

**THE SHORTER
BERGEY'S MANUAL OF
DETERMINATIVE
BACTERIOLOGY**

Eighth Edition

**JOHN G. HOLT
EDITOR**

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BERGEY'S MANUAL OF
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BACTERIOLOGY**

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The Williams & Wilkins Company / Baltimore



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Preface to *The Shorter Bergey's Manual of Determinative Bacteriology*, Eighth Edition

This is not the first time that *Bergey's Manual of Determinative Bacteriology* has been produced in an abridged form. In 1948 the editors compiled and published an abridged edition of the Sixth Edition of the *Manual*, especially "... for the use of students in identifying the cultures of bacteria used in beginning courses...." The Board of Trustees of Bergey's Manual Trust has decided once again to publish an abridged version of the *Manual* for students and laboratory workers who desire a more portable, less monetarily valuable compendium of information useful for the identification of bacteria.

Briefly, *The Shorter Bergey's Manual* contains the outline classification of the bacteria; the descriptions of all genera and higher taxa; all of the keys and tables for the diagnosis of species; the glossary; all of the illustrations; and two of the introductory chapters. The *Shorter* version does not contain the descriptions of species; most of the taxonomic comments; the etymology of names; and references to authors. This latter omission brings up a special point about reference to the *Manual* in published works. All the material in the complete *Manual* is the work of many contributors who are identified by obvious bylines at the beginning of each section. The *Shorter* version is derivative of the larger book and often has material added and much original material deleted in the abridgment process. We believe that it is not appropriate to refer to the *Shorter* version in a scientific publication; rather, reference should always be to the complete *Manual*. Additionally, reference to the *Manual* should be to the *author* of the section being noted and not to the editors (Buchanan and Gibbons in the case of the 8th edition). A reminder and example of the proper form of citation is given throughout the text of the *Shorter* version.

The reader is well advised to read the introductory chapter on "The Mechanism of Identification" before starting out to use either form of the book as a guide for identification. Use of the criteria and suggestions for methodology outlined in that chapter will often lead the reader to the proper Part. There is also a short key to the 19 Parts which follows the chapter to provide an alternative access to the proper Part.

Once the proper placement in a Part has been made, the reader should study the keys and tables in that Part to determine which additional tests will need to be performed in order to use the identification devices. Key characteristics are listed for the reader's convenience for the longer, more involved keys. Most keys are short and the characteristics used are quite obvious. A word about methods is needed here. There are few standardized methods in use in bacteriology, and each taxon or major group may be classified on characteristics which are based on very specific methods. Usually, in the *Shorter* version, reference is made to methodology if it differs from the usual laboratory practice. The reader should consult the text before planning further tests.

Sometimes synopses are used instead of dichotomous keys. A synopsis is not a key; i.e., it does not offer the user alternative statements that logically lead to a determina-

tion of identity of an unknown organism. Rather, a synopsis is a device which gives abbreviated descriptions for a group of related taxa. Some, fortunately not many, of the original keys in the *Manual* are synopses; this is a reflection of a paucity of taxonomic data, which does not allow a logical classification. One must remember that an identification device is only as good as the classification upon which it is constructed and that in many groups of bacteria there still is not a good, logical classification possible. The goal of the *Manual*, of course, is to continue to present the latest thinking on the classification of all of the bacteria and the best keys and tables which can be constructed from these classifications.

All species in a genus are mentioned in some way (with a few exceptions): by key, table, or editorial note. If there is no mention of constituent species, then the genus is monotypic and only the type species will be given. Once a determination has been made, say to the level of species, it may be necessary to consult the *Manual* for further information. This *Shorter* version does not contain detailed descriptions of species, except in the case of some tables, and the reader will have to return to the *Manual*, which is, it is hoped, close by in a safe place, to check the more complete description for confirmation. Or, one may need to consult the *Manual* for more information on where one went wrong or for a lengthy discussion of the taxonomic problems of the group. The *Manual* is liberally salted with "further comments" by the authors on classification or identification problems.

There has been an addition of some new material to this *Shorter* version of the *Manual*. Occasionally there were no keys to the constituent sections or families in a Part or there was no way to gain access to the genera of uncertain affiliation. To correct these situations new keys or synopses have been added that should help to provide better determinations of some of the groups. Also, there have been a number of new genera described since the completion of the *Manual*, and many of these have been noted in the proper place.

JOHN G. HOLT

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Published reference to any or all material from *Bergey's Manual* must always be made to the complete eighth edition, *Bergey's Manual of Determinative Bacteriology*, with credit being given to the author(s) of the section being cited. For example:

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INTRODUCTION

A Place for Bacteria in the Living World

R. G. E. MURRAY

"What's in a name? that which we call a rose
By any other name would smell as sweet . . ."
Romeo and Juliet, Act II. W. Shakespeare

One of the most difficult tasks for the Editor-Trustees of all previous editions of *Bergey's Manual* was the provision of an intelligible and recognizable description of the bacteria as a taxon and a scientifically acceptable placing among the realms of living things. Without doubt most thoughtful bacteriologist-taxonomists since the time of Ferdinand Cohn have been convinced on an intuitive base and slender morphological evidence, that there was something unique about bacteria and that a degree of morphological similarity existed between the bacteria (*Schizomycetes*) and the blue-green algae (*Cyanophyceae* or *Schizophyceae*) whatever the arrangements made at the highest hierarchical levels. This was recognized in the many and various versions of the familiar classifications of the living world by placing these two taxa together as equivalent classes in the Division *Protophyta* of the Plant Kingdom, as was done in the 7th edition. A consequence of the morphological alliance, together with the evident physiological similarity of photosynthesis by the blue-green algae to that of plants, was a continuing adherence to descriptions in a botanical context. The definition of the *Schizomycetes* in the 7th edition was framed in terms of this long established prejudice despite misgivings (see 7th edition, p. 9). The essential operative state-

ment is that the bacteria are "typically unicellular plants," which was not then and certainly is not now defensible in terms of the description of a typical or idealized plant cell. In fact, it is surely true that the intuitive feeling of the bacteriologist rejected this view, but without solid evidence to buttress his faltering steps, as shown by the acceptance and continual refinement of the Code of Bacteriological Nomenclature independent of the Botanical Code. Resolution of the dilemma became possible as soon as the microbes could be described in terms of cellular organization.

The change in our view of the nature of bacteria was slow in coming to full expression. It derives from the application of three sets of experimental-observational approaches to the microbial world and bacteria in particular: (1) comparative cytology using the light microscope and classical staining methods to describe the form and behavior of the DNA-containing portions of nuclei; (2) the development of appropriate techniques of electron microscopy for the extension of comparative cytology to the ultrastructural level; and (3) the extension of biochemical and biophysical observations to the definition of unique features of cellular organization.

Cytologists who studied the protists became aware that the chromatin of bacteria, which they assumed correctly to be the equivalents of nuclei, was markedly different in appearance and behavior during segregation in comparison to the nuclei and component chromosomes of other protists, plant and animal cells. This was sufficient for some to make fresh attempts to circumscribe a taxon at the highest level to include the bacteria. Among these were the proposals of Copeland (1938), Stanier and van Niel (1941) and Whittaker (1959). In essence, these proposals (derived in part from attempts to rationalize Haeckel's concept of the Protists) placed the bacteria in a kingdom of anucleate organisms in contrast to those with true nuclei. Stanier and van Niel (1941) invoked two other negative features—the seeming absence of sexual reproduction and of plastids; however, it was soon to be established that photosynthetic bacteria possessed chromatophores derived from the plasma membrane and that the bacterial genome was capable of recombinative processes. Most significant of all, early electron microscopic observations of sections of cells showed that the genophore of the bacteria and the blue-green algae consisted of a nucleoplasm that was not separated from the cytoplasm by a nuclear membrane as found in fungi, protozoa, plants and animal cells. Further structural and biochemical studies established new constellations of features unique to bacterial cells in the form of heteropolymers and constituent molecules of the intimate make-up of cell walls (see Salton, 1964). In the face of this level of understanding, the kingdom designations of *Mychota* (Enderlein, 1925) or *Monera* (Copeland, 1938) were not appropriate in their definitions. However, Chatton (1937) had proposed a most appropriate conceptual basis for taxa at the highest level by recognizing two general patterns of *cellular organization*—the procaryotes and the eucaryotes. The truth of this prescient generalization was recognized by Stanier (1961) and is now amply supported by a wealth of data derived from comparative cytology involving microscopical, biochemical and physiological approaches. Stanier and van Niel (1962) put the matter in clear perspective, with an accompanying statement of the evidence: "The distinctive property

of bacteria and blue-green algae is the procaryotic nature of their cells." Furthermore, it was possible to justify the use of the inclusive term, the cell, for the unit of structure of both procaryotic and eucaryotic organisms as an expression of equivalence of function; the differences between the broad groupings concern the detailed organization of the cellular machinery. The broad canvas was now sketched in and the bacteria could be confidently placed in perspective with other cellular organisms. The viruses, alone among organisms, remain without a clear position in the scheme of things.

There is no real need to repeat here all the arguments that have been presented to embroider and support the cytological recognition of procaryotic organization as the cornerstone for a coherent view of the nature of bacteria. The case has been made several times (Stanier, 1961; Stanier and van Niel, 1962; Murray, 1962; Allsopp, 1969; Stanier, 1970) and the student should consult these essays for details and references.

The essential features are:

I. The nature of the genophore (a term used by Ris (1961) to avoid the connotations of "chromosome" and "nucleus") constituting the morphologically distinct nucleoplasm of the procaryotic cell. This consists of a skein of double-stranded DNA fibrils that is not separated from cytoplasm by any membranous boundary. Structural and genetic evidence, based on bacterial examples, indicate that the genophore is in the form of a closed loop (often described as a "circular chromosome") and the constituent genes form a single linkage group. The fibrils are not associated in any regular way with a protein in contrast to the histones of the eucaryotic chromosome. For the moment it must be assumed, because of fragmentary genetic or cytogenetic evidence, that the morphologically similar nucleoplasm of blue-green algae has parallel properties.

II. The lack of unit membrane-bounded cytoplasmic organelles is the second most important distinction of the procaryotes. This belies their metabolic diversity and the simplest form is provided by some bacteria whose "membrane system" consists of the plasma membrane alone, smoothly enclosing the protoplasm. Simple intrusions of membrane are common and complex systems of unit membranes do exist (e.g. for photosynthesis, nitrification, etc.), but in all cases there is good support for the view that they are derived by invagination of the plasma membrane into the cytoplasm and in most cases the connection is maintained. There is a possible exception in the blue-green algae whose photosynthetic apparatus is located in an extensive system of thylakoids, which do not appear to be in direct continuity with the plasma membrane.

III. A further distinction attributable to all procaryotes is that the ribosomes are of the small 70 S type as opposed to the consistently larger 80 S ribosomes of the eucaryotes (Taylor and Storck, 1964). They are distributed in the cytoplasm and are not arrayed on membranes as in the endoplasmic reticulum of eucaryotes.

There are a number of positive characters that can be considered as features of many but not all procaryotes, which further strengthen the distinction. For example (1) *cell walls* are not confined to procaryotes but the components are unusual to a degree that is taxonomically significant. Without doubt the now well known peptidoglycan (murein or mucopeptide) component of the cell walls,

shared by the majority of bacteria and the blue-green algae, is a uniquely constituted heteropolymer with distinctive subunits in both the amino sugar backbone (muramic acid) and the peptide (D-amino acids and unusual diamino acids) portions. It cannot be used to characterize the procaryotes because the wall-less *Mycoplasma* and exceptional bacteria (e.g. *Halobacterium*) do not possess it. Other constituents may yet prove to have taxonomic value but the peptidoglycan is particularly important as a bridging character with the blue-green algae. (2) *Flagella* are distinctive organs of swimming motility confined to certain genera of bacteria. This complex tubular assembly of protein subunits with an elaborate anchorage in both wall and plasma membrane cannot be confused with the cilia of eucaryotes. (3) *Gas vacuoles* are common in blue-green algae and are found in a few widely separated genera of bacteria. *Chlorobium* vesicles are unique containers for the chlorophylls and carotenoids of the green bacteria. What they have in common is that they are organellar inclusions that are not bounded by unit membranes but rather by special single layers. They are without counterpart among eucaryotes.

It is no longer possible to support two negative features that have been proposed as characterizing procaryotes: lack of cytoplasmic microtubules and an inability to synthesize sterols. It is now apparent that some *Treponema* may possess microtubules and sterols have been isolated from some *Mycoplasma* and blue-green algae.

Bacteria are remarkable for an extraordinary variety of metabolic mechanisms and, particularly, for a wide range of anaerobic energy-yielding reactions; these are in marked contrast overall to the glycolysis utilized by the eucaryotic cell. The result is that many bacteria are obligate anaerobes and share this condition of existence with only a few protozoa among the eucaryotes. Apart from this generalization and the synthesis of unique cell wall polymers, already mentioned, it should be noted that the ability to fix nitrogen and to accumulate poly- β -hydroxybutyrate as a reserve material are metabolic attributes widely distributed among procaryotes but completely absent from eucaryotes.

The fossil record, although indicative of microbial life long ages before recognizable complex forms of life appeared, is not able to tell us anything of the order of appearance and thus contribute to phylogeny. Those groupings that we can observe today seem likely to represent a coherent segment of the terminal branches of an evolutionary tree. Photosynthesis probably originated when the procaryotic stem was already well developed. The precise forms of photosynthesis represent the derivatives of, most likely, a single evolutionary event (Stanier, 1970) since many elements of the machinery are common to all existing phototrophs.

It has been pointed out by Stanier (1970) that the plasma membrane of procaryotic organisms is not adapted to the transfer of particulates or large molecules either in or out of the living cell; indeed, transforming DNA fragments are about the only example. Furthermore, there is no evidence for endocytosis (viz. phagocytosis and pinocytosis) and its directional counterpart, exocytosis, as mechanisms of import or export of soluble material or particulates. Yet this is a very generalized characteristic of eucaryotic cells. Many protozoa ingest pro-

caryotic organisms as food into food vacuoles. It is not surprising, then, that a good number of stable associations have been set up so that distinctly recognizable endosymbionts are characteristic of the cytoplasm of certain cells. These are also enclosed in a sac of host cell membrane. The most notable studies are on the endosymbionts of *Paramecium aurelia*. Although they are generally not cultivable, many of them are structurally recognizable as procaryotes and some even exhibit bacterial flagella and bacteriophages of the tailed type (Beale *et al.*, 1969; Preer *et al.*, 1972). Some endosymbionts have the characteristics of a eucaryotic green alga (as in *Paramecium bursaria*) and other protozoa have blue-green inclusions (cyanelles) that have been interpreted, with insufficient rigor, as blue-green algae. It is clear that endosymbiotic associations are widespread in a great variety of metazoa (Buchner, 1965), as well as in the vascular plants, such as the well known *Rhizobium* association in the root nodules of legumes. Identification, description and classification rests, in the absence of verifiable cultivation, on morphological and biochemical features. It appears that the capacity to take up external cells brings with it the possibility of endosymbiosis. No stable endosymbiosis within procaryotes has yet been identified. (Bacterial parasitism by *Bdellovibrio* is best described as a nonsymbiotic multiplication between cell wall and protoplast causing death of the host.)

One of the excitements of recent years is the realization that the mitochondria and the plastids of eucaryotes could represent the most extreme form of endosymbiotic parasitism by procaryotes. These unit membrane-bounded structures have physical, genetic and biochemical features that suggest the possibility of their procaryotic nature; furthermore, the DNA from the very small genophore can be isolated in circular form and has a very different base composition in comparison with that of the host cell. At this stage the observations provide the base for fascinating and possibly unverifiable speculation concerning an event (or set of events) of the greatest significance in eucaryotic evolution (see Stanier, 1970; Allsopp, 1969).

There is little doubt, at this time and in the face of the arguments that have been presented, that biologists can accept the division of cellular life (as opposed to virus "life") into two groupings at the highest level expressing the encompassing characters of procaryotic and eucaryotic cellular organization. Those who have written concerning the topic have generally avoided committing themselves to a formal nomenclature. So far as we know there are only two formal proposals, both based on recognizable descriptions. Murray (1968) proposed *Procaryotae* as a taxon "at the highest level" and described it as "a kingdom of microbes... characterized by the possession of nucleoplasm devoid of basic protein and not bounded from cytoplasm by a nuclear membrane." *Eucaryotae* was suggested as a possible taxon at the same level to include other protists, plants and animals. Allsopp (1969) declared that these groups merit the status of "kingdom or even superkingdom" and he proposed with an extended assessment of characters that the Kingdoms should be *Procaryota* and *Eucaryota* (Allsopp, 1969, 607). The Bergey's Manual Trust has discussed these names and the various alternatives on many occasions and agreed that *Procaryotae* was the most appropriate, as a plural feminine noun, for such a taxon.