# ORGANISMIC EVOLUTION

Verne Grant

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FOREWORD BY

George Gaylord Simpson

W. H. FREEMAN AND COMPANY
SAN FRANCISCO

**Library of Congress Cataloging in Publication Data**
Grant, Verne.
Organismic evolution.

Bibliography: p.
Includes indexes.
1. Evolution. I. Title.
QH366.2.G68 575 76–54175
ISBN 0–7167–0372–6



Printed in the United States of America

2 3 4 5 6 7 8 9

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# Foreword

The present book gives an overall view of the most important things in our current knowledge of organic evolution. This foreword seeks to place the book within a comparative framework. To do so in full detail would require another book or several of them, but it can be done in an abbreviated way by focusing attention on some of the most significant features of studies of evolution in three periods: the first about a hundred years ago, the second now some fifty years past, and the third the present. For each period the focus can be further sharpened and the account further abbreviated by special attention to a general book on evolution characteristic for its time: first, Darwin's masterpiece, which, more than any other one work, started it all; second, a work by Lull that was the most popular general textbook on the subject fifty years ago; and third, the book now in your hands.

A hundred years ago Darwin was still alive, and was to be actively at work almost to the day of his death at the age of 73 in 1882. His master work, the long title of which is usually abbreviated to *The Origin of Species* or simply *The Origin,* had first appeared in 1859, and the last edition revised by Darwin (the sixth edition) had been published in 1872. In the 1870s the reality of evolution had been accepted by almost all competent and well-informed biologists. The two most notable exceptions were Louis Agassiz, but he died in 1873 and his followers were already evolutionists, and Richard Owen, who lived to the age of 88 in 1892 and whose late works hinted obscurely that he objected not so much to acceptance of evolution as to Darwin's particular ideas about its course and causes.

Thus a century ago anyone who studied biology under a qualified teacher was already introduced to evolution as a general element of that subject. As

far as I know there were no courses explicitly devoted to evolution as a distinct topic, and although there were many publications on one aspect or another, there was no truly general text other than *The Origin* itself. Anyone who studied *The Origin* would learn first of all that evolution is the only rational explanation of a multitude of observed facts. Next he would learn that the Darwinian theory, properly speaking, ascribed evolutionary change primarily to natural selection—inadequately summed up in the expression "survival of the fittest" —and in lesser degree to inherited effects of the use and disuse of organs, to the effects of the environment, and to "variations which seem to us in our ignorance to arise spontaneously." Most later discussants combined Darwin's second and third factors as inheritance of acquired characters. His fourth factor entailed what we would call mutations, but for the most part mutations with larger and more obvious effects than are usual. The student would also observe that Darwin was quite positive on the role of natural selection and adduced strong evidence for it, but was less emphatic and had weaker evidence for his other three factors.

During the next fifty years, which bring us into the 1920s, many more factual and relevant observations were made. All indicated evolution as the only rational and judicious interpretation of the history of organisms, and opposition to this view was no longer possible on any scientific grounds, although it does continue even now in some nonscientific or antiscientific circles, as noted in the last part of the present book. Nevertheless scientific unanimity on that general point had not produced a definite consensus as to the specific factors or causes of evolution.

In the 1920s college courses in organic evolution were being given. That by Richard Swann Lull was among the most popular lecture courses at Yale. His textbook *Organic Evolution,* published in 1917 and in revised form in 1929, was probably the most widely used of the several then available, and may serve as indicative of the state of knowledge and of pedagogy in this subject fifty years ago. Only a small part of the book, less than 15 percent of the text, was devoted to the theories, principles, or causes ("mechanisms") of evolution. Here there are two striking differences between Lull's and almost any now current treatment, such as that of the present book: the multiplicity of theories given serious attention—some now considered worthy of no more than passing historical mention, at most—and the minimal involvement of genetics.

Lull's discussion of natural selection was brief and anecdotal, with the conclusion that ". . . whereas natural selection may be conceded to be a factor of importance, it is apparently not the only factor nor indeed the only important factor in the evolution of organic life." The inheritance of acquired characters was treated at almost equal length. Lull's verdict on that was that it was "unproved," but he added that "one can not help feeling" that in some unknown way the inheritance of acquired characters may occur. In the present book

such inheritance, in the sense hitherto given it, is quite properly considered not even worthy of discussion.

Lull maintained Darwin's distinction between natural and sexual selection, with some emphasis on the latter. Sexual selection is now considered a real but somewhat minor special case of natural selection. Lull also singled out for consideration rectigradation and kinetogenesis. Both the terms and the concepts have been discarded and are now forgotten except by historians. Orthogenesis, lengthily and rather favorably discussed by Lull, is still named and briefly discussed but rejected in the present book.

The most important development bearing on evolutionary biology in the interval between a hundred years and fifty years ago was the rise of what is often, but somewhat misleadingly, called Mendelian genetics. Lull gave only an elementary and brief account of "Mendel's law" and concluded in his first edition (1917) that it "does not apply universally to all cases of inheritance." In the revision (1929) the account was even shorter but the conclusion then was that "Mendel's laws" (now in the plural) do "apply universally to all cases of inheritance." No clear connection was made between "Mendel's laws," or the then rapidly advancing science of genetics, and the explanation of evolution. A supposed connection then made by some geneticists was anti-Darwinian in that the control of evolution was presumed to be by mutations, especially those that were saltatory in their phenetic effects, whereas natural selection was given only a negative role, if any.

Here is the most marked difference between a textbook of the 1920s and those of today, and this reflects a sort of subrevolution in evolutionary biology supplementing and extending the Darwinian revolution of a century and more ago. In the present book the approach to basic evolutionary theory is primarily genetical. Natural selection, although it involves a broader interplay of factors, is consonant with the genetical approach and can be discussed in terms of causes and effects in genetic systems, which are now considered far more broadly than as simple Mendelism.

Grant has noted in this book that the new movement in evolutionary theory started at the end of the 1920s and in the 1930s in the work of a number of biologists, but most prominently, at first, in that of R. A. Fisher, an English statistician, of J. B. S. Haldane, an English biologist who was successively a professor of physiology, genetics, and biochemistry, and of Sewall Wright, an American geneticist. This new approach to evolutionary theory expanded in the 1940s as contributions came in from every branch of organismal biology, including most noticeably at that time population genetics, systematics, paleontology, and botany. The modified and extended evolutionary theory, or rather body of theory, thus became a synthesis from many sources and so is commonly called the synthetic theory, as it is in this book.

As in any science, or for that matter any subject at all, there are differences of opinion about parts of this body of theory, but its general approach and broader conclusions are now adopted by a great majority of organismal biologists. The synthesis also continues as new discoveries are made and new relationships studied. Grant suggests (in Chapter 17) that if the genetic phenomenon of induction proves to have a significant role in evolution this would go beyond the synthetic theory. I may add the suggestion that it would not remain outside the scope of that theory but would enlarge that scope.

There is a rather widespread human tendency, to which human scientists are also liable, to rediscover, enlarge, and embellish old ideas that seem new when expressed in a later vocabulary. A major part of Lull's text was devoted to adaptive radiation, a fruitful evolutionary concept that Lull ascribed to Henry Fairfield Osborn, although he did mention in passing and incorrectly that Lamarck had had the same idea under a different term, and correctly that Darwin had. In fact it was stated with perfect clarity and for the first time by Darwin, who noted in his autobiography the exact moment when that insight occurred to him. I bring this up here just to emphasize Grant's skill in this book at avoiding the confusion of new terms with new concepts and ideas. It is necessary to use the vocabulary now usual among evolutionists. For example, the term "character displacement" is current and is used as such, although this is another instance of new words and new examples for a phenomenon clearly noted by Darwin. In other instances, as the reader will find for himself, Grant quietly rejects or quite demolishes terminological fallacies.

Here the synthetic theory is not merely expounded. This book is by an active research contributor to that body of theory. The author does not hesitate to express his own opinions and to put forward new ideas. The book has personality.

Finally, it may surprise some readers of this extensive and intensive treatment that some aspects of current evolutionary studies are barely mentioned, or even omitted. To support that statement, and for no other purpose, a simple example should be given: there is no discussion here of mathematical models of faunal changes on islands and in other isolated communities. The point is that no single book can cover all of a subject as vast and complicated as organismal evolution. Darwin considered the first edition of *The Origin,* which ran to 490 text pages, a mere abstract of the book on evolution that he had prepared to write. A single book on this topic has to be highly selective. Darwin selected well, and so has Grant.

*Tucson, Arizona* *George Gaylord Simpson*
*December 31, 1976*

# Preface

This book deals with the processes that bring about evolutionary changes in organisms and with the principal factors that affect these processes. The title, *Organismic Evolution,* is meant to be taken literally, since the emphasis is on the evolution of organisms, particularly animals and plants, rather than on molecular evolution or primitive organic evolution or mathematical models of evolution.

Furthermore, the emphasis in this book is on principles rather than details, on fundamentals rather than current topics, and on well-chosen examples rather than catalogs of facts.

*Organismic Evolution* has grown out of a one-semester, senior-level course that I have been teaching since 1952. The classes typically contain juniors, seniors, and graduate students, and occasionally a professional biologist as a visitor. This is the range of readers I have had in mind in writing *Organismic Evolution.* In short, *Organismic Evolution* was designed and written as an advanced text.

Let me hasten to enter a caveat. Students do not particularly like textbooks that read and look like textbooks, but they do like good books, and I share the same predilection. My primary goal, then, has been to write a good general book on evolution, of potential interest to a wide range of readers; and, within this broader objective, the secondary goal was to shape the book to fit the specific needs of students.

The subject matter is organized into groups of chapters corresponding to three broad levels of evolutionary change: microevolution (Parts II and III), speciation (Part V), and macroevolution (Part VI). These parts can be read

separately. Since macroevolution is underemphasized in many recent books on evolution, a special effort was made to give an adequate introduction to that subject here. Human evolution is dealt with in Part VII. The evolution theory has had in the past, and continues to have, implications for human thought and culture; these social aspects of evolution are considered briefly in Part VIII.

The chapters are short. Only by keeping the individual chapters short was I able to cover a very wide range of topics within the limits of one medium-sized book. The first corollary is that the chapters provide introductions to, not exhaustive treatises on, their respective topics. The second corollary is that a need will often exist for supplementary reading on a specific topic introduced in the text. I have attempted to meet this need in two ways: by providing lists of selected collateral readings at the end of most chapters, and by giving bibliographical citations in the body of the text.

The technical terminology of evolutionary biology is now quite extensive and contains a considerable amount of redundancy. I have grouped the technical terms into two categories for the purpose of this book. The first category consists of terms that are essential for an understanding of basic concepts. These terms are defined and illustrated in the text. In the second category I place those terms that I regard as unnecessary, but that other workers evidently do not, since the terms in question are being used currently in one school or another; consequently students will encounter them in readings, seminars, and lectures. These second-category terms are mentioned parenthetically in the text, usually as synonyms or near-synonyms of the primary terms.

The reader will find an overall list of technical terms—both the essential and the secondary ones—at the end of the book. This list is not a glossary, but rather a thesaurus or index. It gives the page numbers where the terms are either defined in context or placed in synonymy.

*March 1976*

*Verne Grant*
UNIVERSITY OF TEXAS

# Acknowledgments

I am very greatly indebted to Dr. George Gaylord Simpson of Tucson, Arizona, for critical reading of Chapters 26, 28, 29, 30, 31, 32, and 37. The criticisms, suggestions, and information provided by Dr. Simpson led to numerous corrections and improvements in this group of chapters. I also had the benefit of Dr. Simpson's comments concerning the chapter outline.

Dr. Robert Flake of the University of Texas critically read Chapters 6 and 14, making some helpful suggestions.

Dr. Theodore Downs of the Los Angeles County Museum of Natural History provided information from his published and unpublished studies of fossil horses; this information is incorporated in Chapter 26.

The entire manuscript was read by Mrs. Karen A. Grant with a critical eye for ambiguities and prolixities. Mrs. Grant also did a great deal of the proofreading.

My secretary, Ms. Helen Barler, typed the manuscript with care and accuracy, hunted up special items in the library, and skillfully handled the secretarial side of book production.

Mr. John Painter of W. H. Freeman and Company took a serious interest in the book from the start, and has been helpful in every way possible throughout the course of production. Mr. Fred Raab, also of W. H. Freeman and Company, edited the manuscript with understanding and skill.

Let me take this opportunity to express my sincere gratitude to all of these individuals.

Several book publishers kindly granted permission to use previously published illustrations in this book. The credit notes are given in the captions. The cooperation of the various publishing firms is gratefully acknowledged.

*V.G.*

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PART

# I

# INTRODUCTION

CHAPTER

# 1

# The Problem

## Introduction

The world of living organisms exhibits several general features that have always aroused feelings of wonder in mankind. The first of these general phenomena is the great structural complexity of organisms. The second feature is the apparently purposive or adaptive nature of many of the characteristics of these organisms. The third striking general feature is the existence of a tremendous diversity of forms of life. The problem of biological complexity and adaptation is thus compounded by the fact that there are many diverse kinds of organisms with these properties in the world.

The questions evoked by these phenomena are obvious: How have complex organisms come into being? What forces have molded their adaptive characteristics? How has organic diversity originated and how is it maintained? To which can be added the special but relevant questions: What is the place of mankind in the organic world, and what is the ancestry of man?

In all ages man has sought intellectually satisfying answers to these questions. In pre-scientific societies the explanations have taken the form of myths, some of which have been carried over into the world religions. The scientific explanations are embodied in the theory of evolution. Before entering into our discussion of evolutionary theory, however, let us outline the problems that this theory has to explain in somewhat greater detail.