The Life of Bacteria

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The Life of Bacteria

THEIR GROWTH, METABOLISM, AND RELATIONSHIPS

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THE LIFE OF BACTERIA

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"Lieve God, wat zijnder al wonderen in soo een kleyn ' schepsel!"*

Leeuwenhoek's draughtsman
(Letter 76, Oct. 15, 1693)

"The most important discoveries of the laws, methods and progress of Nature have nearly always sprung from the examination of the smallest objects which she contains."

J. B. Lamarck
Philosophie Zoologique, 1809

* "Dear God, what marvels there are in so small a creature!"

PREFACE

The accelerated pace of biological research is stimulating to those in it, but discouraging to those who are endeavoring to put together its glittering fragments into a balanced and satisfying picture. Because this book has been in preparation for more than fifteen years, with numerous breaks (including a complete one of over four years for the war), the subject matter has had to be continually changed. Samuel Johnson lamented in 1755 that "no dictionary of a living tongue can ever be perfect, since, while it is hastening to publication, some words are budding, and some falling away." The same is true for a book on a living science, whose ideas and conclusions are constantly being modified.

Furthermore, the emphasis and the perspective have shifted considerably during the book's preparation. In part this is due to a shift in biology itself, but in part also it represents a change in the conception of the book. Originally written largely to fill a gap (there was no full-length treatment of the physiology of microorganisms at that time), the book slowly came to be envisaged as a text for an advanced course. Meanwhile the gap was partially filled, first by the several editions of the late Marjorie Stephenson's *Bacterial Metabolism* and more recently by several other books, especially those of J. R. Porter (1946), E. F. Gale (1948), and Werkman and Wilson (1951).

There is reason to believe, however, that the gap has not been completely filled. Indeed, it has widened, for it has gradually become apparent that bacteriology as a science is being blurred out, and instead students are being taught such specialties as bacteriological chemistry, agricultural microbiology, dairy bacteriology, industrial fermentations, and medical bacteriology (arrogantly called "bacteriology" by many, mistaking the part for the whole). "The division of science into sciences," writes George Sarton, the historian of science, "is to a large extent artificial, and apparent only in concrete cases. It is clear that a collector of butterflies need not study thermodynamics, and that an observer of

meteors can do very well without botany or palaeontology. It is also clear that the great mass of our scientists and technicians are so deeply specialized that they can no longer see the wood for the trees, or the tree for the twigs."

The development of the specialties has certainly made it next to impossible to see bacteriology as a whole, let alone the still broader topic of microbiology. In the special case of bacteriology, there is an additional unfortunate result, namely, that it is not thought of as a subject in itself but as an adjunct to other activities. To some biochemists, bacteria are merely something which grows on agar and which can be used for the preparation of enzymes or for the assay of vitamins. There are medical, industrial, and agricultural counterparts of this viewpoint. Thus the science by specialization has not only lost its unity (that happens to nearly all the sciences), but it has lost its self-consciousness.

Now while it is only within recent years that great progress has been made in understanding the life of bacteria, microbiology is not a particularly modern science. Its roots go deep into man's simple needs and activities—the yield of crops, the making of bread, the fermenting of wine and cheese, and the preservation of food. These ancient arts, the applied microbiology of the past, have made a profound impression on our culture, which needs to be borne in mind as background to the modern scientific development.

For these reasons the book has come to be an attempt not only to see bacteriology as a whole—that is, as a branch of biology—but also to see it in its perspective as a development from the past and as an active area of modern investigation. How far these dual aims may have been achieved it will be for the reader to determine. The original idea of including all of microbiology has been abandoned as too sweeping; a broader mind will be required to accomplish this very necessary synthesis. The book deals with the structure and activities of the bacteria, and with their influence on the surrounding world.

But even with limitation to the bacteria, the question of where to draw boundaries is a difficult one. No apology need be made for treating some aspects of the physiology of fungi along with that of the bacteria. The fermentations, for instance, can hardly be treated in a unitary manner without the alcoholic fermentation of yeast, the study of which has largely pioneered the unraveling of carbohydrate metabolism. This and certain other activities of yeasts, which are interwoven with similar activities of bacteria, have had to be treated in detail. There is a corresponding

problem in presenting photosynthesis, though it is somewhat eased by the clear-cut differences between the process in bacteria and that in other plants: however, even here it was found necessary to draw on the behavior of the algae at some points. The field of the viruses and bacteriophages seemed too large to attempt to bring within the scope of the book, and accordingly these entities have been given brief treatment at the outset followed only by occasional consideration wherever they could not well be excluded.

The complexly interrelated state of modern biology makes the drawing of area-boundaries *within* the field of bacteriology almost as difficult as plotting its external limits. Once the general plan of the book is laid down, the problem of subdivision in large part resolves itself into choosing topics around which to group the facts. Thus some topics appear as chapter heads which might not be expected to do so, while others become divided up. Nutrition, for instance, is taken up not as a whole but in connection with amino acids and vitamins in one place, uptake of materials in another, and the synthesis of assimilates and of protoplasm in a third. In the same way genetics appears in several places, under cellular fusion, adaptation, transference of characters, and so forth. Such points of arrangement are to some extent arbitrary and every author might make a different choice. In this book the dominant theme of the second and third parts is that of the natural processes caused by bacteria, and many details of selection and arrangement stem from this plan.

The enormous and growing literature on the subject is very difficult to cover completely, and equally difficult to present selectively. Naturally, advantage has been taken of reviews in many cases, but not in all, for reviews, however competent, seldom give the "flavor" of the original research, and the writer has found as a matter of teaching practice that the detailed reading of one original paper often gives more insight into a subject than the coverage of twenty times as much literature through reviews. Recourse has therefore been had primarily to original papers, and students are urged to do the same. For this reason, rather large bibliographies are given with each chapter, and references rich in additional citations are marked with an asterisk. The long bibliography has the disadvantage that titles of papers cannot be quoted, but this is partly offset by giving first and last pages, to indicate length of papers, and by giving titles in the case of reviews and dissertations.

Although a very large number of facts has unavoidably been included, it is still hoped that the book will be found useful for teaching. Naturally,

it can be used only where a course beyond the elementary is given. In spite of the widespread adoption of General Education, some biology courses are still given at a genuinely advanced level. The physiology of bacteria can be taught only as an advanced course, for several reasons. One is that no physiological subject can be presented adequately in these days without a good working knowledge of organic chemistry. This book assumes such a knowledge, and organic chemistry is used throughout without introduction or explanation. In the writer's experience, however, the average biology student's command of physical chemistry is considerably less fluent, and for this reason thermodynamics and other physicochemical matters have been introduced more gingerly and with what may seem to some readers excessive explanation.

Another reason for postponing the physiology of bacteria to the senior or even the first graduate year is the need for some knowledge of the other plant groups, especially the fungi and algae. An elementary acquaintance with these has also been taken for granted in the book, and a more than elementary one would be of great value in setting the subject into perspective and into relation with the rest of experimental biology.

In addition to teaching the subject, the author has had the advantage of many discussions with research workers, and in particular of critical reviews of some of the chapters by outstanding experts. The chapter on Bacteria in relation to other Organisms was reviewed by E. G. Pringsheim; that on Deamination by Ernest Gale; that on Oxidations by F. Lipmann; that on the Butyric Fermentation by H. A. Barker; that on the Oxidative Fermentations by R. Y. Stanier; that on Fermentations using inorganic Hydrogen Acceptors by A. J. Kluyver; that on Antibiotics by J. W. Foster; that on Photosynthesis by C. S. Yocum; and the three chapters on the Propionic Fermentation, Photosynthesis, and Autotrophic life, as well as an early draft of Chap. I, by C. B. van Niel. The criticisms of these men were given without mercy, and many of them were extensive. Their suggestions have been adopted wherever possible. Nevertheless the book cannot claim the weight of their authority and the responsibility for everything in it must be the author's.

Acknowledgment must be made to the many workers who have supplied me with original prints or negatives for the plates. Many of them have gone to considerable trouble to locate and sort out long-forgotten illustrations which seemed to me appropriate. Some of those printed before the war were unfortunately not available, but this loss has been offset in part by the advent of the electron microscope with its splendid

contributions to our knowledge of the anatomy of bacteria. The author desires to thank also the many editors and publishers who have kindly permitted the reproduction of figures. The sources of these are acknowledged in the legends. In some cases figures have been redrawn, data replotted, or other liberties taken for which tolerance is earnestly requested.

Here I want to thank my tireless and extremely efficient secretary, Mrs. J. Lockwood Chamberlin, whose ability to read and type heavily "corrected" and well-nigh illegible manuscript has been invaluable. And lastly I owe a great deal to my wife, without whose patient understanding and encouragement the book would never have been brought to completion.

KENNETH V. THIMANN

NOTE ON NOMENCLATURE

The naming of bacteria is a matter for endless discussion. Though a "rose by any other name" may be acceptable to the poet, it is rejected with horror by the systematist, because the name implies assignment to a definite genus and species. Agreement on classification of the bacteria is far from being reached, however, and for a good reason—namely, that it is not clear what constitutes a species. Among higher organisms the concept of species rests on the phenomena of sexuality; for example, the zoologist Ernst Mayr defines a species as a population which regularly interbreeds. The bacteria, in which sexuality is a rare exception, if it occurs at all (see Chap. III), are not subject to such clearcut and practical definitions. "Species," as recorded in the literature, may differ from one another only in size, in the possession of a single enzyme, or in the hosts they parasitize. Modern geneticists recognize enough "strains" of *B. coli* to staff a whole family of the older taxonomic type, with subdivision into dozens of genera and species. Furthermore, the criteria of species are different in different groups, and in the hands of different taxonomists.

If the border line of a species is difficult to draw, that of a genus is equally so. Hence the names of bacteria are constantly changing. While these problems are taken up again in the closing chapter, they are mentioned here to justify a certain conservatism in the use of names. Some readers may be surprised to find that the author has chosen not to adhere to Bergey's classification slavishly, but the fact is that "Bergey" is not universally accepted, especially outside of America. For this reason, older names which seem more logical have often been retained. Generally, however, the Bergey synonymy has been given as well, so that there should be no difficulty in recognizing the organisms referred to. This is particularly to be noted in the treatment of the lactic and the coliform bacteria (Chaps. XII and XIV). It is hoped that lovers of Bergey will be no more shocked at finding their sacred text occasionally

not followed than medical bacteriologists will be to find that some of their "Bacilli" have been assigned to quite other and varied groups.

A minor departure has been made also in the use of abbreviations. The common practice of using a single letter for the genus is quite unsatisfactory. The abbreviation *C.* may mean Corynebacterium, Clostridium, Chromatium, or Cytophaga (to offer only a few choices). This may be acceptable in scientific papers, which commonly deal only with the members of a single genus, but in a book like the present, where many genera may be discussed in juxtaposition, it would be much too confusing. Accordingly, two or more letters have been adopted for most genera. As far as possible these have been chosen for their immediate recognizability, and in some cases they are already in the older literature. One simple rule is that *B.* means Bacterium (*Bac.* = Bacillus) whether alone or in compound names, so that *Mycob.* (pronounced "myco-bee") naturally means Mycobacterium. Other abbreviations are equally obvious. A list of those adopted throughout the book follows.

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LIST OF ABBREVIATIONS FOR ORGANISMS USED IN THIS BOOK

A.	Acetobacter
Act.	Actinomyces
Aerob.	Aerobacter
Aerobac.	Aerobacillus
Asp.	Aspergillus
Azotob. or Az.	Azotobacter
B.	Bacterium
Bac.	Bacillus
Butyrib.	Butyribacterium
C.	Corynebacterium
Chlorob.	Chlorobacterium
Chr.	Chromatium
Cl.	Clostridium
Cyt.	Cytophaga
D.	Diplococcus
E.	Escherichia
F.	Fusarium
H.	Hemophilus
L. or Lactob.	Lactobacillus
Ln.	Leuconostoc
M.	Micrococcus
Mb.	Methanobacterium
Mm.	Micromonospora
Ms.	Methanosarcina
Mycob.	Mycobacterium
Myxob.	Myxobacterium
N.	Neisseria
Noc.	Nocardia
P.	Proteus
Pen.	Penicillium
Pr.	Propionibacterium
Ps.	Pseudomonas
R.	Rhizobium
Rh.	Rhizopus
Rhodo-ps.	Rhodo-pseudomonas
Rhodo-sp.	Rhodo-spirillum
S.	Salmonella
Sacch.	Saccharomyces
Sc.	Streptococcus
Sp.	Spirillum
Sporocyt.	Sporocytophaga
Sporov.	Sporovibrio
Str.	Streptomyces
T	Thiobacillus
V	Vibrio
Zygosacch	Zygosaccharomyces
Zs.	Zymosareina

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PART 1

The Morphology and General Physiology of Bacteria