Essential Readings in Evolutionary Biology

Edited by

Francisco J. Ayala
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JOHNS HOPKINS UNIVERSITY PRESS
Baltimore

Printed in the United States of America on acid-free paper
9 8 7 6 5 4 3 2 1

Johns Hopkins University Press
2715 North Charles Street
Baltimore, Maryland 21218-4363
www.press.jhu.edu

Library of Congress Cataloging-in-Publication Data

Essential readings in evolutionary biology / edited by Francisco J. Ayala and John C. Avise.
pages cm
Includes index.
ISBN-13: 978-1-4214-1305-1 (hardcover : alk. paper)
ISBN-10: 1-4214-1305-1 (hardcover : alk. paper) 1. Evolution (Biology)—History. 2. Biology—History. I. Ayala, Francisco José, 1934– editor of compilation. II. Avise, John C., editor of compilation.
QH361.E87 2014
576.8—dc23 2013027718

A catalog record for this book is available from the British Library.

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Johns Hopkins University Press uses environmentally friendly book materials, including recycled text paper that is composed of at least 30 percent post-consumer waste, whenever possible.

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Introduction

A famous phrase in the biological sciences conveys a pithy truth: "Nothing in biology makes sense except in the light of evolution." When the evolutionary geneticist Theodosius Dobzhansky penned those words in 1973 (reproduced in this volume), he was wrestling with a striking contradiction: an overwhelming majority of scientists fully acknowledge evolution, whereas a thorough acceptance of evolution by the general populace remains notoriously low in many countries (including the United States). This disconnect has several causes, not the least being a widely perceived antagonism between objective science and faith-based religion. But, as Dobzhansky pointed out, it is possible to be an evolutionist and a theist: "Evolution is God's, or Nature's method of creation."

It remains true that modern science has not been particularly effective in conveying the many wonders of the evolutionary sciences to a broader audience. This book represents one attempt to ameliorate this educational shortfall. We provide an historical overview of evolutionary biology by reprinting nearly 50 classical papers from the field. These seminal articles helped to chart the course of scientific developments in evolution across the one-and-a-half centuries since Darwin.

When we conceived this project, we were surprised to discover that no such compilation of essential readings in evolutionary biology existed, despite the centrality of evolutionary thought in biology, and despite the availability of analogous collections of classical reprints in several biological fields such as ecology and wildlife management and conservation.

We begin this book with a short chapter that encapsulates the broad timeline of evolutionary thought across the past two millennia, beginning with the philosophers of ancient Greece and Rome, continuing to the dawn of modern evolutionary ideas in the late nineteenth century, and culminating with an entrance into the ongoing era of modern genomics that began in the waning years of the twentieth century. After this historical overview, the book then proceeds to its bulk: a collection of 48 papers reprinted from the primary scientific literature of evolutionary biology. Each classic paper is introduced by a commentary in which we explain why the article is important, place it into a broader conceptual context, and provide a short list of source papers that readers might wish to consult for further information.

The seminal reprints are arranged in chronological order, beginning with selected readings from Darwin's (1859) *On the Origin of Species* and *The Descent of Man and Selection in Relation to Sex* (1871). The readings then proceed through the dawn of the twentieth century with such accomplishments as the birth of biochemical genetics, the rediscovery of Mendelian principles, and an elucidation of the chromosomal basis of inheritance. During the first half of the twentieth century, notable achievements included an illumination of the nature of mutations, the conception and development of mathematical population genetics, the origin of biological species concepts, and an early account of biochemical operations in metabolic networks. Near midcentury, the so-called Modern Synthesis was ascendant, which integrated Darwinian thought with Mendelian principles, amalgamated mathematical population genetics with organismal biology, and incorporated ecological and speciation principles with all of the above.

The 1960s and 1970s witnessed the inception and early growth of the molecular revolution in evolutionary biology, which included such path-breaking developments as the rise of neutrality theory and the inauguration of the selection/neutrality controversies, the birth of molecular phylogenetics, and early ideas about possible contrasts between the evolution of biological molecules versus organismal phenotypes. The 1970s through the 1990s were also a time when many tenets of the Modern Synthesis were revisited in the light of new information from molecular biology, developmental biology, and possible levels at which natural selection operates with greatest efficacy.

Other noteworthy happenings included a controversy centered on punctuated equilibrium versus phyletic gradualism, the birth and gestation of phylogeography, which seeks to unify the study of microevolution (population genetics) with macroevolution (phylogenetics), the delineation of many branches in the tree of life, reconsideration of the evolutionary significance of sexual recombination, the emergence of "evo-devo" (the ontogenetic basis of evolutionary change), and the proliferation of experimental approaches to evolutionary studies. The 1900s concluded with the rise of genomic approaches to evolutionary analyses, thanks to vast improvements in DNA-sequencing techniques and genetic annotation methods. These efforts continue today as we enter the era of population genomics in which the management and interpretation of molecular data have become even more demanding than data acquisition itself. The book concludes with a brief epilogue on the challenge of conveying evolutionary reasoning to the broader public.

We hope that this collection of classic reprints will be a useful reference for students and practitioners of the evolutionary sciences and that it will also inform a broader audience of science historians and biologists in related disciplines such as genetics, ecology, molecular biology, and developmental biology. After all, "there is grandeur in this view of life" (Darwin 1859), and nothing in biology makes sense except in evolution's light.

RELATED READING

Darwin, C. 1859. On the origin of species by means of natural selection. Murray, London, England.

Real, L. A., and J. H. Brown, editors. 1991. Foundations of ecology: classic papers with commentaries. University of Chicago Press, Chicago, Illinois, USA.

Krausman, P. R., and B. D. Leopold. 2013. Essential readings in wildlife management and conservation. Johns Hopkins University Press, Baltimore, Maryland, USA.

A Brief Timeline of Evolutionary Thought

ca. 600 BC. The idea that different kinds of organisms can be transformed one into another, including humans into animals and dragons into human form, is a familiar theme in the mythology of many cultures. Among the philosophers of ancient Greece, Anaximander proposed that animals could metamorphose from one kind into another, and Empedocles speculated that organisms were made up of various combinations of preexisting parts. Some of these new organisms would be successful and thus become, by a kind of natural selection, those that continue to exist.

ca. 400 BC. The Greek philosopher Plato advanced that the objects, including organisms, that we perceive with our senses are imperfect representations of *forms*, which are perfect and timeless but transcend our perceptions.

ca. 350 BC. Plato's student Aristotle envisioned a *scala naturae,* or ladder of life, to establish the relationships of living things. Taoist philosophers in China speculated that species develop different features in response to their environments and that nature is always in flux.

ca. 70 BC. The Roman philosopher Titus Lucretius Carus asserted that the development of living things occurred by means of purely naturalistic (rather than preternatural) mechanisms.

ca. 400 AD. Augustine of Hippo, a Christian theologian, maintained that not all species of plants and animals were initially created by God; rather, some had evolved in historical times from God's creations.

9th century. The Muslim biologist and philosopher al-Jahiz described a struggle for existence among animals as being influenced by their environmental conditions.

12th and 13th centuries. Christian thinkers updated the ancient Greek concept of *scala naturae* to arrange God-made forms of life into a great chain or hierarchy from lowly worms to intermediate humans to higher angels and heaven. Albertus Magnus (1200–1280) and his student, Thomas Aquinas (1224–1274), asserted that Genesis and other Christian scriptures should not be read literally. Aquinas concluded, after consideration of the arguments, that the development of living creatures, such as maggots and flies, from nonliving matter, such as decaying meat, was not incompatible with Christian faith or philosophy, although he left it to others to decide whether this actually happened.

14th century. The Islamic writer Ibn Khaldun mused that humans may have developed from monkeys and also discussed broader notions of ascent and descent along a biological continuum.

17th and 18th centuries. Several theories with evolutionary overtones were proposed by various philosophers and biologists including René Descartes, Benoît de Maillet, Gottfried Leibniz, J. G. Herder, and Pierre Louis Maupertuis. Such theories generally were in opposition to the Christian wisdom of the time (natural theology and the argument from design) that species had been sculpted in their current forms by special Creation.

1762. The word *evolution* (from the Latin *evolutio*, "to unroll like a scroll") was introduced by Charles Bonnet, albeit strictly applied to the embryological development of individual organisms.

18th century. The French philosopher and naturalist Comte de Buffon referred to species as well-marked varieties that became modified through time through environmental factors; another French philosopher, Denis Diderot, somewhat anticipated natural selection when he wrote that species were constantly changing through trial and error (after having originally arisen via spontaneous generation).

18th and 19th centuries. Work by geologists—including James Hutton, William Smith, Alexandre Brongniart, and Georges Cuvier—helped to establish the Earth's great antiquity. Cuvier described fossils, making it evident that species could go extinct. In a published essay (*On the Principle of Population*) that was to greatly influence Charles Darwin, Thomas Malthus emphasized the capacity of organismal reproduction to outstrip available resources, leading to a "struggle for existence."

1796. Erasmus Darwin (Charles Darwin's grandfather) expressed evolutionary notions that involved connections among diverse animals in a temporal framework.

1802. William Paley published a highly influential book, *Natural Theology*, claiming that God had designed features of life for the functional purposes they serve.

1809. Jean-Baptiste Lamarck advanced the first complete theory of evolution, asserting a progression over time from simpler to more complex kinds of organisms by use and disuse in response to specific changes in the environment.

1831. The word *evolution* is used for the first time in the modern sense of species' change through time by Etienne Geoffroy Saint-Hilaire.

1830s. Charles Lyell challenged accepted scenarios of catastrophism by taking a uniformitarian stance that the Earth's geologic features register cumulative effects over time of the same gradual geologic forces that are observable today. Charles Darwin went on a five-year voyage aboard the *HMS Beagle* and began a series of private notebooks on the transmutation of species.

1844. The Scottish publisher Robert Chambers proposed an evolutionary scenario for origins of the solar system and life on Earth.

1858. Theories on natural selection by Charles Darwin and Alfred Russel Wallace are read jointly before the Linnean Society of London.

1859. Charles Darwin publishes the first edition of *On the Origin of Species*.

1871. Charles Darwin publishes *The Descent of Man, and Selection in Relation to Sex* in which he extends his evolutionary concepts to *Homo sapiens* and identifies sexual selection as a key driver (in addition to natural selection) of the evolutionary process.

2nd half of the 19th century. The British biologist Thomas H. Huxley defends and promotes Darwin's ideas to sometimes skeptical audiences. Evolution by natural selection becomes the mainstream scientific explanation for biological adaptations and the origin of species. Ernst Haeckel, a German biologist, launches a program to reconstruct the evolutionary history of life. Methodological naturalism or scientific materialism gradually supersedes divine intervention as a favored explanation for evolutionary processes. Neo-Lamarckism (the inheritance of acquired characteristics) continues to enjoy favor as a mechanism of heredity underlying evolution.

1900. Gregor Mendel's work on hereditary factors from the mid-1860s is rediscovered, demonstrating the laws of inheritance.

Early 20th century. Biologists split into two camps (Mendelians and Biometricians) regarding how Mendel's factors (genes) might underlie organismal phenotypes and evolution.

1920s–1940s. Theoretical work by population geneticists Ronald Fisher, J. B. S. Haldane, and Sewall Wright resolve the Mendelian/Biometrician controversy and pave the way for what would later become known as the modern evolutionary synthesis. Other major contributors to this synthesis are Theodosius Dobzhansky (genetics), Ernst Mayr (animals and systematics), George Gaylord Simpson (paleontology), and G. Ledyard Stebbins (plants).

2nd half of the 20th century. Technological advances allow molecular genetics and genomics to be added to the evolutionary synthesis.

Contents

Darwin, C. 1859. *On the origin of species by means of natural selection*. Murray, London, England. Chapter III, pp. 60–69; Chapter IV, pp. 80–81, 87–90.

Charles Darwin (1809–1882) occupies a prominent place in the history of Western thought, deservedly receiving credit for the theory of evolution. On December 27, 1831, a few months after graduating from the University of Cambridge, Darwin sailed as a naturalist on a round-the-world trip on the HMS *Beagle* that lasted until October 2, 1836. He often disembarked for extended trips ashore to collect natural specimens. The discovery of fossil bones from large extinct mammals in Argentina and the observation of giant tortoises and numerous species of finches in the Galápagos Islands were among the events that stimulated Darwin's interest in how species originate. The diversity of natural selection, Darwin's' awareness that it was a greatly significant discovery because it provided an explanation of the design of organisms, and Darwin's designation of natural selection as "my theory" can be traced in his "Red Notebook" and "Transmutation Notebooks B to E," which he started in March 1837, a few months after returning from his voyage on the *Beagle*, and completed in late 1839.

It was in the *Origin*, however, published in 1859, that he assembled the evidence demonstrating the evolution of organisms. In doing so, Darwin accomplished something much more important for intellectual history than demonstrating evolution. The *Origin* is, first and foremost, a sustained effort to account scientifically for the "design" of organisms, their complexity, diversity, and marvelous contrivances as the result of natural processes, which he accomplishes with his theory of natural selection. The evidence for evolution is brought in because it is a necessary consequence of natural selection as the explanation of design. Evolutionary change through time and evolutionary diversification ensue as byproducts of natural selection's fostering the adaptation of organisms to their milieu.

The introduction and chapters I through VIII of the *Origin* explain how natural selection accounts for the adaptations and behaviors of organisms. Natural selection implies that biological evolution occurs, which Darwin therefore seeks to demonstrate in most of the remainder of the book (chapters IX–XIII). In the concluding chapter, XIV, Darwin returns to the dominant theme of adaptation and design and concludes with an eloquent paragraph asserting that "there is grandeur in this view of life . . . , from so simple a beginning endless forms most beautiful and most wonderful have been, and are being evolved."

RELATED READING

Barlow, N., editor. 1946. Charles Darwin and the voyage of the *Beagle*. Philosophical Library, New York, New York, USA.

Berra, T. M. 2009. Charles Darwin: the concise story of an extraordinary man. Johns Hopkins University Press, Baltimore, Maryland, USA.

Desmond, A., and J. Moore. 1991. Darwin: the life of a tormented evolutionist. Warner Books, New York, New York, USA.

Eldredge, N. 2004. Darwin: discovering the tree of life. Norton, New York, New York, USA.

Jones, S. 1999. Darwin's ghost: the *Origin of Species* updated. Doubleday, London, England.

Reznick, D. N. 2010. The *Origin* then and now: an interpretive guide to the *Origin of Species*. Princeton University Press, Princeton, New Jersey, USA.

Weiner, J. 1994. The beak of the finch: a story of evolution in our time. Alfred Knopf, New York, New York, USA.

On the Origin of Species

BY

CHARLES DARWIN

BEFORE entering on the subject of this chapter, I must make a few preliminary remarks, to show how the struggle for existence bears on Natural Selection. It has been seen in the last chapter that amongst organic beings in a state of nature there is some individual variability; indeed I am not aware that this has ever been disputed. It is immaterial for us whether a multitude of doubtful forms be called species or sub-species or varieties; what rank, for instance, the two or three hundred doubtful forms of British plants are entitled to hold, if the existence of any well-marked varieties be admitted. But the mere existence of individual variability and of some few well-marked varieties, though necessary as the foundation for the work, helps us but little in understanding how species arise in nature. How have all those exquisite adaptations of one part of the organisation to another part, and to the conditions of life, and of one distinct organic being to another being, been perfected? We see these beautiful co-adaptations most plainly in the woodpecker and missletoe; and only a little less plainly in the humblest parasite which clings to the hairs of a quadruped or feathers of a bird; in the structure of the beetle which dives through the water; in the plumed seed which is wafted by the gentlest breeze; in short, we see beautiful adaptations everywhere and in every part of the organic world.

Again, it may be asked, how is it that varieties, which I have called incipient species, become ultimately converted into good and distinct species, which in most cases obviously differ from each other far more than do the varieties of the same species? How do those groups of species, which constitute what are called distinct genera, and which differ from each other more than do the species of the same genus, arise? All these results, as we shall more fully see in the next chapter, follow inevitably from the struggle for life. Owing to this struggle for life, any variation, however slight and from whatever cause proceeding, if it be in any degree profitable to an individual of any species, in its infinitely complex relations to other organic beings and to external nature, will tend to the preservation of that individual, and will generally be inherited by its offspring. The offspring, also, will thus have a better chance of surviving, for, of the many individuals of any species which are periodically born, but a small number can survive. I have called this principle, by which each slight variation, if useful, is preserved, by the term of Natural Selection, in order to mark its relation to man's power of selection. We have seen that man by selection can certainly produce great results, and can adapt organic beings to his own uses, through the accumulation of slight but useful variations, given to him by the hand of Nature. But Natural Selection, as we shall hereafter see, is a power incessantly ready for action, and is as immeasurably superior to man's feeble efforts, as the works of Nature are to those of Art.

We will now discuss in a little more detail the struggle for existence. In my future work this subject shall be treated, as it well deserves, at much greater length. The elder De Candolle and Lyell have largely and philosophically shown that all organic beings are exposed to severe competition. In regard to plants, no one has treated this subject with more spirit and ability than W. Herbert, Dean of Manchester, evidently the result of his great horticultural knowledge. Nothing is easier than to admit in words the truth of the universal struggle for life, or more difficult—at least I have found it so—than constantly to bear this conclusion in mind. Yet unless it be thoroughly engrained in the mind, I am convinced that the whole economy of nature, with every fact on distribution, rarity, abundance, extinction, and variation, will be dimly seen or quite misunderstood. We behold the face of nature bright with gladness, we often see superabundance of food; we do not see, or we forget, that the birds which are idly singing round us mostly live on insects or seeds, and are thus constantly destroying life; or we forget how largely these songsters, or their eggs, or their nestlings, are destroyed by birds and beasts of prey; we do not always bear in mind, that though food may be now superabundant, it is not so at all seasons of each recurring year.

I should premise that I use the term Struggle for Existence in a large and metaphorical sense, including dependence of one being on another, and including (which is more important) not only the life of the individual, but success in leaving progeny. Two canine animals in a time of dearth, may be truly said to struggle with each other which shall get food and live. But a plant on the edge of a desert is said to struggle for life against the drought, though more properly it should be said to be dependent on the moisture. A