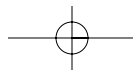
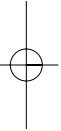
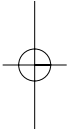


## **MICROBIAL DIVERSITY**



“If I could do it all over again, and relive my vision in the twenty-first century, I would be a microbial ecologist. Ten billion bacteria live in a gram of ordinary soil, a mere pinch held between thumb and forefinger. They represent thousands of species almost none of which are known to science. Into that world I would go with the aid of modern microscopy and molecular analysis. I would cut my way through clonal forests sprawled across grains of sand, travel in an imagined submarine through drops of water proportionately the size of lakes, and track predators and prey in order to discover new life ways and alien food webs. All this, and I need venture no farther than ten paces outside my laboratory building. The jaguars, ants, and orchids would still occupy distant forests in all their splendor, but now they would be joined by an even stranger and vastly more complex living world virtually without end. For one more turn around I would keep alive the little boy of Paradise Beach who found wonder in a scyphozoan jellyfish and a barely glimpsed monster of the deep.”

E.O. Wilson on “The Diversity of Life” in *Naturalist* (1994).

# MICROBIAL DIVERSITY

**Form and Function in Prokaryotes**

**Oladele Ogunseitan**

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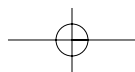
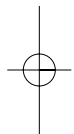
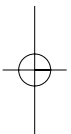
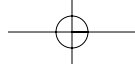
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# FOREWORD

When we contemplate “evolution of life on Earth” we tend to imagine changes in animals and plants. We picture little ape-men who yelp at their hairy wives or small running Paleocene mammals who run on the third (“middle finger”) digits of their fore and hind legs that enlarge and harden to become hooves. We see forests of ancient scaly *Lepidodendron* trees descend to become the little club mosses (also called ground pine or Christmas fern). Mostly the word “evolution” conjures the grunting caveman to singing cave painter transition in northern Spain and southern France. Although we know that no *Eohippus* ever awoke one fine and sunny spring morning, to stretch his legs and watch his toes transform to horny hooves, nor did any bone-splitting, marrow-chomping hairy Neanderthal survey the snowscape to return inside the limestone cavern to outline horned antelope before the fire, such exaggerated evolutionary images enchant and attract us. What is seldom conjured up by the phrase “evolution of life on Earth” is bacteria.

A thorough read of *Microbial Diversity* will alter our worldview. We moderns are grossly biased in our perspective; we are far too preoccupied with far too few forms of life. Of most concern to us are vertebrates that live on land (ourselves, our pets, our draft animals); flowering grasses that do most of the production upon which we depend for sustenance (i.e., barley, corn, rye, wheat); and the fungi as mushrooms, the yeast of bread and beer, or as agents of ringworm, athlete’s foot, or allergens. Reminiscent of the five-year old, our anthropocentric view toward the natural world is one of “what’s in it for me?” When, in *The Progress of the Soul* (c.1610), John Donne wrote, “Nature’s great masterpiece, an Elephant . . .”, he was only partly right. He could not have guessed the truth that Professor Ogunseitán builds in this splendid text and, I paraphrase, “Nature’s great masterpiece, the bacterium”. In *Microbial Diversity* Ogunseitán has written well about the fundamental units of life, the bacteria. His work is surprisingly comprehensive and up to date. By implication and even in explicit reference, he explains their spectacular evolution. But he has not even opened the expansive landscape to their most gifted and crucial descendants: the eukaryotic microorganisms. These larger beings, are the coevolved and integrated communities of bacteria, the immediate kin from which the larger forms of life on Earth evolved. What other denizens of the glorious microbial world, the microcosmos, are omitted from detailed treatment here? The filamentous fungi and the protists, microscopic eukaryotic organisms, refractory to simple classification and to short accurate description are underrepresented.

The fundamental lesson of this book turns our cultural myths inside out. The abundance and diversity of life on Earth has come not from fossil horses or club mosses but from the flourishing of the oldest, most omnipresent life forms, the bacteria. For all intents and purposes the bacteria invented everything of importance: growth, metabolism and reproduction, swimming and chemical sensitivities, oxygen respiration and desiccation-resistant propagules. Some perfected predatory behavior and the kill. They are masters of efficiency and recycling of waste. They invented sex and indulge in it with abandon. They cover the mountaintops, the prairie, and the plains with their offspring. They swim with no thought

## Foreword

of sleep. They fashion fuel like methane and ethanol from far less energetic forms of carbon such as CO<sub>2</sub>. The prodigious bacteria have created sexual communication and gender, genetic recombination, and consortial living. Some thrive exposed to ferocious winds and blinding sunlight on open cliffs, others burrow into hard limestone rock and photosynthesize right through their chalky covers. As metal workers, bacteria have no peers: some precipitate gold and others mine iron; some manufacture metallic sheens of manganese and others work copper or etch glass. In Ogunseitán's learned tome the crucial importance of bacterial life to our environment is laid bare at a sobering level of scholarship. He pays heed to the recent literature. He does not overstate or overconclude, rather he gives the advanced student access to the professional literature on its own terms.

Microbes, by consent, are live beings too small to be seen as individuals with the unaided eye. Nature's energetic gyration has generated two vast groups, easily distinguished by direct microscopic inspection of their cells. Because no single life form intermediate between these groups has ever been found, all microbial life is unambiguously classified into the Eukarya, organisms with nuclei or the bacteria in the broad sense (the Prokarya). Apparently small and simple when visualized by light microscopy, bacteria are amazingly complex and diverse when studied by more devious means. Chemical, metabolic, macromolecular, and other indirect analyses have revealed the world of diversity in prokaryotes that is the subject of this book. Prokaryotes are single or multicellular organisms in which each cell is of the bacterial kind. Since they were discovered by Antoni van Leeuwenhoek in the late-17th century and analyzed by Louis Pasteur in the late-19th century, bacteria have been studied by chemists, oil scientists, food industry advisers, and especially by physicians. Lately prokaryotes have been the focus of attention of sewage engineers, space scientists, and environmental analysts. Biologists, whether zoologist, botanist, or cell biologist, have tended to exclude prokaryotes from their foci of study. The activities of these wily, insinuating hordes impinge so heavily on human lives that a new vocational term was coined to describe the scientist whose profession it is to study the greater bacteria: he is the microbiologist. Although, by tradition and practice, the microbiologist studies all the prokaryotes and one group of eukaryotes, the smallest fungi (the yeast), he systematically, by tradition, excludes the eukaryotic microbes. Microbes composed of cells that contain nuclei, an estimated 250,000 species alive today, form another world. They tend to be studied by zoologists (the protozoa), botanists (the algae), and mycologists (the fungi including the slime molds). Ogunseitán rests squarely in the microbiologist's traditions but he is aware of its deficiencies.

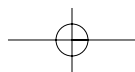
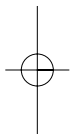
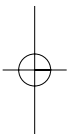
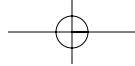
His subtitle admits that this is a book about the bacteria as units of life itself. It deals with all organisms made of cells that lack membrane-bounded nuclei. All prokaryotes are still members of the bacterial world, whether in ribosomal composition eubacterial or archaeobacterial, or in cell wall structure (two-membraned gram-negative, single-membraned gram-positive, gram-variable, or the aflagellate that lack cell walls entirely). Bacteria lack chromosomes. In spite of the widespread terminology, "bacterial chromosomes", in my opinion, do not exist. The naked DNA structures of the bacterial genophores are chromonemes, not chromosomes. The histone protein-draped chromatin of animals, plants, protoctists, and fungi provide the material basis of meiotic-fertilization forms of sex. Mitotic spindle movements of real chromosomes assure alternate production of haploids (e.g., plant spores and germ cells) and diploids (plant sporophytes and animal body cells). Such elaborate sexuality in the Eukarya, which requires the breach of the individual haploid cell and the acceptance in toto of a "foreign" nucleus or cell within a common membrane, is a feature essential to eukaryotes and their behavior. The cell-level "emboitement" (known in many guises: fertilization, pinocytosis, phagocytosis, cell fusion, karyogamy, invasion, endocytosis, incorporation) marks as unique all eukaryotes relative to Ogunseitán's prokaryotes. The ability to evolve "a genome at a swallow" is entirely lacking at the prokaryotic level of cell organization.

The paucity of endosymbionts and absence of cyclical cell fusion is what makes Carl Woese's currently preferred term "Archaea" an anathema, as it implies that these microorganisms somehow are not bacteria. Whereas Woese's original concept of "Archaeobacteria"

led to an immense contribution to the literature of the analysis of microbial life, “Archaea” is a misnomer. Archaeobacteria (usually methanogens, halobacters, or sulfoacidophils) are, after all, bacteria in every sense. Like all their prokaryotic brethren they are homogenomic, have small ribosomes and chromonemic organization, transfer small pieces of DNA, and are not products of symbiotic fusions. The great group of bacteria, including archaeobacteria, with its incredible diversity, may be characterized by many criteria in addition to the ribosomal RNA DNA genes or a chromonemal gene sequence for a single protein. Unique physiological pathways and environmental distribution are two examples. A singular strength of Ogunseitán’s text is its exhaustive, measured, and fair comparison of ways to measure and handle the unruliness of the prodigious diversity of bacteria. He knowingly slights the eukaryotes although he realizes they are composites of bacteria. Clearly, a detailed treatment of them would bring him into a far different realm. Because eukaryotes are all merged complexes of a limited set of prokaryotes another entire book would be required to do them justice. The ecological, behavioral, developmental, metabolic, and genetic magnitude of prokaryotic diversity is staggering enough. Beside it the diversity of all eukaryotes pales. Whether microbial (small fungus or protoctist) or visible with the unaided eye (large fungus and protoctist, animal or plant), the uniformity of the sexual and metabolic biology of eukaryotes is striking relative to the evolutionary diversity of bacteria. Only in morphological splendor, easily delineated species and the production of certain specific metabolites such as plant and fungal hallucinogens, toad and dinomastigote nerve toxins, plant skin irritants, Chinese and English speech, phosphate–nitrate mountains and cities, do the eukaryotes have any claim to unique and original diversity. All important features of life on this planet evolved in bacteria. Enter here and see for yourself.

**Lynn Margulis**

Distinguished University Professor  
Department of Geosciences, University of Massachusetts



# PREFACE

Conservation biology is a relatively new academic discipline that is currently enjoying a remarkable popularity among students, researchers, and the public. Its success is striking because it is primarily an exploratory science with few reproducible theories or generalizable concepts. Habitat preservation and species protection programs implemented through government regulations such as the U.S. Government's Endangered Species Act of 1973 have been modestly successful experiments to conserve biological diversity. However, to microbiologists, these landmark steps toward popular appreciation of ecological biology must seem partial and inadequate. Years dedicated to learning that microorganisms sustain the global ecosystem have not reduced the gap between the appreciation of large animal and plant organisms (macrodiversity) and the widely acknowledged ignorance of the diversity of microorganisms (viruses, bacteria, protists, and small fungi—microdiversity).

In nature, the large population densities and rapid growth rates inferred from working with many microorganisms in the laboratory support the view that prokaryotes cannot be in danger of extinction (Staley, 1997). Microbial pathogens that humans have deliberately tried to extinguish with antibiotics and antiseptics for centuries are still very much with us. However, occasions do arise that raise the prospect of microbial extinction, at least locally. For example, the debate at the end of the twentieth century about whether to terminate the last remaining stocks of the smallpox virus only slightly included discussions about microbial diversity. Instead, the debate was framed by concerns for future bioterrorism and access to vaccines.

This book presents a comprehensive analysis of the concepts and methods that have facilitated recent advances in the understanding of microbial diversity, and a clear linkage to the importance of this understanding for global physicochemical and biological processes that are easily recognizable to investigators in the natural sciences. Microbial diversity is presented here as highly relevant to processes that are proximal to human affairs, a treatment that will be of interest to investigators in other disciplines.

Taxonomy and systematics are unquestionably important to concepts of microbial diversity, but they are treated here only as means to the goal of understanding the diversity of microbial function in nature. Therefore, in certain contexts, it is reasonable to discuss the diversity of specific microbial processes with limited scientific data on the exact number and names of microbes that are responsible for the processes at a particular time and place. The inability to identify and quantify particular microbial species involved in a given ecological process has long been recognized as a major impediment in microbial ecology and environmental microbiology, but the shortcomings are treated here as an opportunity for scientific advancement. The advancement will undoubtedly ameliorate the hindrance that methodological limitations have placed on research programs aiming to understand the contributions of microbial diversity to defined states of ecological and human health.

The book is organized in two major sections with chapters representing major themes within each section. Part I focuses on conceptual and methodological issues, whereas Part

## Preface

It focuses on principles, applications, and opportunities for research and the advancement of knowledge. Chapter 1 introduces the theoretical and empirical difficulties entailed in defining a microbial “species” as a fundamental unit of microbial diversity, and on the methods for identifying varieties in microbial populations. Chapters 2 through 5 present critical analyses of the major techniques employed for investigating microbial diversity including microscopic, culture, molecular, and phylogenetic systematic methods.

Chapter 6 lays the foundation for integrating microbial diversity with Earth system science through the historical evidence for the influence of the origin of microbial life on the early Earth environment. The sojourn into environmental evolution places contemporary concerns about human impacts on the global ecosystem into the robust context of the coevolution of life and environment. The constant flow of novel and controversial theories about the geological roots of microbial life on Earth makes this topic also of great interest for astrobiology (e.g., see Gold, 1999). Chapters 7 and 8 focus on the relevance of microbial diversity to biogeochemical cycles. This is a well-researched area of microbial ecology, but rather than focusing on the activities of well-known microbial species or specific biochemical pathways, the approach used in these chapters focuses on the interconnectedness of microbial communities and their role in maintaining balanced biogeochemical pathways. In addition, the discussion deals with the consequences to microbial communities, of geochemical disequilibria attributed to human-dominated ecosystems. Chapters 9 and 10 focus on the relationship of microbial diversity to biotic interactions. Many of the commercial applications of microbial diversity fall within this topic area.

The axenic culture conditions that have been very useful in elucidating the characteristics of microorganisms are unfortunately not the state in which microorganisms exist in nature, therefore, it is clearly not appropriate to draw far-reaching conclusions about the driving forces of microbial speciation and diversity from axenic laboratory experiments. Advances in microcosm design have facilitated research on natural microbial communities, but it is difficult to reproduce how these communities behave under natural environmental conditions. As the progenitors of eukaryotic life forms, most microorganisms that have been studied engage in complex multifaceted interactions with plants, animals, and with other microorganisms. The inevitable human-value system prejudices these interactions as either beneficial such as in nitrogen fixation or detrimental such as in the case of pathogens, but there is no question that these biotic interactions and all their ramifications are essential for the sustainability of natural ecosystems. The approach used in these chapters does not underestimate the significance of the categorization of microbial biotic interactions, but the emphasis is on the importance of microbial diversity to such categorizations, and how human impacts on existing diversity may reinforce or modify the biotic interactions in consequential ways.

The final chapter deals with the relevance of microbial diversity to global environmental problems that have been exacerbated recently by inefficient industrial ecology, population growth and urbanization. In many ways, the recognition of dynamic environmental phenomena as intractable problems is rooted in impatience with, and poor understanding of, biogeochemical cycles, some of which are discussed in Part II. An optimistic view is that solutions to these global environmental “problems” may depend in part on better understanding and scientific management of microbial diversity for “correcting” the balance of chemical fluxes in various environmental compartments.

For students majoring in microbiology, this book will be useful for one of the quartet of core courses recommended by the American Society for Microbiology, namely “Introduction to Microbiology”, “Microbial Physiology”, “Microbial Genetics”, and “Microbial Diversity” (Baker, 2001). The order in which this sequence of courses is taken should not adversely affect comprehension of the materials presented in this book, although it is recommended that a solid foundation in general microbiology should come first. The book is presented in a format that can also serve as an accessible resource for a graduate-level, one-semester course in departments where knowledge of applied microbiology is required to sustain specific research programs. The book is also designed for active researchers to reveal the current

state of knowledge, including conceptual inconsistencies and existing analytical gaps. All biological diversity can be traced back in time to prokaryotic diversity. In this sense, the Earth is a planet of prokaryotes, and the treatment of microbial diversity here leans heavily on prokaryotic forms and functions. Excellent treatments of eukaryotic microbial diversity already exist (notably Margulis *et al.*, 2000). These texts and handbooks should be indispensable supplements to this book for a complete view of microbial diversity.

Special features of the book include:

- Extensive illustrations including charts, maps, graphs, and diagrams.
- Four-color plate inserts with high resolution images of microorganisms, maps, and satellite images.
- Text and image boxes presenting extended discussions of critical concepts and case studies, for those interested in a deeper exploration of the material.
- Challenging questions for further investigation in each chapter offer opportunities for direct field investigation.
- A list of suggested readings in each chapter and an extensive list of references at the end of the book provide up-to-date sources for further exploration.
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**Oladele A. Ogunseitn**

