The Evolutionary Synthesis

Perspectives on the Unification of Biology

EDITED BY

Ernst Mayr and
William B. Provine

The Evolutionary Synthesis

Perspectives on the Unification of Biology

EDITED BY

Ernst Mayr and William B. Provine

Harvard University Press
Cambridge, Massachusetts, and London, England 1980

Printed in the United States of America

Library of Congress Cataloging in Publication Data
Main entry under title:

The Evolutionary synthesis.

Bibliography: p.
Includes index.
1. Evolution. 2. Evolution—History. I. Mayr, Ernst, 1904- II. Provine, William B.
QH366.2.E87 575 80-13973
ISBN 0-674-27225-0

THE EVOLUTIONARY SYNTHESIS

Preface

The theory that the diversity of life (plants and animals) is the product of evolution by common descent was almost universally accepted by biologists soon after the publication of *On the Origin of Species* (1859). Although Darwin's specific explanation—gradual evolution by natural selection—was immediately adopted by Wallace, Hooker, Gray, Bates, Poulton, and Weismann, it was rejected by most biologists and bitterly attacked by many others. It seemed to make some temporary headway in the 1870s, but lost ground again in the 1880s and 1890s and almost received a fatal setback through the mutationist theories of the early Mendelians. In the first decades of the twentieth century the schools of saltationism, orthogenesis, and neo-Lamarckism had decidedly more followers than selectionism. Indeed, only a handful of authors between 1900 and 1920 could be designated as pure selectionists. On the whole—and admittedly this is an oversimplification—two camps were recognizable, the geneticists and the naturalists-systematists. They spoke different languages; their attempts in joint meetings to come to an agreement were unsuccessful. In the early 1930s, despite all that had been learned in the preceding seventy years, the level of disagreement among the different camps of biology seemed almost as great as in Darwin's days. And yet, within the short span of twelve years (1936-1947), the disagreements were almost suddenly cleared away and a seemingly new theory of evolution was synthesized from the valid components of the previously feuding theories. Huxley (1942) referred to this episode in the history of biology as the "evolutionary synthesis."

The historian would like to know what happened during these crucial years. What factors were responsible for the breaking down of the barriers between the separate camps? What important insights were contributed by the specialists of the various biological disciplines that constitute the field of evolutionary biology? What misunderstandings had to be removed? Why were the thirties and forties so favorable to the synthesis?

The Committee on the Recent History of Science and Technology of

the American Academy of Arts and Sciences conceived the idea of organizing a conference composed of two workshops charged with the task of attempting to answer these questions. Happily, some of the architects of the synthesis were still alive and they were invited. Also invited were some of the leading evolutionists of the next generation, as well as a number of historians of biology and philosophers of science. J. Huxley, B. Rensch, and G. G. Simpson, unfortunately, were prevented from participation by illness or conflicting engagements. That the conference was none too early is sadly demonstrated by the subsequent death of three participants (Th. Dobzhansky, I. M. Lerner, and E. Boesiger) and two correspondents (J. Huxley and B. L. Astaurov).

The major objective of the conference was to elicit as much information as possible about any factor, scientific or otherwise, that had had a positive or negative influence on the occurrence of the synthesis. Some participants had prepared formal papers; others presented their views informally. All of them made major additional contributions in response to questions in the ensuing discussion periods. Alexander Weinstein, who had been invited as a former student of T. H. Morgan, provided particularly valuable information.

The entire conference was recorded on tape and transcribed. Most unfortunately, the machine went on strike during E. B. Ford's presentation, and it was impossible to restore the missing part. All participants were asked to edit the transcripts of their own discussions, while the overall supervision and coordination were in the hands of Ernst Mayr and William Provine. During this editorial process most of the discussions were consolidated with the major presentations, and material was eliminated that did not relate directly to the synthesis. Biographical essays were gathered in a separate section.

Following Ernst Mayr's prologue, we have divided the book into two major sections with a smaller concluding section. The first section contains analyses of the contributions of the various biological disciplines to the evolutionary synthesis. The evolutionary synthesis was, however, genuinely different in different countries. Because a historical understanding of the progress of the synthesis must encompass this diversity, the second major section is devoted to analyses of the evolutionary synthesis in different countries.

The two sections are closely interrelated. Nearly every essay in the second section deals with the contributions to the synthesis of several of the fields examined in the first section.

The third section contains a discussion of general interpretive issues in the evolutionary synthesis, Will Provine's epilogue, and the biographical essays.

We should note here that because of the variety of acceptable systems of transliteration from the Russian, we have made no attempt to impose consistency in this respect from one chapter to another; rather, we have permitted the individual contributors to follow the method of their choice.

ACKNOWLEDGMENTS

The workshops could not have functioned so successfully, without the efficiency and never failing helpfulness of John Voss, Patricia Flaherty, and Shirley Hazen, of the staff of the American Academy. Our special thanks are due Alexandra Oleson, conference coordinator.

We are deeply grateful to William Kimler for his preparation of the detailed index to this book.

The conference was made possible by National Science Foundation grant GS-42934 to the American Academy of Arts and Sciences.

E.M.

W.B.P.

Contents

Prologue: Some Thoughts on the History of the Evolutionary Synthesis*

Ernst Mayr

The term "evolutionary synthesis" was introduced by Julian Huxley in *Evolution: The Modern Synthesis* (1942) to designate the general acceptance of two conclusions: gradual evolution can be explained in terms of small genetic changes ("mutations") and recombination, and the ordering of this genetic variation by natural selection; and the observed evolutionary phenomena, particularly macroevolutionary processes and speciation, can be explained in a manner that is consistent with the known genetic mechanisms. The objective of this conference is to examine the rapid changes in evolutionary biology that occurred in the period of the synthesis (from approximately 1936 to 1947), to reconstruct the sequence of events leading to the synthesis, and to identify the factors responsible for the preceding disagreements.

To meet these objectives, the conference faces a formidable task. It is extremely difficult to explain and reconstruct something that happened forty years ago. Memories of past events have become dim; the situation looked then, and probably still looks today, different to representatives of different specialized fields; and finally, the situation was different in each country and sometimes even in different scientific centers in the same country. To resolve these problems, we have invited some speakers to report on the relation between the synthesis and various disciplines of biology (such as systematics, genetics, paleontology, and botany), others to speak on its occurrence (or not) in various countries (USSR, Germany, France). We hope that this approach will illuminate the synthesis from many different angles.

Historiography of science must avoid two great dangers. Chauvinism exaggerates the importance of whatever field or country a given scientist represents and tends to belittle the contribution of others. Butterfield

*Dedicated to Bernhard Rensch, one of the architects of the evolutionary synthesis, on his eightieth birthday (January 21, 1980).

(1957) has called the second danger the "whiggishness" of science writing —that is, the application of the hindsight of modern understanding in the evaluation of past events, combined with a suppression of all inconvenient phenomena.

No one can entirely avoid either of these shortcomings; sometimes they even provoke illuminating controversy. Yet all of us must keep a careful watch for manifestations of both pitfalls so that we can correct misleading statements before still other inaccuracies are added to the all too rich repertory of myths in science.

The conference has five specific objectives:

(1) To define the concepts that were dominant in various fields of biology and in various countries in the period preceding the synthesis
(2) To identify misunderstandings and other factors that delayed a reaching of consensus
(3) To identify the respective contributions made by various individuals and various biological disciplines, such as genetics, cytology, systematics, and paleontology
(4) To determine the factors that induced some authors to resist the synthesis
(5) To determine how the actual synthesis was achieved.

My own task in opening the conference is to attempt to specify the principal problems posed by the synthesis. I shall try to describe the state of evolutionary biology as it existed in the 1920s and early 1930s. I shall attempt to specify the objections raised by the opponents of the Darwinian theory and to identify the source of these objections. Finally, I shall try to focus attention on the relative importance of the contributions made by various branches of biology and the specific role played by certain key figures.

Most of what has so far been written about developments in evolutionary biology in the 1920s and 1930s has been written from the viewpoint of genetics. My own treatment is clearly affected by the fact that I am a systematist by background. Inevitably my interpretation of many developments differs from that of a geneticist. Future historical research must determine which of opposing interpretations seems to represent the situation more accurately. My major purpose here is to tickle the memory of the participants and to give them an opportunity to elaborate on my comments or to correct them if my recollections or interpretations are faulty. Nothing would be worse for our purposes than to gloss over existing difficulties, discrepancies, and contradictions.

The Opposition to the Darwinian Theory

The Darwinian (selectionist)[1] interpretation of evolution is now so nearly universally accepted among biologists that the present generation of evolutionists can hardly comprehend the opposition that the theory of natural selection still encountered in the 1920s and 1930s. During that period, nearly all the major books on evolution, including those by Berg, Bertalanffy, Beurlen, Boeker, Goldschmidt, Robson, Robson and Richards, Schindewolf, and those of all the French evolutionists (such as Cuénot, Caullery, Vandel, Guyénot, and Rostand) were more or less antiselectionist. The general texts on zoology and botany, even when adopting Darwinism, usually gave a good deal of space to Lamarckism as a legitimate possible alternative (see chapter 9). Darwinism was even less popular among nonbiologists. The philosophers, in particular, were almost unanimously opposed until relatively recent years (Cassirer, 1950; Grene, 1959; Popper, 1972).

The Darwinians were fully aware of the continuing popularity of non-Darwinian evolutionary theories. As recently as 1932, T. H. Morgan found it advisable to use an entire chapter to refute the hypothesis of an inheritance of acquired characters. An extraordinary amount of space is likewise devoted to the refutation of anti-Darwinian arguments by Haldane (1932), in the various books of the synthesis (Dobzhansky, 1937; Huxley, 1942; Rensch, 1947; Simpson, 1944) and in the postsynthesis literature (see, for example, Fisher, 1954).

The very few books on evolution written by authors who were firm adherents to neo-Darwinism (such as Haldane, 1932) had various shortcomings. None of these was greater than their attempt to explain evolution in terms of changes in gene frequencies. This explanation left most nongeneticists thoroughly dissatisfied because events at the level of the gene did not at all explain the organismic phenomena studied by paleontologists, systematists, ecologists, and students of behavior.

A peculiar myth popular among the geneticists at that time illustrates their failure to understand the real meaning of the Darwinian theory. Many held that the acceptance of evolution by natural selection depended on the maturation of genetics. The facts do not support the validity of this claim. First, Darwinism together with all of its consequences

1. The term "Darwinism" in the following discussions refers to the theory that selection is the only direction-giving factor in evolution.

was accepted not only by Darwin, Hooker, Wallace, and Weismann, but also by Poulton, K. Jordan, and many naturalists in the nineteenth century before the birth of genetics. More important, Darwinism was rejected by three of the founders of Mendelism—Bateson, de Vries, and Johannsen—the first evolutionists who truly understood Mendelian inheritance. Nevertheless, genetics subsequently did make a decisive contribution to the synthesis, but it is only one of the multiple sources of the synthesis.

Different Schools of Evolutionism

The number of competing theories of evolution in vogue before the synthesis is quite bewildering. The frequently used dichotomy, Darwinism versus Lamarckism, is not very satisfactory because both labels usually lumped rather different theories. Evolutionary theories can be classified by numerous criteria; my own arrangement is only one of many possible ones. I have chosen two classifying criteria: whether the author was an essentialist or believed in the uniqueness of individuals (population thinking), and whether the author allowed only for hard inheritance or admitted also "soft" inheritance. By "soft" I mean whether the author believed that the genetic basis of characters could be modified either by direct induction by the environment, or by use and disuse, or by an intrinsic failure of constancy, and that this modified genotype was then transmitted to the next generation. Soft inheritance is usually referred to as a belief in an inheritance of acquired characters, but soft inheritance includes a broader range of phenomena. It is also sometimes called Lamarckism or neo-Lamarckism, even though Lamarck's own theory was only one subdivision in this group of theories. Using these two criteria, I have designed a discrimination grid (table 1) that separates the best-

Table 1 Criteria for classifying evolutionary theories

Based on—	Also allowing for soft inheritance	Exclusively hard inheritance
Essentialism	Orthogenesis Geoffroyism	Saltationism
Populationism	Darwinism	Neo-Darwinism Synthetic theory

known theories of evolution. I have avoided the term Lamarckism because it refers to several heterogeneous theories and most often to ones not supported by Lamarck himself.

These various theories may be characterized as follows:

(1) Geoffroyism, which ascribes evolutionary change to the direct influence of the environment. The product of this induction is transmitted to future generations, by means of an inheritance of acquired characters. Geoffroyism was adhered to by most neo-Lamarckians.

(2) Orthogenesis, a rather heterogeneous assortment of theories, all of which ascribe evolution to a built-in tendency or drive toward progress and ever greater perfection.[2] Lamarck's original thesis, widely adopted not only by biologists but particularly by sociologists, anthropologists, and philosophers, H. F. Osborn's aristogenesis, and Teilhard de Chardin's ideas belong to this tradition.

Population thinking (see chapter 4) is absent in both Geoffroyism and orthogenesis. However, it is also not strictly correct to list them under essentialism, as I have done, because both schools believe in a change through time. Their representatives, however, never make it quite clear whether they believe in genuine change or merely the unfolding of an immanent potentiality.

(3) The saltationism (macrogenesis) school, which postulates the origin of new types by discontinuous variation. Belief in such a process goes as far back as the Greeks and was particularly strong in the eighteenth and nineteenth centuries. The mutation theory of de Vries and other Mendelians is in this tradition as well as the later theories of R. Goldschmidt ("systemic mutations") and of certain paleontologists, particularly Schindewolf. T. H. Morgan had a strong saltationist tendency in his earlier writings that had not yet entirely disappeared from his 1932 book.

(4) The original Darwinism, which postulates slow, gradual evolution through natural selection utilizing abundantly available genetic variation. However, it also admits a certain amount of effectiveness of use and disuse and other manifestations of soft inheritance.

(5) Neo-Darwinism, which differs from the original Darwinism primarily by excluding all possibility of an inheritance of acquired characters. Neo-Darwinism was established by Weismann (1883) and adopted by Wallace (1889) and other Darwinians.

This classification into five schools of evolutionism is an oversimplification. Most authors between 1860 and 1940 adopted a mixture of these

2. Adherents of this theory might be referred to as orthogenesists. It would be as inappropriate to call them orthogeneticists as it would be to call believers in Genesis geneticists.

theories. For instance, a simultaneous belief in "mutations" for discontinuously varying characters and in Geoffroyism for continuously varying characters was particularly widespread. It was often not realized that certain elements in some of the mixed theories were incompatible. As time went on, the existence of a certain amount of natural selection was more and more widely admitted, but this was considered by many evolutionists to be quite compatible with an inheritance of acquired characters. Table 1 is only a first guide, but many of the authors of mixed evolutionary theories do not fit readily in any one of the four categories. The only thing these various non-Darwinian theories of evolution had in common was that they denied natural selection as the exclusive mechanism of evolution. This opposition to selection was based on a great variety of objections.

The Widening Split in Biology

The rise of evolutionism after 1859 coincided with an increasing separation of zoology and botany into new special fields, such as embryology, cytology, genetics, behavioral biology, and ecology. Simultaneously, the gap widened between the experimental biologists and those anatomists, zoologists, botanists, and paleontologists who had been raised as naturalists and who worked with whole organisms. Each group not only dealt with different subject matter but also asked basically different questions. When it came to the interpretation of evolutionary phenomena, their conclusions often were diametrically opposed. As early as 1894 Bateson suggested that "the Discontinuity of Species results from the Discontinuity of Variation" (p. 568), whereas most zoologists more than ever believed in Darwin's gradual evolution.

The rift became aggravated by the rediscovery of Mendel's rules in 1900, which resulted in the birth of genetics and eventually led to an ever increasing understanding of the principles of inheritance and of the nature of the genetic material. As essential as a knowledge of genetics is for a full understanding of the process of evolution, it spread only slowly through biology. Most naturalist-evolutionists learned about genetics from the writings of those geneticists who wrote books about evolution —that is, from Bateson, de Vries, Johannsen, and T. H. Morgan. Unfortunately none of these four geneticists understood evolution. All four tended to think as essentialists and failed to appreciate the nature of species as biological populations. All four downgraded or denied altogether the importance of natural selection, but instead considered mutation pressure as the major directive force in evolution.

These authors wrote more extensively on evolutionary questions than