THE ORIGIN OF EUKARYOTIC CELLS

Edited by

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and

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To Lynn Margulis

In non-living habitats, an organism either exists or it does not. In the cell habitat an invading organism can progressively lose pieces of itself, slowly blending into the general background, its former existence betrayed only by some relic. Indeed one is reminded of Alice in Wonderland's encounter with the Cheshire cat. As she watched it, "it vanished quite slowly, beginning with the tail, and ending with the grin, which remained some time after the rest of it had gone." There are a number of objects in a cell like the grin of a Cheshire cat. For those who try to trace their origins, the grin is challenging and truly enigmatic (D. C. Smith, Paper 9).

SERIES EDITOR'S FOREWORD

The Systematic and Evolutionary Biology series reprints classic scientific papers on the evolution and systematics of organisms. The volumes in this series do more than just provide scholars with facsimile reproductions or English translations of classic papers on a particular topic. The interpretative commentaries and extensive bibliographies prepared by each editor provide busy scholars with a review of the primary and secondary literature of the field from a historical perspective and a summary of the current state of the art.

Biologists employ comparative methodology to scientifically reconstruct phylogenies—the evolutionary history of life on this planet. Scientists studying the fossil record have identified microfossils of prokaryotes (bacteria) in rocks known to be 3.7 billion years old. Microfossils of eukaryotes have been found in rocks as old as 1.4 billion years. Most of what we know now of the fossil records of these organisms has been discovered within the last 20 years. Most of the classic papers comparing living prokaryotes with living eukaryotes have also been published within the last 20 years. Drs. Betsey Dexter Dyer and Robert Obar have chosen the classic comparative studies of living as well as fossil prokaryotes and eukaryotes for inclusion in *The Origin of Eukaryotic Cells*.

The philosopher of science, Alfred North Whitehead, is reported to have said "We give credit for an idea not to the first man to have it, but to the first one who takes it seriously." It is for this reason that we give a woman scientist credit for developing the symbiotic theory of the origin of eukaryotes from prokaryotes. Lynn Margulis first championed her theory in 1967, only 18 years ago. She has successfully employed hypothetico-deductive-testing scientific methodology in her research. Many of the predictions she has deduced from her theory that eukaryotes originated as the result of symbiotic interactions among prokaryotes have been tested and verified by her as well as others.

Evolutionary biology is a successful science because its theories are testable and have been scientifically tested against empirical evidence; its theories have unified many diverse problems in biology and solved them with the same problem solving strategy; and its theories have been fruitful in opening up new dimensions of scientific investigation. Lynn Margulis's symbiotic theory of the origin of eukaryotic cells from prokaryotic cells is an example of such a successful evolutionary theory.

CARL JAY BAJEMA

PREFACE

The present understanding of the origin of eukaryotic cells is based on the development of two new fields of research in the past 20 years: micropaleontology (the study of microfossils of prokaryotes and early eukaryotes) and biochemical and genetic research on the origin and nature of eukaryotic organelles (mitochondria, plastids, motility organelles). The second of these two fields is the topic of our book.

The publication of the discovery of microfossils in 2 billion-year old rocks by S. Tyler and E. Barghoorn in 1965 exploded the notion that the fossil record began abruptly and inexplicably with large, hard-bodied eukaryotes about 500 million years ago. The field of micropaleontology continues to grow. Microfossils of prokaryotes are now known in 3.7 billion-year old rocks while presumptive eukaryotic fossils have been found in rocks as old as 1.4 billion years. Micropaleontology is an integral part of any understanding of early life and the initial stages of eukaryote evolution.

The first full length treatment of the theory of a symbiotic origin for eukaryotic cells was presented by L. Margulis in 1967 (Paper 3). Opposition to this paper was so strong that it nearly remained unpublished. The theory stated that the mitochondria, plastids, nucleocytoplasm, and motility organelles (that is, most of the major components of eukaryotes) originated as separate prokaryotes (bacteria) that came together in symbiotic associations, forming the first eukaryotes. In her 1967 paper, Margulis unified data and observations on eukaryotic cells into one theory and made specific predictions, many of which were tested and verified in subsequent years. As a result, the theory of a symbiotic origin of eukaryotes is no longer controversial at this writing (1984) and is even included in most discussions of cell evolution in new elementary biology textbooks.

In this book we have assembled classic and in some cases difficult-to-obtain papers that deal with the symbiotic origin of eukaryotes, as well as several early papers of historical interest. A collection of this sort has never before been published in one volume. We believe that it will become a valuable and convenient reference for college libraries and for educators and advanced students in most fields of biology and biochemistry. Many of the experiments described are elegant and inspirational, and many of the papers are exemplary for their literary style as well.

We hope that our introductory list of research criteria for determining whether an organelle or other intracellular structure is of symbiotic origin will be particularly useful to theorists and researchers. Also included is a section on the still relatively controversial symbiotic origin of motility organelles, with a collection of the classic papers on this topic. We hope that this volume will encourage potential researchers in the field, as well as provide a collection of background references.

We thank Carl Bajema for critical reading of the manuscript. We thank Lynn Margulis with love, for years of generosity, support, inspiration, tolerance, and enthusiasm.

BETSEY DEXTER DYER
ROBERT OBAR

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INTRODUCTION

The category *eukaryotic organisms* includes animals, plants, fungi, and protoctists. The cells of eukaryotes contain nuclei (double membrane-bound packages containing a DNA genome) and, in most cases, mitochondria (double membrane-bound packages in which oxidative respiration occurs). Some eukaryotes (plants and some protoctists) have plastids, which are double membrane-bound packages containing the light-capturing pigments and enzymes for photosynthesis. Eukaryotes undergo mitotic cell division in which the chromosomes (DNA genome plus associated proteins) are moved by microtubule spindle fibers made primarily of tubulin protein. The eukaryotic motility organelle (undulipodium) is a bundle of tubulin microtubules usually with a 9 + 2 cross-sectional arrangement of the microtubules (e.g., cilia and sperm tails) (Paper 30). In addition to tubulin, the motility organelles (undulipodia) are made of about 200 other proteins and the structure is intrinsically motile if provided with an energy source.

Prokaryotes (i.e., the bacteria) differ from eukaryotes in that the DNA of prokaryotes is not contained within a nucleus, and metabolic processes such as photosynthesis are not contained in separate packages or organelles. Prokaryotes also have no tubulin-based motility systems, although at least three species reportedly have tubulin-like proteins (Part IV), the functions of which are unknown. Prokaryotes do not undergo mitosis with tubulin spindle fibers. The prokaryotic flagellar motility system is based on a unique set of proteins, *flagellins,* which are not intrinsically motile (Paper 30).

Eukaryotes are divided into four distinct kingdoms: protoctists, fungi, animals, and plants (Papers 35A, B, C, D, and E). The protoctists make up an extremely diverse group of uni- and multi-cellular organisms that are mostly aquatic. The group lacks extensive tissue differentiation and embryonic stages and includes members that are probably direct descendants of the first eukaryotes, which began to evolve about 2 billion years ago. There are about 30 distinct phylum-level groups of protoctists. Examples of some photosynthetic protoctists are *Chlamydomonas, Euglena, Volvox,* diatoms, dinomastigotes, red algae, and brown algae. These are distinct from the heterotrophic protoctists, organisms that either ingest or absorb their food such as amoebae, sporozoans (a parasitic group), mastigotes, and myxomycetes (slime molds).

Fungi form thread-like cells called *hyphae* that absorb nutrients from the environment. The group has no tubulin-based motility organelles (undulipodia), but it does have mitosis, with tubulin spindle fibers, and mitochondria. The fungal kingdom includes the mushrooms and molds.

The plants and animals both have extensive tissue differentiation and embryonic stages. The animals are heterotrophic, ingesting or absorbing their food. They have mitochondria and, in at least one stage of their life cycles, eukaryotic motility organelles (undulipodia). Plants are oxygenic green photosynthesizers. Descendants of the earliest plants (mosses, ferns, ginkgos) have motile sperm. Motile forms were entirely lost in later plant groups (gymnosperms, angiosperms). Plant cells have mitochondria and chloroplasts.

All organisms interact with other organisms in nature; there are no solitary individuals. The environment of every organism is filled with other organisms, thus the selection pressure on a community of organisms is not a result of merely the physical environment but of other organisms as well. The limitation of resources on Earth causes part of the selection pressure by which interactions between organisms evolve. Metabolic reactions are not perfectly efficient; there are extra products and reactants and usually waste products. Organismal interactions evolve to use these products. The problem of limited space on Earth is also solved in part by interactions in which organisms live upon and inside of each other. Interactions range from situations where one organism benefits from the relationship and the other does not (as in predator/prey relationships and host/parasite relationships) to interactions in which both organisms benefit (symbioses). The boundaries are blurred between the definitions of organismal interactions. Many parasites are benign or are harmful only in a certain life-cycle stage of the host. Most symbioses probably originate as less equitable relationships. The ongoing tendency to interact is probably one of the major mechanisms by which the first eukaryotes began to evolve 2 billion years ago.

The first evidence for life on Earth is 3.7 billion years old and includes microfossils of bacteria-like organisms and laminated sedimentary structures (stromatolites) formed by communities of bacteria-like organisms (Fig. 1). It may be extrapolated that life originated at least 4 billion years ago in order for a diversity of organisms to be present 3.7 billion years ago. The "age of bacteria," in which prokaryotes

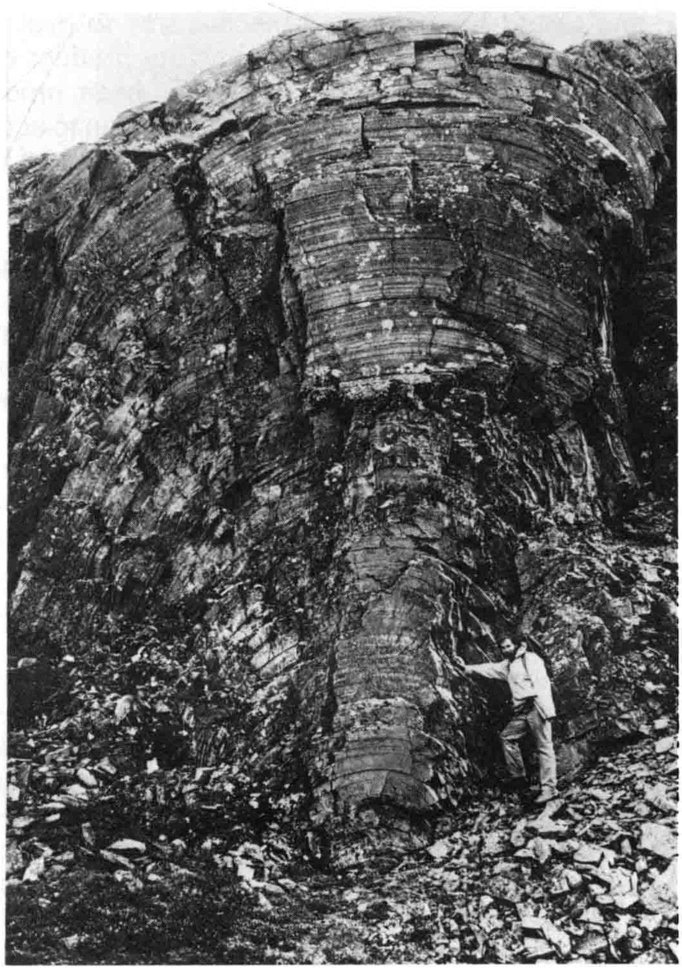

Figure 1. Proterozoic stromatolite (bacterial skyscraper) (*photo:* Geological Survey of Canada).

diversified and covered every available part of the Earth, lasted for about 2 billion years. During that period almost all of the metabolic processes of prokaryotes and eukaryotes were evolved by the prokaryotes. Fieldwork indicates that modern prokaryotes tend to live in complex communities, and there is evidence for such communities in the fossil record. Modern prokaryotes also have many interactions (ranging from predator/prey to symbioses) with each other and it is presumed (although evidence has not been preserved in the fossil record) that ancient prokaryotes also interacted extensively.

About 2 billion years ago a crisis occurred. Oxygen began to accumulate in an atmosphere which, up to that point, had been