



# *The Bacteria*

A TREATISE ON STRUCTURE AND FUNCTION

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VOLUME I: STRUCTURE

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*The Bacteria*

VOLUME I: STRUCTURE

# **THE BACTERIA**

## **A TREATISE**

**Volume I: Structure**

**Volume II: Metabolism**

**Volume III: Biosynthesis**

**Volume IV: Growth**

**Volume V: Heredity**

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## PREFACE

Bacteriology developed in the late nineteenth and early twentieth centuries very largely as an applied science, with momentous consequences for human health and welfare. Its outlook was largely empirical, and its growth was influenced only to a minor extent by general biological theory. During the past twenty-five years, a radical change has occurred. Although the applied aspects of this science have continued to grow, there has emerged a vigorous and widespread interest in the bacteria as biological entities. This originated historically from the realization of the fundamental unity of biochemical processes in living organisms, coupled with the recognition that bacteria provide ideal experimental systems for the investigation of many biochemical problems. Somewhat later, the experimental analysis of bacterial variation by scientists aware of the concepts of classical genetics led to the emergence of bacterial genetics as an important branch of genetic science. Here again, it was quickly realized that the biological properties of bacteria make them particularly suitable for the study of certain genetic problems; in addition the unique mechanisms of gene transfer in bacteria enriched genetic theory with new insights. Lastly, the study of bacterial cell structure has made great strides, aided particularly by the development of electron microscopy and of modern cytochemical techniques.

Heretofore, there has been no comprehensive source of information about modern knowledge of the general biological properties of bacteria. The present treatise will, it is hoped, help to fill this gap in the bacteriological literature. When the editors first discussed plans for the treatise some five years ago, they recognized the desirability of covering also the special properties of the various bacterial groups. However, it soon became apparent that a treatise which dealt with both the general and special aspects of bacteriology would prove an enormous undertaking, and it was accordingly decided to confine the work to general aspects. These will be treated in five volumes, concerned, respectively, with: structure; energy-yielding metabolism; biosynthesis; growth and general physiology; and heredity.

An undertaking of this sort, which involves the collaboration of many different specialists, inevitably lacks the unity and cohesiveness of a work produced by one or two authors. This is unfortunate, but the tremendous expansion of science in our time allows comprehensive coverage of a broad field only at this price. The editors have refrained from attempts to impose a single format, or to delineate in detail the area assigned to individual

authors, beyond attempting to eliminate obvious large overlaps. The willingness with which the authors have responded to our appeals for contributions and have accepted suggestions for revisions has made the task of the editors a pleasant one. We are also greatly appreciative of the understanding, enthusiasm and practical assistance extended by the publishers and their staff. We trust that this undertaking will prove to be of value to the community of microbiologists.

I. C. GUNSALUS  
R. Y. STANIER

*December, 1959*



# *The Bacteria*

## A TREATISE ON STRUCTURE AND FUNCTION

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W. A. WOOD

Fermentation of Nitrogenous Organic Compounds

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## CHAPTER 1

# The Bacterial Protoplasm: Composition and Organization

S. E. LURIA

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## I. Living Matter, Cell Theory, and the Unity of Biochemistry

### A. LIFE AND ORGANIZATION

When we examine living beings, the feature that immediately strikes us is organization. The organization of the world of life expresses itself at various levels. Some are taxonomic levels, which reflect the historical aspects of life and define the common descent and degree of relationship among living beings. Other levels of organization are detected within the individual units of living matter, which are in fact called *organisms*. The organized features of living beings reach all the way from the macroscopic to the molecular level, and one of the major tasks of biology is to understand and describe this organization, its interdependent levels, its stability, and its variability. In fact, life can be defined as the set of processes by

which the organization of organic matter is maintained and reproduced, that is, imposed upon other matter which becomes assimilated into living organisms. We may define as *living matter* or *protoplasm* that portion of matter endowed at any one time with this self-maintaining organization.

The progressive evolution and diversification of living forms result from the flexibility of the organization of living matter, which, by reproducing its own pattern with accurate but not always absolute fidelity, makes it possible for new forms of life to arise, to be tried out in the ever-changing material environment, and to persist or disappear, depending on their fitness to carry out the processes of maintenance and reproduction.

## B. CELL THEORY AND THE UNITY OF BIOCHEMISTRY

The unique features and historical continuity of the organization of living matter or protoplasm are embodied in two basic generalizations: the cell theory and the theory of the unity of biochemistry.

The *cell theory*<sup>1</sup> recognizes that all living matter consists of units, called *cells*, which have a common basic pattern of organization and which represent the simplest elements that can carry out all processes of life. The *theory of the unity of biochemistry*<sup>2</sup> recognizes that these life processes involve the same basic chemical reactions in all cells, because the common pattern of organization is embodied in a chemically common material substrate.

The cell theory was founded on a morphological basis. The microscope showed that all tissues and organs of animals and plants consisted of cells and of intercellular materials. The essential steps in the formulation of the cell theory were, on the one hand, the realization that in any organism only the cells are living, that is, are capable of assimilation and reproduction, while the extracellular materials, no matter how specific or complex, are nonliving, incapable of assimilation, metabolically inert products of cell activity; and, on the other hand, the recognition that all cells have a common basic structure, and that the almost infinite variety of cells represent differentiations and modifications of the common pattern—modulations and variations on a basic theme.

### 1. CELL THEORY AND CELLULAR STRUCTURE

The common pattern of organization of all cells is embodied in the idealized cytological picture of a *generalized cell*. The generalized cell has a nucleus, which, within a nuclear membrane, contains one or more nucleoli and a characteristic number of chromosomes. These are identified by cytogenetic experiments as the seat of the discrete genetic determinants that obey Mendelian heredity rules in sexual reproduction. Outside the nucleus is the cytoplasm, consisting of a basic substance or *hyaloplasm*, in which are immersed a variety of organelles and granules, including functional struc-

tures—*mitochondria*, *centrosomes*, *plastids*, *kinetosomes*—and reserve materials—starch granules, fat globules, and vacuoles.

The electron microscope recognizes further levels of morphological organization, which reflect more and more closely the patterns of molecular organization. For example, in the hyaloplasm we recognize the *ergastoplasm* or *endoplasmic reticulum*<sup>3</sup> with its constituent granules or *microsomes*; in the mitochondria, elaborate systems of lamellae. On the outer edge the cell is bounded by a *cytoplasmic membrane*, which contains lipids, acts as a semipermeable barrier, and is the site of active transport mechanisms, retaining the larger cellular constituents and regulating the exchanges of smaller molecules between the cell and its environment.

The actual cell types may deviate morphologically from the generalized cell in a number of ways. They may acquire an outer rigid *cell wall*, as many plant cells do. They may develop complex surface structures, such as cilia, flagella, and even “mouth parts,” as in certain protozoa, probably by differentiated functions of kinetosomes.<sup>4</sup> They may acquire contractile functions by synthesizing fibers of contractile proteins. They may lose irreversibly their reproductive ability, as in differentiated nerve cells, or even lose their nuclei, as in mammalian erythrocytes. Supracellular or apparently acellular complexes may arise by failure of cellular division to accompany nuclear division, as in fungi with nonseptate hyphae, or by actual fusion of preexistent cells.

## 2. UNITY OF BIOCHEMISTRY AND CELLULAR FUNCTION

In the same way as the cell theory recognizes a general cell pattern and interprets the multitude of actual cell types as modifications of the general pattern, so does the theory of the unity of biochemistry recognize a common chemical substrate of all protoplasm and a common set of chemical reactions providing the energy and the building blocks for the construction of protoplasm. The functionally diverse types of cells represent modifications of the basic chemical pattern, specifically adapted to certain functions and environments.

The unity of protoplasmic chemistry reveals itself in two ways. The first and most basic aspect is the composition of the macromolecules—proteins and nucleic acids—that carry out the specific chemical activities of protoplasm, *enzyme action* and *genetic action*; that is, chemical catalysis and control of the specific patternization of new macromolecules—the so-called “template action.” All proteins and all nucleic acids consist of a limited number of common ingredients, in the same way as all words of a language consist of a limited number of letters and syllables: the proteins, of amino acids; the nucleic acids, of nucleotides. As the meaning of language results from combinations and permutations of letters and syllables and from the



arrangements of words into sentences, thus all functional specificity or "information" in cells results from the combinations and permutations of about 20 amino acids in proteins or 4 nucleotides in nucleic acids, respectively, and from the folding and juxtaposition of the macromolecules. Folding and mutual relations of the macromolecular chains are probably themselves fully determined by the inner sequence of digits<sup>4a</sup>.

Such a system of chemical alphabets makes available innumerable functional specializations embodied in a common substrate; but the actual chemical processes by which proteins and nucleic acids carry out their catalytic or template functions are still largely not understood.

The second way in which the unity of biochemistry expresses itself is that a given chemical result is accomplished in different cells and organisms, not by a great variety of mechanisms, but in only a few alternative ways, sometimes in a unique way. This limited number of alternative pathways reflects the opportunism of evolution, which tends to select and preserve any successful device among the chemically, thermodynamically and ecologically possible ones. Clear examples are observed in energy-yielding and biosynthetic pathways. There are four known prototypes of energy-yielding mechanisms:<sup>5</sup> anaerobic fermentation, pentose phosphate cycle, tricarboxylic acid cycle\* and photosynthesis. One or more of these are found with minor variations in all cells and organisms, with similar or identical substrates, key intermediates, and cofactors. Even the enzymes have enough common features to bespeak a common molecular structure. Likewise, each of the necessary chemical ingredients of protoplasm, or *essential metabolites*, is synthesized in different organisms by one of a few alternative pathways. Even the processes involved in all forms of motion of living organisms seem to share a common basic mechanism: stimulation of contractile proteins with ATPase activity by the common substrate adenosine triphosphate (ATP).<sup>6</sup>

All quantitative and qualitative differences among cells and organisms can be traced biochemically to variations of the basic pattern, which fall into three main categories: (1) failures to synthesize some essential metabolite, which thereby becomes a *required nutritive* (or "growth factor," or "vitamin") and must be supplied from the outside, either by other cells or from the external milieu; (2) specific stimulation or inhibition of chemical processes by endogenous or exogenous substances that regulate enzyme function, like hormones, or enzyme synthesis, like "inducers"<sup>7</sup> or "repressors,"<sup>7a</sup> or agents which alter cell permeability; (3) production of specific functional differentiations, such as contractile proteins for motion,

\* The glyoxylate bypass is here considered as an essential variant of the tricarboxylic acid cycle permitting net synthesis of four-carbon compounds for cellular biosynthesis during growth on two-carbon compounds exclusively.<sup>5a</sup>