldwin that the SAB should cede the rights to the *Manual*, the royalties to come, and the accumulated fund to Dr. Bergey to do with as he would wish, and the Council agreed (December 28, 1935). In large part it was a gesture of respect for Dr. Bergey because both of them stated in letters that they did not expect the *Manual* to go through more editions, in which respect they were mistaken.

In preparation for the Fourth Edition, and recognizing that Bergey was not well and that Harrison, Hammer, and Huntoon would not stay for long, Breed added E.G.D. Murray (Fig. 1d) to his corps of editors/authors, so that with Harrison still enlisted there were two Canadian members. With the Fourth edition published in 1934, from late 1935 until early 1936 was a time of negotiation. It is clear that Bergey, Breed, and Murray wanted an independent entity, while Buchanan with his own ideas was presenting a plan to Baldwin involving sponsorship by the Society, and Breed was trying unsuccessfully to make peace with Buchanan. Bergey, for his part, was (January, 1936) consulting with the SAB and advisors in preparation for developing a deed of trust for the future development of the *Manual*, and asking that there be no further controversy. His feeling about the whole sad tale was voiced on January 29, 1936: "The arrangement I have made will be without hindrance from a group of persons who appear to have no kindly feeling toward advances in bacteriology in which they could not dictate every step". The *Bergey's Manual* Trust was indentured on January 2, 1936 in Philadelphia, Pennsylvania, and the Trustees were Bergey, Breed, and Murray. The only concession to the SAB, that continues to the ASM today, is that one of the Trustees is chosen as a representative who reports annually to the Society on the state of the Trust and its work.

Mr. R.S. Gill, the representative of the Williams & Wilkins Co., informed Breed in December, 1934 that copies of the Fourth Edition were exhausted and sought agreement for a new edition; Breed prevaricated because the situation was not yet clear. However, by 1937 he was seeking contributions from a number of colleagues for a future volume. Sadly, D.H. Bergey died on Sep-

tember 5, 1937 at age 77, but the trustees retained his name on the masthead of the Fifth Edition published in 1939. Breed was now Chairman of the Trust and remarked in a letter to E.B. Fred and I.L. Baldwin (January 26, 1938) that Dr. Bergey, who was so interested in seeing the *Manual* revised, would have liked "... to know how well his plans are developing and how ... interested specialists are cooperating with us in making this new edition much better than anything we have had before". So a new way of producing the *Manual* with many contributors was now in place for elaboration in future editions. The first printing of 2000 copies of the Fifth Edition (Bergey et al., 1939) was sold out before the end of the year and 1000 more copies were printed. It was obvious that the *Manual* was needed and served a useful purpose, vindicating the optimism Bergey and Breed had maintained in the face of opposition. Breed, Murray, and A.P. Hitchens (who was appointed to the Board of Trustees in 1939) had to organize a Sixth Edition, which needed to be completely revised and required much to be added. There were 1335 species descriptions in the Fifth Edition and the Sixth, when accomplished, would have 1630. They were faced not only with the need to make changes in the outline classification but also to make decisions about the inclusion or exclusion of large numbers of dubious and inadequately described bacteria. Furthermore, the exigencies of World War II took some of the trustees and many of their contributors out of contention for the duration. Nevertheless, the Sixth Edition was published in 1948 (Breed et al., 1948a) and acknowledged the assistance of 60 contributors. Some of the incompletely described species appeared in appendices following the listings in genera and the book included an index of sources and habitats as an attempt to be helpful. A novelty, and an approach not to be fully realized until 35 years later in the *Systematic Manual*, was a section on the *Myxobacterales* containing a preliminary discussion of the nomenclature and biological characteristics of members of that Order. For this, credit is given to J.M. Beebe, R.E. Buchanan, and R.Y. Stanier; it seems likely to those who knew all of them that this approach originated with Stanier. Additions to the Sixth Edition were sections on the classification of *Rickettsiales* prepared by I.A. Bengston and on the *Virales* or Filterable Viruses prepared by F.O. Holmes. The former was appropriate but the latter pleased very few, certainly preceded an adequate understanding that would have allowed for a rational classification, and never appeared again.

The original Board of Trustees went through changes due to death and the enlargement of the Board. H.J. Conn, a colleague of Breed's at Cornell, was added in 1948 to join Breed, Murray, and Hitchens. The next year A.P. Hitchens died and was replaced by N.R. Smith, an expert on *Bacillus* species. R.E. Buchanan was added as a member in 1951 and began to take an active role in the affairs of the Trust. In 1952 Breed expressed a desire to step down as Editor-in-Chief, he was 75, and the Board debated about his successor. Among those considered were E.G.D. Murray, who was about to retire from McGill University, L.S. McClung of Indiana University, and C.S. Pederson of Cornell, but no decision was made. In correspondence to Breed, Smith wrote that "No doubt, Dr. Buchanan would like to take over when you step aside . . . In fact one can read between the lines that 'no one besides Buchanan is capable of editing the *Manual*' ". This change, however, did not come to pass as Breed stayed on until his death in 1956.

Breed pursued actively the production of a Seventh Edition in the 1950s with the active support of Murray and Smith (Breed et al., 1957). The task was no less formidable, and there were many new authorities mounting increasingly pointed discussions about shortcomings in bacterial taxonomy in the dinner sessions that Breed arranged at the annual SAB meetings. It was to be the last edition in which the bacteria are classified as Schizomycetes within a Division of the Plantae, the Protophyta, primordial plants. In fact, the Preface tells us, the opening statement describing the Schizomycetes as "typically unicellular plants", was hotly debated without attaining a change, yet there were some concessions to cytology in the rest of that description, particularly concerning nucleoids. Ten Orders were recognized, adding to the five in the Sixth Edition, and these now included *Mycoplasmatales* and considerable division of the Order *Eubacteriales*. The keys to the various taxa were improved for utility and, recognizing the many difficulties involved in determination, an inclusive key to the genera described in the book was devised by V.B.D. Skerman and appended. This key, which was referred to as a comprehensive key, was designed to lead the user by alternative routes to a diagnosis of a genus when a character might be variable. It proved to be extremely popular and useful with readers and was repeated as an updated version in the Eighth Edition. Overall, the substance of the Seventh Edition of the *Manual* was due to the efforts of 94 contributors from 14 different countries. The *Manual* was becoming an international effort; however, Breed complained that the slowness of communication between the USA and Europe hampered their efforts.

Breed did not see the fruits of his labors as Editor-in-Chief; he died February 10, 1956, with many of the contributions arranged and the form of the book decided, but leaving a serious problem of succession. The position of Chairman of the Board of Trustees and Editor-in-Chief was decided, appropriately, and given to R.E. Buchanan whose interest in bacterial nomenclature and taxonomy, with direct and indirect involvement in the *Manual*, dated back to its origins. There was the immediate problem of finishing the editorial work on the Seventh Edition after Breed's death. E.F. Lessel Jr. had been working as a graduate student with Breed in Geneva, NY on the *Manual*, but was called into military service before the job was finished, and was stationed at a camp in Texas. Upon taking over the Chairmanship, Buchanan contacted W. Stanhope Bayne-Jones, of the Army's Office of the Surgeon General and Lessel's superior, to ask that Lessel be assigned to work on the completion of the *Manual* while in the service. Bayne-Jones agreed and assigned Lessel to the Walter Reed Hospital in Washington, DC. Thus the last editorial polishing of the book could take place without undue delays. After his service commitments were fulfilled Lessel went to Iowa State and finished his Ph.D. under Buchanan's direction and acted on occasion as recording secretary for Trust meetings.

R.E. Buchanan for many years had held three important administrative posts at Iowa State (Bacteriology Department Head since 1912; Dean of Graduate College since 1919; and Director of the Agricultural Experiment Station since 1936), retiring from all three in 1948. After 1948 some of his energies went to compiling and annotating the text for the 1952 publication of the Bacteriological Code and starting the *International Bulletin of Bacteriological Nomenclature and Taxonomy*. The *International Bulletin* received its initial monetary start in 1950 with a $150 gift from the *Bergey's Manual* Trust, to which Murray objected, saying "the *Journal* would be ephemeral." Fortunately he was wrong because the *Bulletin* later changed its name to the *International Journal of Systematic Bacteriology* and is still being published by ICSB (IAMS) with about 1200 pages in the 1997 volume. When Buchanan became Editor-in-Chief of the *Manual*, he induced the Department of Bacteriology at Iowa State to provide him an office suite

and the title of Research Professor, from which position he obtained grants from the National Library of Medicine to support the office. This support continued until his death in 1973 at the age of 89 years.

Buchanan's twenty-year involvement in the Trust was to see, near its end, the start of a new era, despite his many objections to change. The chief change to come arose from a growing lack of confidence in the sanctity of higher taxa, there being few and often no objective tests of correctness. In the production of the Seventh Edition, it was recognized that an expanding synonymy and the ever-growing list of species that were unrecognizable or inadequately described provided a burden that made for wasted space and unreasonably extensive appendices. The addition of Breed's collection of reprints to Buchanan's considerable collection formed an extensive taxonomic archive in the Trust headquarters. With this resource in mind the Trust decided that a separate publication was needed to assemble as complete a listing as possible of the names and references of all the taxa included in the *Manual*, as well as "species formerly found as appendices or indefinitely placed as *species incertae sedis*" that might or should have appeared in the *Manual*. These, together with an assessment of whether or not each name was validly published and legitimate, formed a monster book of nearly 1500 pages, published as *Index Bergeyana* (Buchanan et al., 1966). Each and every reference was checked for accuracy, for Buchanan rightly stated that there "was a lot of gossip about the description of each name." These labors were a personal interest of R.E. Buchanan, who directed several years of effort by J.G. Holt (then at Iowa State), E.F. Lessel Jr., and a number of graduate students and clerks in the undertaking. The lists served as a finder mechanism, an alphabetical listing of the names of the bacteria, and of special use as a reference after the new starting date for nomenclature, January 1, 1980, mandated by the revised Code (Lapage et al., 1975). Addenda were inevitable and more names were collected as a *Supplement to Index Bergeyana* published in 1981 under the direction of N.E. Gibbons, K.B. Pattee and J.G. Holt. These substantial reference works assisted the refining of the content of the Seventh and Eighth Editions of the *Manual* and allowed concentration on effectively described and legitimate taxa.

There were seemingly interminable discussions about what needed to be done for an effective new edition. This was particularly true in the period 1957–1964 after Breed's death, when the Trust membership changed and new ideas and new scientific approaches to taxonomy became available. In the late 1950s the Board of Trustees was enlarged with the addition of S.T. Cowan, C.F. Niven Jr., G. Edsall, and A.G. Lochhead (the record is unclear on the exact date of their appointment). The election of Cowan from the UK added a European member and continued the internationalization of the Board (Fig. 2). Each of these new members brought expertise in different areas of bacteriology and that policy of diversity of interest among members has continued to this day. Later, in 1962, Arnold Ravin, a bacterial geneticist, was added to replace the retiring Lochhead. Of primary concern in the late 1950s and early 1960s was the position of Editor-in-Chief and location of Trust headquarters. An arrangement with Iowa State University to have a candidate assume a professorship at the University and house the headquarters there was made. The position was offered to P.H.A. Sneath, who had gained renown with his invention of numerical taxonomy and production of a masterful monograph on the genus *Chromobacterium*. By 1963, however, Sneath chose to stay in England and Buchanan stayed on as Editor-in-Chief. All other efforts to find a new editor failed until Buchanan's death in 1973. As he grew older, more difficult, and more autocratic, progress on a new edition slowed considerably. Even the replacement of E.G.D. Murray, Conn, Smith, and Edsall by R.G.E. Murray, J. Liston, R.Y. Stanier, and N.E. Gibbons did not change the speed of Board actions. It became a war of wills between Buchanan and the others on what was important and where progress could be made. Until decisions on the taxa to be included and their circumscriptions were made, there was slow progress in naming and putting to work the 20 or more advisory committees needed to direct the authors of the final texts on genera and species. One novel (to the Trust) approach for obtaining consensus on taxonomic matters was the organization of a conference of advisory committee members and trustees held in May, 1968 at Brook Lodge in Augusta, MI, under the auspices of the Upjohn Co. and chaired by R.G.E. Murray. Fifteen advisory committee members joined in discussions with the Trust to assess the status of current knowledge on the major groups of bacteria to be included in the Eighth Edition. Despite this helpful preliminary, it brought no agreement between Buchanan as Chairman, whose main focus was then on nomenclature, and the rest of the Trustees, whose interests mostly focused on biological, functional, and eco-physiological attributes. It was clear that many of the higher taxa rested on shaky ground and were hard to assess on strict taxonomic terms. Accordingly, there was a long argument over abandoning formal names above family level wherever possible, agreeing that a large number of genera were of uncertain affiliation or, at least, could only be related on the basis of some diagnostic characters, such as gliding motility, shape and Gram reaction, and methane production, all of which might or might not have phylogenetic significance. All former ideas about phylogeny and relationships were discarded. The Eighth Edition was planned as a book divided into "Parts", each with a vernacular descriptor. The Advisory Committee for each part (some needed more than one) was assigned a member of the Trust who was responsible for action and who, eventually, had to see that each genus had an assigned author (131 in the end) who was willing to write.

Molecular/genetic technology was well established by 1974 when the Eighth Edition was published, but was not yet widely applied to play a role in broad decisions in taxonomy. The procaryotic nature of bacteria and all cells related to them (i.e. including the Cyanobacteria) could be recognized and used to define the Kingdom *Procaryotae*. *Monera* was the old and partially applicable higher taxon but the description was not cytologically based. The molecular composition of DNA was useful for separating phenotypically similar but genetically distinct groups (e.g., *Micrococcus* and *Staphylococcus*) and many descriptions could include mol% G + C as a character. Genetic and subsequent biochemical-molecular data told us that species were only relatively "fixed" in their expressed characters. This concept needed to be addressed in the circumscriptions and aids to identification. Greater use was made of diagnostic tables and wherever possible there were indications regarding uncertainties and the percentages of positive or negative reactions for tests. The value of the Eighth Edition for identification purposes was increased by the emphasis of both the Trustees and the authors on refining descriptions (in terms as up-to-date as possible), tables, keys, and illustrations. As in previous editions, many old names of dubious or unrecognizable entities were discarded and synonymy was reduced to essentials; the old information and its location was not lost because it was available in the *Index Bergeyana* (Buchanan et al., 1966), or later in the *Supplement to Index Bergeyana* (Gibbons et al., 1981).

The Eighth Edition was a long time in gestation—17 years—

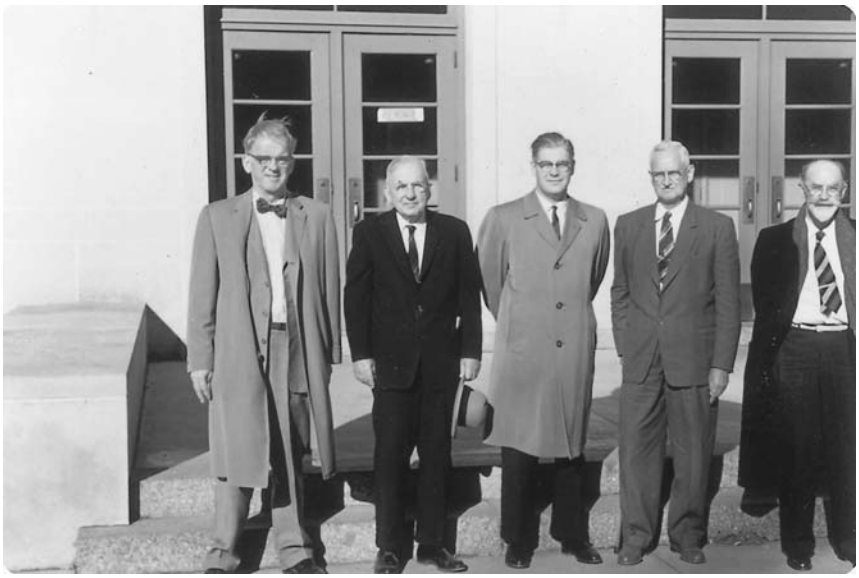

FIGURE 2. Photograph of Trustees meeting at Iowa State University, Ames, November, 1960. *L. to R.*, G. Edsall, R.E. Buchanan, C.F. Niven, Jr., N.R. Smith, and E.G.D. Murray.

but its success (40,000 copies over the next 10 years, and more than half outside of North America) was a testament to its necessity and utility. Most of the primary journals involved in publishing microbiological papers suggested or required the *Manual* as the nomenclatural resource for bacterial names, all this despite the treatment of some groups (e.g., the *Enterobacteriaceae*) not being universally accepted. But it was truly an international enterprise, with authors from 15 countries who could, at last, be named in literature citations as authors.

The editing of the Eighth Edition became a major operation requiring sharing of responsibilities and some redirection of effort. This was in part due to the age and increasing infirmities of R.E. Buchanan who had been both Chairman of the Trust and Editor, directing his efforts to nomenclature, synonymy, and etymology. It became evident that a Co-Editor was required and fortunately N.E. Gibbons, recently retired from the National Research Council of Canada, agreed to undertake the task. Shortly thereafter Gibbons became the *de facto* editor, due to Buchanan's illness and death in January, 1973, and did all the general technical editing from his home in Ottawa with help from his wife, Alice Gibbons (who handled the Index of Names), and a number of Trustees, especially S.T. Cowan. The book was published in 1974 (Buchanan and Gibbons, 1974).

With publication of the Eighth Edition the Board of Trustees went through another major change of membership, and over a period of two years Niven, Ravin, Liston, Gibbons, and Stanier left the Board. At the first meeting after Buchanan's death, held in October, 1973, J.G. Holt, who had served as Secretary to the Board from 1963–1966 and co-edited the *Index Bergeyana*, was elected member and Secretary. In 1974–1975, H. Lautrop, S. Lapage, and M. Bryant were added, and later in 1976 N.R. Krieg and J.T. Staley joined the Board. In 1975 Holt was appointed Editor-in-Chief. With the publication and healthy sales of the Eighth Edition and increasing international profile, it was decided to meet at locations separate from the ASM venue and to meet every other year outside North America, and the 1975 meeting was held in Copenhagen, Denmark, at the Statens Seruminstitut. From then on a segment of each meeting was devoted to consultation with taxonomically inclined colleagues in that area.

The Trust had recognized, in the process of deciding the format of the book, that students and technologists were important users, with primary interests in identification and a lesser need for the extensive descriptions of individual species. An abridged edition of the Sixth Edition of the *Manual* had been produced (Breed et al., 1948b), but was only a modest success and not carried forward to the Seventh Edition. In 1974 the need seemed to be greater, so preparations were made to assemble an outline classification; the descriptions of genera, families and such higher taxa as were recognized; all the keys and tables for the identification of species; the glossary; all the illustrations; and two informative introductory chapters. It was recognized that there were both deletions and additions (new keys and synopses as well as new genera) to the material from the parent edition, so that at the most the abridged version would be considered an abstract of the work of the authors of the larger text. Therefore, citation could only be made to the complete Eighth Edition. It was published as *The Shorter Bergey's Manual of Determinative Bacteriology* in 1977 (Holt, 1977). It too was a great success, selling 20,000 copies over a span of 10 years. A few years later it was translated into Russian and sold throughout the USSR, with royalties accruing to the Trust.

The development of bacteriology, as we now appreciate, required the recognition and differentiation of the various groups of microbes as taxonomic entities. At the time that *Bergey's Manual* started, the nature of bacterial cells was not known. Bacteria were classified and named under the Botanical Code of Nomenclature as Schizomycetes and no one could then have substantiated present understanding that *Cyanophyceae* are really bacteria. The international discussions of bacterial classification were minimal and took place at Botanical Congresses, as befitted the view that the Schizomycetes and the *Schizophyceae* within the Phylum Schizophyta (later Protophyta) belonged in the plant kingdom. This interpretation was maintained in *Bergey's Manual*s up to and including the Seventh Edition (1957); however, it was stated in an introductory chapter that E.G.D. Murray "... felt most strongly that the bacteria and related organisms are so different from plants and animals that they should be grouped in a kingdom equal in rank with these kingdoms". As expressed by Stanier

and Van Niel (1962) in their seminal paper "The concept of a bacterium" it is "... intellectually distressing (for a biologist) to devote his life to the study of a group that cannot be readily and satisfactorily defined in biological terms ...". This marked the beginning of the useful and directive description of bacteria as cells of unique nature. With this approach it was clear that the cyanobacteria were included and there was, at last, a satisfactory unity. This was to be slowly elaborated in the next three decades by the recognition of phylogenetic information recorded in molecular sequences of highly conserved macromolecules, but in the meantime the Eighth Edition (1974) subscribed to the view based on cytological data that the bacteria (all the procaryotes) belong in a separate kingdom, the *Procaryotae*. This was not a surprising decision because two Trustees, Stanier and R.G.E. Murray, were then involved in the description of bacteria as cells with unique features.

International Efforts to Regulate Taxonomy

The founders of *Bergey's Manual* were fully aware of the substratum of opinion, albeit not supported then by strong data, that the bacteria were a special form of life, requiring special methods and a different approach to classification, not necessarily the same as that required by the Botanical Code. In fact, between 1927 and 1930 there was a considerable international correspondence between bacteriologists interested in taxonomy in the varied fields of application in agriculture, medicine, soil science, etc, expressing their concerns. The correspondence also concerned what should be done about discussing bacteria at the forthcoming Botanical Congress to be held in Cambridge, England, in 1930, and about resolutions adopted by the Bacteriological Section of the Botanical Congress, of which J.M. Sherman had been Secretary, held in Ithaca, NY, in 1926. The resolutions were (1) exclusion of the requirement for a Latin diagnosis in bacteriological nomenclature; (2) greater emphasis on the "type concept"; (3) a special international and representative committee was needed to coordinate the special nomenclatural interests of bacteriologists; and (4) that a permanent International Commission on Bacteriological Nomenclature should be formed. Sherman, then Secretary-Treasurer of SAB, wrote to Prof. J. Briquet of the Permanent International Committee on Botanical Nomenclature pointing out that the past two Congresses had authorized a bacteriological committee on nomenclature, that it should be organized, and that the Bacteriological Section had prepared a distinguished list of nominations for membership. The list included three of the major contributors to discussions of systematics in the SAB (Buchanan, Breed, and Harrison) and two of them were intimately involved with *Bergey's Manual*.

A lively correspondence among the authorities resulted and much of it was stimulated by Breed writing to bacteriologists in Europe as well as America. He sums up an impression of the responses in a letter to the Secretary of the Botanical Congress, as follows: " . . . there is a general feeling that unless the Congress welcomes us into the ranks of botanists with the recognition of our peculiar and perplexing problems in the taxonomic field, we must organize an independent international group". At the same time he recognized the value of the work of Congresses in maintaining useful rules of nomenclature and reiterating the list of resolutions. The British correspondents were generally agreeable to bacteriological discussions but expressed sharp divisions as to associating or not with the botanists. Other players namely the newly formed International Society of Microbiology, and the Cambridge committee charged with organizing the bacteriological component of the 1930 Botanical Congress came on the scene in 1927. The former encouraged some thoughts of an independent base for microbiological congresses and taxonomy committees, while the latter questioned whether or not a Section of Bacteriology was desirable or even feasible, and asked H.R. Dean (Professor of Pathology at Cambridge University) to seek interest and act on it. Dean's correspondents in this matter were numerous and mostly British, but also included Breed, Buchanan, B. Issatchenko (USSR), and K.B. Lehmann (Germany) (letters regarding this information are now filed in The American Society for Microbiology Archives). The responses generally supported a Section at the Congress but the overall opinions on continuing association with the botanists varied from the enthusiastic (mostly general microbiologists) to outright contrary opinion (mostly medical bacteriologists). Paul Fildes wrote: "Personally I am of the opinion that bacteriology has nothing to gain by a close association with botany." And Sir John Ledingham, while agreeing with having general bacteriological discussions, thought in the future "If the botanists will not have us, maybe that is all to the good". J.W. McLeod wrote: "Frankly, I am not very enthusiastic about a Section of Bacteriology at an International Botanical Congress especially if we are going to have an International Association of Microbiology". Other views crept into letters such as one from F. Löhnis: "I know that there exists within ... (the SAB) ... a small but very active minority extremely eager to advance a scheme of classification and nomenclature that seems to me as to others quite contrary to international usage ... this minority has advanced its ideas in the U.S.A. and will probably try the same scheme at Cambridge in 1930 if there should be a separate Section of Bacteriology". Breed wrote Dean that there would be support in the SAB for a delegation and added a few remarks on differences with the botanists, including: "Our troubles, for example, do not concern type specimens kept in a herbarium. They are intimately concerned with the maintenance of type culture collections such as the English bacteriologists have been able to establish so splendidly at the Lister Institute". There were more meetings in 1929 of a subcommittee appointed to settle a program for the Bacteriology Section (Dean as Chairman, with Boycott, Topley, Ledingham, Paine, Thornton, Thaysen, and Murray) and charged to keep Briquet (Botanical Nomenclature Committee) informed of any discussion of bacteriological nomenclature that might take place.

Attitudes to studying and naming bacteria were rather different in the UK and Europe in the 1920s than was evident in the USA and Canada. The influential members of the SAB involved in *Bergey's Manual* seemed to be able to muster support for their views and seek consensus even if there were rumblings of dissent (q.v. Hall, 1927). In Europe many, like Orla-Jensen, believed that individual bacteriologists of substance should prevail because they were the ones who knew their groups of bacteria and he objected to imposition from outside. Internationalism did not and does not come easily.

The International Society for Microbiology (ISM), formed during an international conference on rabies sponsored by the Institute Pasteur in April, 1927, elected Prof. J. Bordet as President and R. Kraus as Secretary-General. It was stated in the brochure that: "It will not only compose the Science of Bacteriology but all the sciences associated with Microbiology" and the concept was based on "the unanimous conviction that Science should unite Nations...". The idea that all Societies of Microbiology may join, and that National Committees may present individual microbiologists as members, was expressed. So, the concept of an international association was born in Europe without anyone from North America among the founding members from 14

countries. There was interest: Harrison wrote to Dean suggesting that contact should be established between the ISM and the Bacteriological Section meeting at the Botanical Congress. Ledingham wrote to Dean in June, 1928, to support a meeting of the Nomenclature Committee of the Pathological Society of Great Britain and Ireland with Breed and others who were visiting, "particularly with regard to joint action on this matter by the botanical bacteriologists and the new International Society for Microbiology. Possibly they might consent to turn the matter over entirely to the new International Society (if adequate guarantees given)". It is not clear what group meeting resulted although hints were made.

1930 was the year of change because the First International Congress for Microbiology was held in Paris and by a vote agreed to follow the rules of nomenclature accepted by the International Congresses of Botany and Zoology *"in so far as they may be applicable and appropriate"* (italics as given by Breed, 1943). This opened the doors for a dedicated committee which would be in action at the following Congress (1936, in London, England), and set in train the development of an International Committee for Systematic Bacteriology, the regulatory mechanisms that were to be so important to taxonomic decisions in years to come, and a bacteriological code of nomenclature. The Microbiology Congress and the Botanical Congress, prompted by its Bacteriology Section (and probably by a questionnaire circulated by Breed), both approved in plenary session that the starting date for bacteriological nomenclature should be May 1, 1753, the date of publication of *Species Plantarum* by Linnaeus.

No doubt, there was much going on behind the scenes and some degree of consensus about the ever contentious matters involved in bacterial taxonomy. However, it was clear that bacterial taxonomy would be a matter of international concern from then on.

The Enlargement of the Scope of the *Manual*

In the period following the death of R.E. Buchanan, John Liston took over as Chairman until 1976 when he retired and was replaced by R.G.E. Murray. It was during this subsequent period, in the late 1970s, that plans were laid to expand the informational coverage of the *Manual*. What started as a discussion of a new edition of the determinative manual developed into a plan to include much more information on the systematics, biology, and cultivation of each genus covered. Hans Lautrop had analyzed the content of the Eighth Edition and suggested a format that would allow authors to expound on further descriptive information, isolation and maintenance, and taxonomic problems. Other planned departures from past editions included the profuse use of high quality illustrations and allowing publication of new names and combinations in the *Manual*. It was also decided to preface the book with essays on general aspects of bacterial systematics such as modern genetic techniques, culture collections, and nomenclature. This expanded coverage meant a large increase in the number of pages and it was decided to publish the book in four volumes, each containing a set of taxa divided along somewhat practical lines. The final arrangement consisted of volumes covering the Gram-negatives of medical importance, the Gram-positives of medical importance, the other Gram-negatives (including the *Archaea* and, for the first time, the Cyanobacteria), and lastly, the Actinomycetes. This division allowed users to purchase separate volumes that suited their special professional requirements. This expansion demanded a more descriptive title and it was decided to call the book *Bergey's Manual of Systematic Bacteriology*. Production of each volume was set up on a cascading schedule with completion planned for the mid 1980s. Trust members were chosen to edit each sub-volume, with the final editing being done in the Ames office. Obviously, such an undertaking was an expensive endeavor, beyond royalty income, and extra funding was provided by a grant from the National Library of Medicine of the US National Institutes of Health for volumes 1 and 2, and an advance on royalties from the publisher. In the end the complete project cost around $400,000. Volume 1 was published in 1984 (Krieg and Holt, 1984), Volume 2 in 1986 (Sneath et al., 1986), and Volumes 3 and 4 in 1989 (Staley et al., 1989; Williams et al., 1989).

The book was a truly international project in which 290 scientists from 19 countries (and 6 continents) participated, and as much of a success as the Trust and its authors could have expected. Each of the volumes sold between 10 and 23 thousand copies in the 1984–1996 period and more than half of the sales were outside of the USA. The total royalties add up to in excess of $450,000, making the *Systematic Manual* both a scientific and business success. The challenge now is to find the finances, energies, and means to keep the *Manual* up to date, affordable and reasonably current.

One of the mandates of the Trust is to further bacterial taxonomy, and the modern Board of Trustees has taken other initiatives besides the publication of books to promote the field. There has been monetary support, however small, for worthwhile causes, such as the aforementioned gift to launch the *International Bulletin of Bacteriological Taxonomy and Nomenclature*. Also in 1980, the Trust contributed $3000 towards the publication of the Approved Lists of Bacterial Names (Skerman et al., 1980). Two ways have been found to honor people who have made important contributions to the field of bacterial systematics. In 1978 the Bergey Award was instituted as a joint effort by Williams & Wilkins and the Trust; the first award went to R.Y. Stanier and is an annual event. Table 2 lists the recipients of this award, which consists of $2,000 and expenses to allow travel to a meeting of the recipient's choice to receive the award. In the 1990s the Trust commissioned a medal, the Bergey Medal (Fig. 3), to be given to individuals who have made significant lifetime contributions to bacterial sys-

TABLE 2. Recipients of the Bergey Award

Roger Y. Stanier	1979
John L. Johnson	1980
Morrison Rogosa	1981
Otto Kandler	1982
Carl R. Woese	1983
W. E. C. Moore	1984
Jozef De Ley	1985
William H. Ewing	1986
Patrick A. D. Grimont	1987
Lawrence G. Wayne	1988
Hubert A. Lechevalier	1989
M. David Collins	1990
Erko Stackebrandt	1991
Wolfgang Ludwig	1992
Wesley E. Kloos	1993
Friedrich Widdel	1994
Michael Goodfellow	1995
Karel Kersters	1996
Rosmarie Rippka	1997
Barry Holmes	1998
David A. Stahl	1999
William B. Whitman	2000
Lindsay I. Sly	2001
Peter Vandamme	2002
Peter Kämpfer	2003
Rudolf Amann	2004