

# THE ORIGIN OF EUKARYOTIC CELLS

---

Edited by  
**Betsey Dexter Dyer**  
and  
**Robert Obar**

---

---

# **THE ORIGIN OF EUKARYOTIC CELLS**

Edited by

**BETSEY DEXTER DYER**  
Wheaton College

and

**ROBERT OBAR**  
Worcester Foundation  
for Experimental Biology

A Hutchinson Ross Publication



**VAN NOSTRAND REINHOLD COMPANY**

*New York*

Copyright © 1985 by **Van Nostrand Reinhold Company Inc.**  
Benchmark Papers in Systematic and Evolutionary Biology, Volume 9  
Library of Congress Catalog Card Number: 85-20261  
ISBN: 0-442-21952-0

All rights reserved. No part of this work covered by the copyrights hereon may be reproduced or used in any form or by any means—graphic, electronic, or mechanical, including photocopying, recording, taping, or information storage and retrieval systems—without permission of the publisher.

Manufactured in the United States of America.

Published by Van Nostrand Reinhold Company Inc.  
115 Fifth Avenue  
New York, New York 10003

Van Nostrand Reinhold Company Limited  
Molly Millars Lane  
Wokingham, Berkshire RG11 2PY, England

Van Nostrand Reinhold  
480 Latrobe Street  
Melbourne, Victoria 3000, Australia

Macmillan of Canada  
Division of Gage Publishing Limited  
164 Commander Boulevard  
Agincourt, Ontario M1S 3C7, Canada

15 14 13 12 11 10 9 8 7 6 5 4 3 2 1

**Library of Congress Cataloging in Publication Data**

Main entry under title:

The origin of eukaryotic cells.

(Benchmark papers in systematic and evolutionary biology; 9)

"A Hutchinson Ross publication."

Includes indexes.

1. Eukaryotic cells—Evolution—Addresses, essays, lectures. 2. Symbiosis—Addresses, essays, lectures.

I. Dyer, Betsey Dexter. II. Obar, Robert. III. Series.

QH371.O73 1985 575 85-20261

ISBN 0-442-21952-0

# **Benchmark Papers in Systematic and Evolutionary Biology**

**Editor: Carl Jay Bajema—Grand Valley State Colleges**

MULTIVARIATE STATISTICAL METHODS: Among-Groups Covariation/  
*William R. Atchley and Edwin H. Bryant*

MULTIVARIATE STATISTICAL METHODS: Within-Groups Covariation/  
*Edwin H. Bryant and William R. Atchley*

CONCEPTS OF SPECIES / *C. N. Slobodchikoff*

ARTIFICIAL SELECTION AND THE DEVELOPMENT OF EVOLUTIONARY  
THEORY / *Carl Jay Bajema*

NATURAL SELECTION THEORY: From the Speculations of the  
Greeks to the Quantitative Measurements of the Biometricians /  
*Carl Jay Bajema*

SEXUAL SELECTION THEORY PRIOR TO 1900 / *Carl Jay Bajema*

PALEOBOTANY, PART I: Precambrian Through Permian / *Thomas N. Taylor  
and Edith L. Smoot*

PALEOBOTANY, PART II: Triassic Through Pliocene / *Thomas N. Taylor  
and Edith L. Smoot*

CLADISTIC THEORY AND METHODOLOGY / *Thomas Duncan  
and Tod F. Stuessy*

*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

## *Preface*

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

## CONTENTS BY AUTHOR

- Adams, G. M. W., 167  
 Agsteribbe, E., 153  
 Barath, Z., 137  
 Beisson, J., 244  
 Bonen, L., 184  
 Boynton, J. E., 167  
 Chase, D., 266  
 Cleveland, L., 288  
 Cutting, J. A., 90  
 Dayhoff, M. O., 68  
 Doolittle, W. F., 83, 184  
 Dutcher, S. K., 276  
 Eaton, J. W., 125  
 Fairfield, A. S., 125  
 Falconet, D., 145  
 Fridovich, I., 116  
 Gibbs, S. P., 177  
 Gillham, N. W., 167  
 Goksøyr, J., 17  
 Goldsmith-Spoegler, C. M., 273  
 Goodner, K., 240  
 Gray, M. W., 145  
 Green, J., 156  
 Grimes, G. W., 273  
 Harris, E. H., 167  
 Heidemann, S. R., 252  
 Huang, B., 276  
 Huh, T. Y., 145  
 Jeon, K. W., 95  
 John, P., 141  
 Kirschner, M. W., 252  
 Knaupp, E. A., 273  
 Küntzel, H., 137  
 Lewin, R. A., 164  
 Lorch, I. J., 95  
 Luck, D. J. L., 276  
 McKenna, M. E., 273  
 Martin, J. P., Jr., 116  
 May, H. G., 240  
 Meshnick, S. R., 125  
 Obar, R., 156  
 Palmer, J. D., 193  
 Ramanis, Z., 276  
 Raven, P. H., 77  
 Sagan, D., 290  
 Sagan-Margulis, L., 18, 223, 266, 290, 311,  
     317, 321, 325, 331  
 Samallo, J., 153  
 Sander, G., 252  
 Schiff, J. A., 198  
 Schnare, M. N., 145  
 Schulman, H. M., 90  
 Schwartz, K., 311, 317, 321, 325, 331  
 Schwartz, R. M., 68  
 Smith, D. C., 97  
 Sonea, S., 113  
 Sonneborn, T. M., 244  
 Spencer, D. F., 145  
 Starr, M. P., 208  
 Stern, D. B., 193  
 Thomas, D. Y., 132  
 Tingle, C. L., 167  
 Van den Boogaart, P., 153  
 Van Winkle-Swift, K., 167  
 Wallin, I. E., 10  
 Whatley, F. R., 141  
 Wilkie, D., 132  
 Withers, N. W., 164

# THE ORIGIN OF EUKARYOTIC CELLS

# CONTENTS

Series Editor's Foreword	xi
Preface	xiii
Contents by Author	xv
Introduction	1

## PART I: HISTORICAL OVERVIEW

Editors' Comments on Papers 1 through 6	8
1 WALLIN, I. E.: The Mitochondria Problem <i>Am. Nat.</i> 57:255-261 (1923)	10
2 GOKSØYR, J.: Evolution of Eucaryotic Cells <i>Nature</i> 214:1161 (1967)	17
3 SAGAN, L.: On the Origin of Mitosing Cells <i>J. Theor. Biol.</i> 14:225-274 (1967)	18
4 SCHWARTZ, R. M., and M. O. DAYHOFF: Origins of Prokaryotes, Eukaryotes, Mitochondria, and Chloroplasts <i>Science</i> 199:395-403 (1978)	68
5 RAVEN, P. H.: A Multiple Origin for Plastids and Mitochondria <i>Science</i> 169:641-646 (1970)	77
6 DOOLITTLE, W. F.: Revolutionary Concepts in Evolutionary Cell Biology <i>Trends Biochem. Sci.</i> , June, pp. 146-149 (1980)	83

## PART II: MECHANISMS NECESSARY FOR SERIAL SYMBIOSIS

Editors' Comments on Papers 7 through 12	88
7 CUTTING, J. A., and H. M. SCHULMAN: The Biogenesis of Leghemoglobin. The Determinant in the Rhizobium- Legume Symbiosis for Leghemoglobin Specificity <i>Biochim. Biophys. Acta</i> 229:58-62 (1971)	90
8 LORCH, I. J., and K. W. JEON: Rapid Induction of Cellular Strain Specificity by Newly Acquired Cytoplasmic Components in Amoebas <i>Science</i> 211:949-951 (1981)	95
9 SMITH, D. C.: From Extracellular to Intracellular: The Establishment of a Symbiosis <i>R. Soc. London Proc., ser. B</i> , 204:115-130 (1979)	97

<b>10</b>	<b>SONEA, S.:</b> Bacterial Plasmids Instrumental in the Origin of Eukaryotes? <i>Rev. Can. Biol.</i> <b>31</b> :61-63 (1972)	<b>113</b>
<b>11</b>	<b>MARTIN, J. P., JR., and I. FRIDOVICH:</b> Evidence for a Natural Gene Transfer from the Ponyfish to Its Bioluminescent Bacterial Symbiont <i>Photobacter leiognathi</i> . The Close Relationship Between Bacteriocuprein and the Copper-Zinc Superoxide Dismutase of Teleost Fishes <i>J. Biol. Chem.</i> <b>256</b> :6080, 6082-6089 (1981)	<b>116</b>
<b>12</b>	<b>FAIRFIELD, A. S., S. R. MESHNICK, and J. W. EATON:</b> Malaria Parasites Adopt Host Cell Superoxide Dismutase <i>Science</i> <b>221</b> :764-766 (1983)	<b>125</b>

### PART III: ORIGIN OF MITOCHONDRIA

<b>Editors' Comments on Papers 13 through 18</b>		<b>130</b>
<b>13</b>	<b>THOMAS, D. Y., and D. WILKIE:</b> Recombination of Mitochondrial Drug-Resistance Factors in <i>Saccharomyces Cerevisiae</i> <i>Biochem. Biophys. Res. Commun.</i> <b>30</b> :368-372 (1968)	<b>132</b>
<b>14</b>	<b>BARATH, Z., and H. KÜNTZEL:</b> Cooperation of Mitochondrial and Nuclear Genes Specifying the Mitochondrial Genetic Apparatus in <i>Neurospora crassa</i> <i>Natl. Acad. Sci. (USA) Proc.</i> <b>69</b> :1371-1374 (1972)	<b>137</b>
<b>15</b>	<b>JOHN, P., and F. R. WHATLEY:</b> <i>Paracoccus denitrificans</i> and the Evolutionary Origin of the Mitochondrion <i>Nature</i> <b>254</b> :495-498 (1975)	<b>141</b>
<b>16</b>	<b>GRAY, M. W., T. Y. HUH, M. N. SCHNARE, D. F. SPENCER, and D. FALCONET:</b> Organization and Evolution of Ribosomal RNA Genes in Wheat Mitochondria <i>Structure and Function of Plant Genomes</i> , O. Ciferri and L. Dure III, eds., Plenum Publishing Corporation, New York, 1983, pp. 373-380	<b>145</b>
<b>17</b>	<b>VAN DEN BOOGAART, P., J. SAMALLO, and E. AGSTERIBBE:</b> Similar Genes for a Mitochondrial ATPase Subunit in the Nuclear and Mitochondrial Genomes of <i>Neurospora crassa</i> <i>Nature</i> <b>298</b> :187-189 (1982)	<b>153</b>
<b>18</b>	<b>OBAR, R., and J. GREEN:</b> Molecular Archaeology of the Mitochondrial Genome <i>J. Mol. Evol.</i> (1985)	<b>156</b>

### PART IV: ORIGIN OF PLASTIDS

<b>Editors' Comments on Papers 19 through 24</b>		<b>162</b>
<b>19</b>	<b>LEWIN, R. A., and N. W. WITHERS:</b> Extraordinary Pigment Composition of a Prokaryotic Alga <i>Nature</i> <b>256</b> :735-737 (1975)	<b>164</b>

- 20** **BOYNTON, J. E., N. W. GILLHAM, E. H. HARRIS, C. L. TINGLE, K. VAN WINKLE-SWIFT, and G. M. W. ADAMS:** Transmission, Segregation and Recombination of Chloroplast Genes in *Chlamydomonas* **167**  
*Genetics and Biogenesis of Chloroplasts and Mitochondria*, Th. Bücher, W. Neupert, W. Sebald, and S. Werner, eds., Elsevier/North-Holland Biomedical Press, Amsterdam, The Netherlands, 1976, pp. 313-322
- 21** **GIBBS, S. P.:** The Chloroplasts of *Euglena* May Have Evolved from Symbiotic Green Algae **177**  
*Can. J. Bot.* **56**:2883-2889 (1978)
- 22** **BONEN, L., and W. F. DOOLITTLE:** Ribosomal RNA Homologies and the Evolution of the Filamentous Blue-Green Bacteria **184**  
*J. Mol. Evol.* **10**:283-291 (1978)
- 23** **STERN, D. B., and J. D. PALMER:** Extensive and Widespread Homologies Between Mitochondrial DNA and Chloroplast DNA in Plants **193**  
*Natl. Acad. Sci. (USA) Proc.* **81**:1946-1950 (1984)
- 24** **SCHIFF, J. A.:** Origin and Evolution of the Plastid and Its Function **198**  
*N.Y. Acad. Sci. Ann.* **361**:166, 167, 172-174, 186, 187-188 (1981)

## PART V: ORIGIN OF NUCLEOCYTOPLASM

- Editors' Comments on Papers 25 and 26** **206**
- 25** **STARR, M. P.:** *Bdellovibrio* as Symbiont: The Associations of Bdellovibrios with other Bacteria Interpreted in Terms of a Generalized Scheme for Classifying Organismic Associations **208**  
*Symbiosis*, Symposia of the Society for Experimental Biology, No. 29, Society for Experimental Biology, London, England, 1975, pp. 95-104, 121-124
- 26** **MARGULIS, L.:** Mitochondria: Acquisition by Whom? **223**  
*Symbiosis in Cell Evolution*, W. H. Freeman and Company Publishers, San Francisco, 1981, pp. 205-213

## PART VI: ORIGIN OF MOTILITY ORGANELLES

- Editors' Comments on Papers 27 through 32** **236**
- 27** **MAY, H. G., and K. GOODNER:** Cilia as Pseudo-Spirochaetes **240**  
*Am. Microsc. Soc. Trans.* **45**:302-305 (1926)
- 28** **BEISSON, J., and T. M. SONNEBORN:** Cytoplasmic Inheritance of the Organization of the Cell Cortex in *Paramecium Aurelia* **244**  
*Natl. Acad. Sci. (USA) Proc.* **53**:275-282 (1965)
- 29** **HEIDEMANN, S. R., G. SANDER, and M. W. KIRSCHNER:** Evidence for a Functional Role of RNA in Centrioles **252**  
*Cell* **10**:337-350 (1977)

## Contents

<b>30</b>	<b>MARGULIS, L., and D. CHASE:</b> Microtubules in Prokaryotes <i>Science</i> <b>200</b> :1118-1124 (1978)	<b>266</b>
<b>31</b>	<b>GRIMES, G. W., M. E. MCKENNA, C. M. GOLDSMITH-SPOEGLER, and E. A. KNAUPP:</b> Patterning and Assembly of Ciliature are Independent Processes in Hypotrich Ciliates <i>Science</i> <b>209</b> :281-283 (1980)	<b>273</b>
<b>32</b>	<b>HUANG, B., Z. RAMANIS, S. K. DUTCHER, and D. J. L. LUCK:</b> Uniflagellar Mutants of <i>Chlamydomonas</i> : Evidence for the Role of Basal Bodies in Transmission of Positional Information <i>Cell</i> <b>29</b> :745-753 (1982)	<b>276</b>
<b>PART VII: ORIGIN OF MITOSIS, MEIOSIS, AND SEX</b>		
<b>Editors' Comments on Papers 33 and 34</b>		<b>286</b>
<b>33</b>	<b>CLEVELAND, L.:</b> Sex Produced in the Protozoa of <i>Cryptocercus</i> by Molting <i>Science</i> <b>105</b> :16-17 (1947)	<b>288</b>
<b>34</b>	<b>MARGULIS, L., AND D. SAGAN:</b> Evolutionary Origins of Sex <i>Oxford Surveys in Evolutionary Biology</i> , R. Dawkins and M. Ridley, eds., Oxford University Press, Oxford, England, 1985, pp. 30-47	<b>290</b>
<b>PART VIII: CLASSIFICATION OF EUKARYOTES</b>		
<b>Editors' Comments on Papers 35A through 35E</b>		<b>310</b>
<b>35A</b>	<b>MARGULIS, L., and K. SCHWARTZ:</b> Monera <i>Five Kingdoms</i> , W. H. Freeman and Company Publishers, San Francisco, 1982, pp. 24-29	<b>311</b>
<b>35B</b>	<b>MARGULIS, L., and K. SCHWARTZ:</b> Protoctista <i>Five Kingdoms</i> , W. H. Freeman and Company Publishers, San Francisco, 1982, pp. 68-71	<b>317</b>
<b>35C</b>	<b>MARGULIS, L., and K. SCHWARTZ:</b> Fungi <i>Five Kingdoms</i> , W. H. Freeman and Company Publishers, San Francisco, 1982, pp. 144-147	<b>321</b>
<b>35D</b>	<b>MARGULIS, L., and K. SCHWARTZ:</b> Animalia <i>Five Kingdoms</i> , W. H. Freeman and Company Publishers, San Francisco, 1982, pp. 160-165	<b>325</b>
<b>35E</b>	<b>MARGULIS, L., and K. SCHWARTZ:</b> Plantae <i>Five Kingdoms</i> , W. H. Freeman and Company Publishers, San Francisco, 1982, pp. 248-251	<b>331</b>
<b>Author Citation Index</b>		<b>335</b>
<b>Subject Index</b>		<b>343</b>
<b>About the Editors</b>		<b>347</b>

# INTRODUCTION

The category *eukaryotic organisms* includes animals, plants, fungi, and protocists. 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 protocists) 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: protocists, fungi, animals, and plants (Papers 35A, B, C, D, and E). The protocists 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 protocists. Examples of some photosynthetic protocists

## Introduction

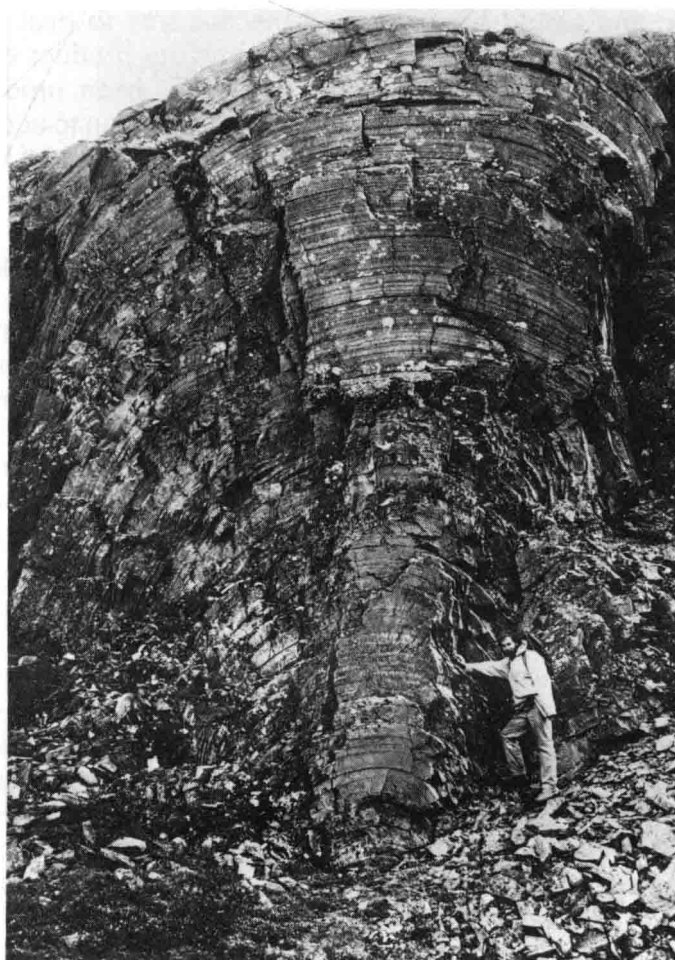
are *Chlamydomonas*, *Euglena*, *Volvox*, diatoms, dinomastigotes, red algae, and brown algae. These are distinct from the heterotrophic protists, organisms that either ingest or absorb their food such as amoebae, sporozoans (a parasitic group), mastigotes, and myxomycetes (slime molds).

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