S. Osawa T. Honjo (Eds.)

# Evolution of Life

## Fossils, Molecules, and Culture

With 125 Illustrations, 2 in Color

Springer-Verlag
Tokyo Berlin Heidelberg
New York London Paris
Hong Kong Barcelona

Syozo Osawa, ph.d.
Professor, Department of Biology, Nagoya University, Chikusa-ku, Nagoya, 464 Japan

Tasuku Honjo, m.d., ph.d.
Professor, Department of Medical Chemistry, Kyoto University, Yoshidakonoe-cho, Sakyo-ku, Kyoto, 606 Japan

*On the cover*: Genetic uniqueness in the genome of each species, *see* p. 436.

ISBN-13:978-4-431-68304-9 e-ISBN-13:978-4-431-68302-5
DOI: 10.1007/978-4-431-68302-5

Library of Congress Cataloging-in-Publication Data
Evolution of life : fossils, molecules, and culture / S. Osawa, T. Honjo, (eds.) p. cm. Includes bibliographical references and index. ISBN-13:978-4-431-68304-9 1.Life—Origin.2.Molecular evolution. 3. Human evolution. I. Osawa, Syozo, 1928– . II. Honjo, T. (Tasuku). QH325.E964 1991. 575—dc20 90-24925



Typesetting: Asco Trade Typesetting Ltd., Hong Kong

# Preface

The origin of life is a most fascinating question, not only for biologists, but for all human beings, since everyone wishes to know from where he has come. Our investigations into the origin of life had been very limited until the recent development of molecular genetics. Examination and comparison of fossils has been the most important approach in understanding the evolution of life. However, quantitative comparison of amino acid sequences of particular proteins among various species has provided a powerful tool for evolution theory. Important new insights, such as the neutral theory of molecular evolution, have been obtained mainly by this approach. Recent advances in molecular biology and genetics have made a profound impact on our understanding of the evolution of life. We are now beginning to understand how our genetic information was created, how it evolved, and how the complex organization and systems of living organisms including humans evolved from simple basic units. Evidently, such developments could not have been achieved without accumulating evidence from other evolutionary sciences including systematic biology, population genetics, paleontology, and anthropology.

The most important character of life is self-replication, the essential part of which is replication of genetic information. Since nucleic acid is the carrier of genetic information, it is reasonable for molecular geneticists to imagine that the creation of nucleic acid is the first step towards the creation of life. However, replication of nucleic acid entirely depends on protein catalysts, or enzymes. It is, therefore, reasonable for biochemists to consider that creation of polypeptides should be the first step in the evolution of life. Until recently this was a kind of chicken-and-egg argument, and we were in a dilemma as to finding an answer. But a discovery by Tom Cech and his colleagues that a specific structure of ribonucleic acid (RNA) can catalyze RNA synthesis, although much slower than protein enzymes, helped us to escape from this dilemma, and convinced us that nucleic acid was created in a self-catalytic manner. This form of RNA, called ribozyme, can elongate RNA by adding ribonucleotides, and can splice RNA by cutting and joining phosphodiester bonds. In other words, RNA can replicate itself.

Discovery of the ribozyme led us to reevaluate the well-known fact that protein synthesis depends on RNA. Protein synthesis is directed by the nucleotide se-

quence of mRNA. Amino acids are aligned according to the genetic code of mRNA by using tRNA adaptors and are polymerized by peptide bond formation on the ribosome. Ribosomal RNA plays a central role in peptide bond formation. It is, therefore, likely that RNA evolved first as a catalyst as well as an information-carrier, and then synthesized the protein according to its information. Since proteins can catalyze a variety of reactions more efficiently, once they were produced the information of RNA became more important than its catalytic activity. We may imagine that the initial life on Earth might be in an "RNA world."/As RNA is chemically unstable, a stable form of nucleic acid, DNA, has taken over the dominant position of RNA as the genetic material of living organisms. Current forms of life must have derived from a common ancestor because the genetic code used by all the present-day organisms is derived from the single "universal code."

Molecular genetic studies on genes involved in the immune system revealed an important strategy of life to create complex and diverse functions in living organisms. A large family of genes, called the immunoglobulin gene superfamily, seems to have evolved from a common ancestor which consisted of a single exon encoding a 100-residue domain with an internal disulfide bond. Immunoglobulins are composed of the light and heavy chains, each consisting of multiple domains. All other members of this gene superfamily have various numbers of immunoglobulin-like domains in addition to other functional units. Comparison of these genes indicates that complex proteins have evolved by repeated duplication of the simplest unit or domain exon. Duplicated exons must have diverged by mutations and must have been selected for functional diversification. Immunoglobulin-like domains are found in growth factor receptors such as those for platelet-derived growth factor and macrophage colony stimulating factor. In these cases, the immunoglobulin domain exon was shuffled into other genes. These studies clearly indicate that complex genes have evolved by duplication and combination of simple elements like exons.

Diversification by combinatorial association of different proteins was used to create complex functional units like receptors and channels on the cell membrane. Immunoglobulins per se are composed of both light and heavy chains. Combination of different light and heavy chains can produce immunoglobulins with different antigen binding specificities. In a similar fashion, proteins which control gene expression can form unique regulatory units by specific combinatorial association. Expression of a particular gene is regulated by combinatorial binding of multiple proteins to the regulatory region of the gene. A single regulatory protein, in turn, can be involved in regulation of multiple genes.

In some cases organisms recruit a functionally unrelated gene for another purpose. The gene for δ-crystallin, a dominant structural protein in lenses of birds and reptiles, is highly homologous to the gene for argininosuccinate lyase that is an essential enzyme for urea synthesis.

The Darwinian view of evolution, which depends on genetic drift and selection of organisms, is now generally accepted and supported by molecular genetic studies on numerous genes. Moreover, the Darwinian principle operates at the somatic level. For example, the genetic variation required for antibody diversity is generated by somatic recombination and somatic hypermutation in the antibody

genes of B lymphocytes. Each B cell thus expresses a different antibody. Among diverse B lymphocytes, those which express antigen-recognizing antibodies are selected by specific proliferation. The processes of genetic drift and cellular selection are able to create enormous diversity, but the price is paid by the huge waste of B lymphocytes which failed in the production of useful antibodies by inaccurate recombination or aberrant mutations.

Such developments in this field set the stage for organizing an international symposium on evolution of life to facilitate interaction between paleontologists, molecular biologists, population geneticists, and anthropologists. This volume comprises the proceedings of the International Symposium of "Evolution of Life" which was held in Kyoto, Japan on March 26–28, 1990 and sponsored by the International Institute for Advanced Studies. This symposium aimed to discuss the motifs of organismic evolution from the viewpoints of biogeo-interactions and diversification of the genetic systems. Based on these fundamental understandings, the last session was devoted to the human evolution that included phylogeny of man as well as evolution of human culture. We believe that such comprehensive discussion gave us the synthesized view of evolution of life, that is undoubtedly one of the most important problems not only for science but also for human culture in general. The symposium took place in a pleasant, friendly atmosphere, with lively discussions and constructive criticism.

The organizing committee which consists of Drs. Sydney Brenner, Takashi Hamada, Takashi Miyata, Keiichi Omoto, and Alan M. Weiner in addition to the editors of this volume, wishes to express its deep appreciation to all participants of the symposium. We are also grateful to Ms. Akiko Morimoto for her excellent and devoted assistance throughout the symposium.

Syozo Osawa
Tasuku Honjo

# Contents

Preface ..... V
Contributors ..... XIII

1 Bio-Geo Interacting Systems

1.1 Fossils and Evolution ..... 3
P.D. GINGERICH

1.2 Biological Extinction in Terms of Overadaptation ..... 21
T. HAMADA

1.3 Revolutions and Colonizations in the History of Life ..... 27
B. HALSTEAD

2 Evolution of Biological Information

2.1 The Genomic Tag Model for the Origin of Protein Synthesis: Further Evidence from the Molecular Fossil Record ..... 51
A.M. WEINER and N. MAIZELS

2.2 Neutral Evolution ..... 67
M. KIMURA

2.3 Recent Evidence for Evolution of the Genetic Code ..... 79
T.H. JUKES and S. OSAWA

2.4 The Grammatical Rule of DNA Language: Messages in Palindromic Verses ..... 97
S. OHNO

2.5 Module Organization in Proteins and Exon Shuffling ..... 109
M. Gō

2.6 Molecular Evolution and the Immunoglobulin Gene Superfamily 123
L. Hood and T. Hunkapiller

2.7 Evolution of the Multigene Family: A Case of Dynamically Evolving Genes at Major Histocompatibility Complex ..... 145
T. Ohta

2.8 Evolution of a Urea Cycle Enzyme to δ-Crystallin ..... 161
M. Mori, T. Matsubasa, Y. Amaya, and M. Takiguchi

2.9 Evolution of Repetitive Sequences ..... 175
N. Okada, M. Aono, H. Endoh, Y. Kido, R. Koishi, K. Matsumoto, M. Matsuo, S. Murata, S. Nagahashi, and T. Yamaki

2.10 Evolution of Organellar Genomes ..... 187
K. Ohyama, Y. Ogura, K. Oda, K. Yamato, E. Ohta, Y. Nakamura, M. Takemura, N. Nosato, K. Akashi, T. Kanegae, and Y. Yamada

3 Diversification of Organisms

3.1 Mechanisms of Speciation: A Review ..... 201
W.B. Provine

3.2 Comparing Life Histories ..... 215
P.H. Harvey

3.3 The Seething Genetics of Health and the Evolution of Sex ..... 229
W.D. Hamilton

3.4 On the Evolution of Reproductive Isolation and the Origin of Species ..... 253
F.J. Ayala

3.5 The Evolution of Cells ..... 271
T. Cavalier-Smith

3.6 Symbiosis in Evolution: Origins of Cell Motility ..... 305
L. Margulis

3.7 Archaebacteria Vs Metabacteria: Phylogenetic Tree of Organisms Indicated by Comparison of 5S Ribosomal RNA Sequences ..... 325
H. Hori, Y. Satow, I. Inoue, and M. Chihara

3.8 Evolution of Archaebacteria: Phylogenetic Relationships Among Archaebacteria, Eubacteria, and Eukaryotes ..... 337
T. Miyata, N. Iwabe, K. Kuma, Y. Kawanishi, M. Hasegawa, H. Kishino, Y. Mukohata, K. Ihara, and S. Osawa

3.9 Early Biochemical Evolution: Speculations on the Biochemistry of Primitive Life ..... 353
T. Oshima

4 Human Evolution

4.1 Man, Culture, and Environment ..... 363
P.V. Tobias

4.2 The Origin of the Genus *Homo* ..... 379
A. Walker

4.3 Sequence Evolution of Mitochondrial DNA in Humans and Chimpanzees: Control Region and a Protein-Coding Region ..... 391
T.D. Kocher and A.C. Wilson

4.4 Evolutionary Relationships of Human Populations at the Molecular Level ..... 415
M. Nei and T. Ota

4.5 Human Genome and Human Evolution ..... 429
S. Ueda

4.6 Some Theoretical Aspects of the Origin of Cultural Transmission 439
K. Aoki

5 Summary and Concluding Remarks

5 Summary and Concluding Remarks ..... 453
S. Brenner

Index ..... 457

# Contributors


Akashi, K. 187
Amaya, Y. 161
Aoki, K. 439
Aono, M. 175
Ayala, F.J. 253
Brenner, S. 453
Cavalier-Smith, T. 271
Chihara, M. 325
Endoh, H. 175
Gingerich, P.D. 3
Gō, M. 109
Halstead, B. 27
Hamada, T. 21
Hamilton, W.D. 229
Harvey, P.H. 215
Hasegawa, M. 337
Hood, L. 123
Hori, H. 325
Hunkapiller, T. 123
Ihara, K. 337
Inoue, I. 325
Iwabe, N. 337
Jukes, T.H. 79
Kanegae, T. 187
Kawanishi, Y. 337
Kido, Y. 175
Kimura, M. 67
Kishino, H. 337
Kocher, T.D. 391
Koishi, R. 175
Kuma, K. 337
Maizels, N. 51
Margulis, L. 305
Matsubasa, T. 161
Matsumoto, K. 175
Matsuo, M. 175
Miyata, T. 337
Mori, M. 161
Mukohata, Y. 337
Murata, S. 175
Nagahashi, S. 175
Nakamura, Y. 187
Nei, M. 415
Nosato, N. 187
Oda, K. 187
Ogura, Y. 187
Ohno, S. 97
Ohta, E. 187
Ohta, T. 145
Ohyama, K. 187
Okada, N. 175
Osawa, S. 79, 337
Oshima, T. 353
Ota, T. 415
Provine, W.B. 201
Satow, Y. 325
Takemura, M. 187
Takiguchi, M. 161
Tobias, P.V. 363
Ueda, S. 429
Walker, A. 379
Weiner, A.M. 51
Wilson, A.C. 391
Yamada, Y. 187
Yamaki, T. 175
Yamato, K. 187


For contributors' addresses, see chapter opening pages.