THE BACTERIA

A TREATISE ON STRUCTURE AND FUNCTION

Consulting Editor
I.C. Gunsalus

Editors-in-Chief
J.R. Sokatch
L. Nicholas Ornston

VOLUME VIII

Archaebacteria

Volume Editors
CARL R. WOESE
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VOLUME VIII

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Volume VIII: Archaebacteria (C. R. Woese/R. S. Wolfe, eds.)

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INTRODUCTION

Archaebacteria: The Third Form of Life

Our concept of what a bacterium is has been strongly conditioned by our understanding of what it is not. It is not a eukaryote. Since the seminal realization by Chatton in the 1930s that all living (self-replicating) forms fall into one of two classes defined by cell morphology, our understanding of cells, their evolution, and their relationships has been fashioned in accord with a deceptively simple and remarkably subtle concept, the so-called prokaryote–eukaryote distinction. (It is also a concept whose etymological development was perhaps never recognized.) As is often the case, epoch-making ideas carry with them implicit, unanalyzed assumptions that ultimately impede scientific progress until they are recognized for what they are. So it is with the prokaryote–eukaryote distinction. Our failure to understand its true nature set the stage for the sudden shattering of the concept when a "third form of life" was discovered in the late 1970s, a discovery that actually left many biologists incredulous. Archaebacteria, as this third form has come to be known, have revolutionized our notion of the prokaryote, have altered and refined the way in which we think about the relationship between prokaryotes and eukaryotes (especially the role the former plays in the evolution of the latter), and will influence strongly the view we develop of the ancestor that gave rise to all extant life (particularly the conditions under which that entity arose). As a background against which to view the archaebacteria—whose physiological, morphological, ecological, and molecular aspects are discussed in this volume—we will trace the history of the prokaryote–eukaryote distinction and the parallel development of the concept of archaebacteria, which would prove its undoing.

Initially the definition of the prokaryotic cell was basically a negative one. The prokaryotic cell did not possess this or that eukaryotic feature—organelles, circumscribed nucleus, etc.—but no converse properties (those possessed by prokaryotes that were lacking in eukaryotes) were recognized. It is remarkable, therefore, that much of a concept of a prokaryote existed at all initially. (If a "car" were to be defined only as not having leaves or bark, etc., one would not have a very clear picture of what a car is.) Yet a definite concept of a "prokaryote" did exist, and it strongly influenced the course of microbiology.

For reasons that are not entirely clear, the prokaryote was taken to be a phylogenetically coherent unit, perhaps in part because the eukaryote was so conceived. The proof of this contention lies not so much in statements made by biologists over the years as in the fact that in defining the molecular phenotype of eukaryotes and prokaryotes, the biologist rarely felt a need to characterize other than the "typical prokaryote"—*Escherichia coli*—and if he did, it was for

reasons unrelated to the matter of phylogenetic coherence of the group. Several generations of biologists have now been raised to believe that prokaryote–eukaryote is both a cytological and a phylogenetic dichotomy.

The term prokaryote also carried with it the implication (in the prefix "pro-") that it was a forerunner of the eukaryote. And so it continued to be regarded. Explanations for the origin of the eukaryotic cell in terms of endosymbioses are testimony to this. While such an idea seems a valid enough explanation for the origin of chloroplasts and mitochondria, it is at best a debatable speculation when applied to the origin of the eukaryotic nucleus and is near nonsense when invoked to account for the species that hosted the endosymbionts (it was a prokaryote that lost its cell wall). The general idea, too, embodies the more subtle implication that endosymbioses among prokaryotes are all there really is to eukaryotic cellular evolution, a notion which at best is misleading. Attempts by biologists to rationalize the origin of eukaryotic mechanisms (e.g., control of gene expression) in terms of their having arisen from their prokaryotic (i.e., eubacterial) counterparts have proved unsatisfying and stultifying exercises. Eukaryotic mechanisms, if anything, seem derived independently of, not from, their prokaryotic counterparts.

The final implication of the prokaryote–eukaryote distinction is that the eukaryote is somehow more advanced than the prokaryote. It is mainly because this view accords with anthropocentrism that it finds acceptance. Prokaryotes may have smaller genomes than do eukaryotes, but these are, if anything, more precisely organized, well defined, and efficiently functioning than are their eukaryotic counterparts. There are as many (or more) reasons to consider that the eukaryotic cell is the more primitive of the two than the reverse.

Conventional wisdom has always regarded the prokaryote, then, as a primitive, less advanced type of cell that arose before the eukaryotic cell and was capable of evolving into the latter. This notion is incorrect and pernicious.

With the onset of the molecular era in biology the prokaryote–eukaryote distinction in effect became redefined. Previously the distinction had been made in terms of noncomparable properties at the cytological level, e.g., whether the cell possessed a nucleus or organelles. Now the definition would be framed in terms of comparable properties at the molecular level. For any number of molecular properties there was a characteristic eukaryotic and a characteristic prokaryotic form—various enzyme quaternary structures, this or that biochemical pathway, the ribosome, control mechanisms, etc. While this drastic redefinition gave the notion of a prokaryote a definiteness it had previously lacked, while it made biologists aware of the true depth of the prokaryote–eukaryote distinction, and while it gave the idea some real evolutionary meaning, biologists approached the redefinition firm in their belief (mentioned above) that the prokaryote was a phylogenetically monolithic grouping, and so never saw fit to explore the phylogenetic diversity of its molecular phenotype. Had they done so, archaebacteria would certainly have been discovered ten to twenty years sooner.

Microbiology is a discipline that has developed virtually untouched by Darwin's grand idea. Despite the concerns and the efforts of the classical microbiologists, the natural, or evolutionary relationships among bacteria remained effectively unknown through the early 1970s, and so exerted no influence on the development of the field of microbiology. We cannot appreciate the profound effect the lack of a bacterial phylogeny has had on the course not only of microbiology but all of biology. Evolution provides the only unifying theme in an otherwise diverse and continually disintegrating discipline. And the evolutionary history of bacteria, because it transcends in time and to a large extent overlaps the evolution of eukaryotes, is the true base for the study of evolution.

In the past, evolutionary relationships were deduced largely from the morphological similarities and differences among the extant representatives of various (eukaryotic) lines and their fossilized ancestors. The success of this approach turned on the complexity of eukaryotic morphologies. Bacteria are not morphologically complex. And we now can see that attempts to use morphological (and other equally unreliable) characters to establish their natural relationships have created only a phylogenetic monstrosity: the current system of bacterial taxonomy. There is no point in attempting to construct a bacterial phylogeny in these terms.

While the bacterial phenotype (at least as classically defined) is too simple to serve as the basis on which to establish a phylogeny, this is not true of the (bacterial) genotype. For any given phenotypic character—the cytochrome *c* function, for example—myriad genotypic (i.e., sequence) equivalents exist. Thus, genotypic "phase space" is enormous compared to the "phase space" of the corresponding phenotypes. This in turn means that the majority of changes in genotypes that become fixed are selectively neutral—which gives the occurrences of such changes a chronometric quality—and that the biologist can use sequence comparisons as a rather precise, reliable, and powerful measure of evolutionary time (distance) and phylogenetic branch points.

The use of macromolecular sequence comparisons for determining evolutionary relationships and distances was developed in eukaryotic systems. However, its great impact will be in prokaryotic systems. Evolutionary distances in the bacterial world far exceed those among eukaryotes. This is readily seen in terms of the cytochrome *c* molecular chronometer. A phylogenetic tree constructed on the basis of cytochrome *c* sequence comparisons for the eukaryotes is no more than a branch of a larger eubacterial tree that itself covers only one of three of the sublines of purple bacteria, which in turn are one of about ten major divisions of the eubacteria. It is no wonder then that a molecule such as cytochrome *c*, which is a superb molecular chronometer for the eukaryotes, proves to be an inadequate chronometer in the case of the bacteria.

Ribosomal RNA (16 S) has proved to be an excellent molecular chronometer by which to measure the evolutionary distances encountered in the bacterial world. Ribosomal RNA sequence comparisons can measure not only the deepest

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