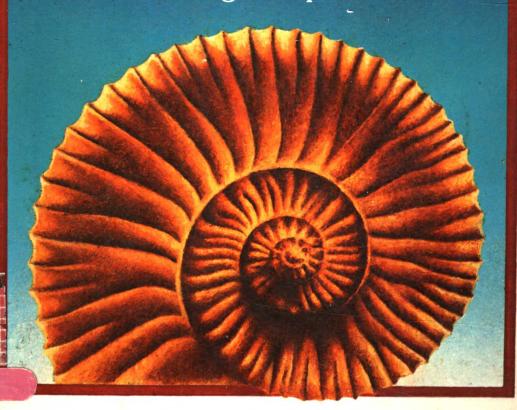
STEVEN M. STANLEY

THE NEW EVOLUTIONARY TIMETABLE

Fossils, Genes, and the Origin of Species



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Basic Books, Inc., Publishers
NEW YORK

Library of Congress Cataloging in Publication Data

Stanley, Steven M.

The new evolutionary timetable.

Includes bibliographical references and index.

1. Evolution. I. Title.

QH366.2.S69 575 81-66101 ISBN 0-465-05013-1 (cloth)

ISBN 0-465-05014-X (paper)

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PREFACE

HE THEORY of evolution is not just getting older, it is getting better. Like any scientific concept that has long withstood the test of time, this one has suffered setbacks but, time and again, has rebounded to become richer and stronger. What I describe in this book is evidence that evolution is not quite what nearly all of us thought it to be a decade or two ago. This evidence comes largely from the record of fossils—a record that until recently was not well scaled against absolute time. The record now reveals that species typically survive for a hundred thousand generations, or even a million or more, without evolving very much. We seem forced to conclude that most evolution takes place rapidly, when species come into being by the evolutionary divergence of small populations from parent species. After their origins, most species undergo little evolution before becoming extinct.

It is only fair to report that, while this "punctuational" view has displaced the traditional "gradualistic" view in the minds of many evolutionists, there remain dissenters. Among these are some physical anthropologists, who continue to assert that modern humans have evolved by the gradual, persistent modernization of an apelike ancestor. In chapter 7 I offer opposition to this traditional portrayal of our ancestry.

This book is not designed to build a rigorous case for the punctuational model of evolution—the goal of my more technical volume, *Macroevolution:* Pattern and Process, published in 1979. Rather, in the present book I attempt to give the interested non-specialist access to the punctuational view and its implications—implications that are by no means trivial. I also explore the history of the traditional, gradualistic view. Among the most fundamental questions here is why Charles Darwin was a gradualist. I hope that my explanations for Darwin's position will be given due consideration by historians of science, and I do not mean to be critical of Darwin here. For many reasons, he could only have been a gradualist.

The emergence of the punctuational model of evolution during the past

decade has at times caused acrimonious debate. This is an exciting time in the history of evolutionary science, and those of us laboring in this complex discipline can only hope that, during the next few years, important truths will float to the top of our collective crucible without occasioning undue rancor. I do not violate this wish by attacking the biblical creationists in chapter 8 of this book. The fact is, the fundamentalist creationists are parading antiscientific views falsely under a counterfeit banner of science. The recent antievolutionary efforts of the creationists constitute a grievous insult to natural science—to astronomy, as well as to geology and biology, and even to physics and chemistry, on which the other three sciences are partly founded. It is, after all, the behavior of atoms that reveals the earth to be more than four billion years old.

I express heartfelt thanks to Léo Laporte, Ledyard Stebbins, and Jim Valentine for thoughtful and kind, but sometimes dissenting, opinions of early drafts of the first seven chapters, and to Alan Walker for the same treatment of the initial version of chapter 7. Finally, I thank Jane Isay of Basic Books for her support and encouragement.

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The New Evolutionary Timetable



CHAPTER

1

Introduction

HE WORD "evolution" means unfolding, and for more than a century biologists have portrayed the evolution of life as a gradual unfolding of new living things from old, the slow molding of animals and plants into entirely different forms. It was this persistent style of change that Darwin described as "The Origin of Species."

Today the fossil record—a rich store of information that was long untapped—is forcing us to revise this conventional view of evolution. As it turns out, myriads of species have inhabited the Earth for millions of years without evolving noticeably. On the other hand, major evolutionary transitions have been wrought during episodes of rapid change, when new species have quickly budded off from old ones. In short, evolution has moved by fits and starts.

I have composed the following description in order to express the traditional view of large-scale evolution:

All around us in nature, life is ceaselessly changing. Species are modified gradually, almost imperceptibly when scaled against human history, yet in the course of millions of years the accumulation of infinitesimal steps amounts to total restructuring. Thus, during some fifty million years, what early in the Eocene Epoch had been the four-toed, fox-terrier-sized "dawn horse" was molded into the large, hoofed animal that today strains in the harness of a two-legged creature of enormous intellect. The master creature descended gradually from apelike animals, in part because changed surroundings forced these simian forebears down from the trees to a life on the savannah.

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This passage would fit comfortably into many accounts of evolution published in recent decades, but its credibility fades rapidly in the light of recently recognized facts. Some of these facts pertain to the ancestry of the two-legged creature who harnessed the horse, and others relate to the ancestry of the horse irself.

Let us first look briefly at the pattern of human evolution. According to the traditional view, modern humans arose by the gradual modification of an apelike animal during an interval of several million years. Fossil evidence now challenges this simple scenario. We now know that the human family tree has included several discrete branches, and that, at certain times, two or more humanoid species have walked the earth side by side. Even more important is the fact that species of the human family have existed almost unchanged for long stretches of geological time. Homo erectus, our evolutionary parent or grandparent, endured for at least a million years, and our own species, Homo sapiens, has undergone almost no bodily change in Europe since appearing there suddenly some forty thousand years ago. I will evaluate these aspects of human evolution and others in chapter 7 of this book, but the fundamental point is easily grasped: human evolution has apparently followed a stepwise course, with important biological change occurring as one species has branched rapidly from another.

The fossil record of horses also testifies to an episodic tempo for evolution, and this is particularly notable because for decades the record of ancient horses was heralded as the classic illustration of gradual transformation. Although this fossil record, like all others, is incomplete, so that it fails to document the full history of the horse family, one of its striking revelations is great evolutionary stability for tiny dawn horses, which, as the earliest representatives of the horse family, browsed on leaves about forty million years ago. For at least three or four million years, two species of these dawn horses roamed through woodlands of western North America. In other words, populations of these small animals replicated themselves through a million generations or so without undergoing appreciable change in form. Looking to the upper end of the horse family tree, we find the same kind of evidence. In North America, at least four species of horses survived virtually unchanged for the better part of two million years, through almost the entire recent Ice Age. In Africa during the same interval of time, four or more species of the zebra variety persisted almost without modification. All of these Ice Age species belong to the Equus group, which includes all living horses and zebras. The Equus kind of animal appears suddenly in the fossil record in North American deposits less than three million years old. This

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familiar creature evolved from an ancestor of quite different form—one that had toes flanking each of its hoofs, as well as much simpler molar teeth than the modern horse. Horses of the modern Equus type obviously evolved rapidly, and apparently for this reason their origin is not documented by known fossil evidence. This abrupt evolutionary birth of the modern kind of animal stands in sharp contrast to the stability of established horse species.

Thus, the new message offered by the ancient remains of humans, horses, and many other animals is that evolution has occurred episodically. Most change has taken place so rapidly and in such confined geographic areas that it is simply not documented by our imperfect fossil record. The resulting view of evolution has become known as the punctuational model, while the contrasting traditional view has been labeled the gradualistic model. The punctuational model is not incompatible with what we now know of modern life on Earth. There is good evidence that certain distinctive living species of animals have formed since the dawning of modern civilization in the Middle East.

The punctuational model might appear to represent a minor modification of the traditional scheme of evolution—an esoteric adjustment that should interest only specialized practitioners of biological science. In fact, its consequences reach much farther. The punctuational view implies, among other things, that evolution is often ineffective at perfecting the adaptations of animals and plants; that there is no real ecological balance of nature; that most large-scale evolutionary trends are not produced by the gradual reshaping of established species, but are the net result of many rapid steps of evolution, not all of which have moved in the same direction; and that sexual reproduction does not prevail in the world for the reasons that have traditionally been offered.

The punctuational model has another implication of particular interest to us, as humans. Because the human family does not consist of a solitary line of descent leading from an apelike form to our species, *Homo sapiens*, we are not as special as we would like to think. Had a perceptive being somehow passively watched human evolution for the three or four million years before our species and its immediate ancestors appeared, it could not have predicted our origin. Our anatomy and the very different anatomy of our stocky Neanderthal cousins are in many ways unpredictable from what went before. We function satisfactorily, but no better than many other configurations of bones and flesh that might have evolved in our place from the distinctive species *Homo erectus*, which was our evolutionary parent or grandparent. Our sharp chin, tall forehead, and weak brow are not the results of long-term evolutionary trends. They are apparently features unique to our species. They represent evolutionary sur-

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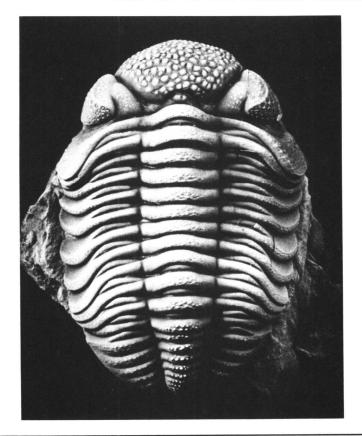


FIGURE 1.1 The Devonian trilobite *Phacops rana*, about 300 million years old, viewed from above. The compound eyes are clearly visible, and the animal is partially enrolled, like a pill bug.

prises, albeit ones that may have been favored by natural selection at a particular time and in a particular place. The gradualistic model is compatible with such reversals, but the punctuational model predicts that they should often be very abrupt and pronounced, as indeed they seem to have been in the evolution of our own family.

We thus have strong motives to understand evolution, one of the most important intellectual concepts of the Western world, and we have every reason to sit up and take notice when it appears that fossils—pieces of inanimate rock—reveal new and surprising things about our biological origins. Fossils played only a minor role in Darwin's conception of an evolutionary process,