The Growth of Biological Thought

Diversity, Evolution, and Inheritance

ERNST MAYR

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Preface to the motion of the manufacture of the state of

MUCH OF MODERN BIOLOGY, particularly the various controversies between different schools of thought, cannot be fully understood without a knowledge of the historical background of the problems. Whenever I made this point to my students, they would ask me in what book they could read up on these matters. To my embarrassment, I had to admit that none of the published volumes filled this need. To be sure, there is much literature on the lives of biologists and their discoveries, but these writings are invariably inadequate as far as an analysis of the major problems of biology are concerned or as a history of concepts and ideas in biology. While some of the histories of individual biological disciplines, like genetics and physiology, are indeed histories of ideas, there is nothing available that covers biology as a whole. To fill this gap in the literature is the object of this work. This volume is not, and this must be stressed, a history of biology, and it is not intended to displace existing histories of biology, such as that of Nordenskiöld. The emphasis is on the background and the development of the ideas dominating modern biology; in other words, it is a developmental, not a purely descriptive, history. Such a treatment justifies, indeed necessitates, the neglect of certain temporary developments in biology that left no impact on the subsequent history of ideas.

When I first conceived the plan to write a history of ideas in biology, the goal seemed impossibly remote. The first years (1970–1975) were devoted to reading, notetaking, and the preparation of a first draft. Soon it became obvious that the subject was too vast for a single volume, and I decided to prepare first a volume on the biology of "ultimate" (evolutionary) causations. But even this limited objective is a hopelessly vast undertaking. If I have been successful at all, it is because I have myself done a considerable amount of research in most areas covered by this volume. This means that I was already reasonably familiar with the problems and some of the literature of the areas involved. I hope to

deal with the biology of "proximate" (functional) causations in a later volume that will cover physiology in all of its aspects, developmental biology, and neurobiology. When a biological discipline, for instance genetics, deals both with ultimate and proximate causations, only the ultimate causations are treated in the present volume. There are two areas of biology that might have been (at least in part) but were not included in this volume: the conceptual history of ecology and that of behavioral biology (particularly ethology). Fortunately, this omission will not be quite as painful as it might otherwise be, because several volumes by other authors dealing with the history of ecology and ethology are now in active preparation.

The professional historian is not likely to learn much from chapters 1 and 3; in fact he may consider them somewhat amateurish. I have added these two chapters for the benefit of nonhistorians, believing that it will help them to see the purely scientific developments of the other chapters with a deepened

perception.

I owe an immense debt of gratitude to numerous individuals and institutions, Peter Ashlock, F. J. Ayala, John Beatty, Walter Bock, Robert Brandon, Arthur Cain, Fred Churchill, Bill Coleman, Lindley Darden, Max Delbrück, Michael Ghiselin, John Greene, Carl Gustav Hempel, Sandra Herbert, Jon Hodge, David Hull, David Layzer, E. B. Lewis, Robert Merton, J. A. Moore, Ron Munson, Edward Reed, Phillip Sloan, Frank Sulloway, Mary Williams, and others have read drafts of various chapters, have pointed out errors and omissions, and have made numerous constructive suggestions. I did not always follow their advice and am thus solely responsible for remaining errors and deficiencies. To P. Ax, Muriel Blaisdell, and B. Werner I am indebted for useful factual information.

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The Museum of Comparative Zoology, through the courtesy of its Director, Professor A. W. Crompton, has provided office space, secretarial help, and library facilities, even after my retirement. Research periods at the Institute for Advanced Study (Princeton, spring 1970), at the library of the Max Planck Institute of Biology (Tübingen, 1970), a senior fellowship of the Alexander von Humboldt Foundation (Würzburg, 1977), a fellowship awarded by the Rockefeller Foundation (Villa Serbelloni, Bellagio, 1977), and a grant (No. GS 32176) by the National Science Foundation have greatly facilitated my work.

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Agoloid to design the Museum of Comparative Zoology
Harvard University

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1 Introduction: How to write history of biology

ANYTHING THAT changes in time has, by definition, a history—the universe, countries, dynasties, art and philosophy, and ideas. Science also, ever since its emergence from myths and early philosophies, has experienced a steady historical change and is thus a legitimate subject for the historian. Because the essence of science is the continuing process of problem solving in the quest for an understanding of the world in which we live, a history of science is first a history of the problems of science and their solution or attempted solutions. But it is also a history of the development of the principles that form the conceptual framework of science. Because the great controversies of the past often reach into modern science, many current arguments cannot be fully understood unless one understands their history.

Written histories, like science itself, are constantly in need of revision. Erroneous interpretations of an earlier author eventually become myths, accepted without question and carried forward from generation to generation. A particular endeavor of mine has been to expose and eliminate as many of these myths as possible—without, I hope, creating too many new ones. The main reason, however, why histories are in constant need of revision is that at any given time they merely reflect the present state of understanding; they depend on how the author interpreted the current zeitgeist of biology and on his own conceptual framework and background. Thus, by necessity the writing of history is subjective and ephemeral.¹

When we compare published histories of science, it becomes at once apparent that different historians have quite different concepts of science and also of history writing. Ultimately all of them attempt to portray the increase in scientific knowledge and the changes in interpretive concepts. But not all historians of science have attempted to answer the six principal questions that must be addressed by anyone who wants to describe the progress of science critically and comprehensively: Who? When? Where?

What? How? and Why? On the basis of the author's selection from among these questions, most of the histories known to me can be classified as follows (cf. Passmore, 1965: 857–861), though it must be recognized that nearly all histories are a combination of the various approaches or strategies:

Lexicographic Histories

These are more or less descriptive histories with a strong emphasis on the questions What? When? and Where? What were the principal scientific activities at any given past period? What were the centers of science where the leading scientists were working, and how did they shift in the course of time? No one will argue about the value of such histories. A correct presentation of the true facts is indispensable because much of the traditional history of science (and its standard texts) is encrusted with myths and spurious anecdotes. Yer, a purely descriptive history provides only part of the story.

Chronological Histories

A consideration of time sequences is crucial to any kind of history writing. Indeed, one can even make chronology the primary organizing criterion, and some authors have done so. They have asked, for instance, what happened in biology between 1749 and 1789, or between 1789 and 1830? Chronological histories present a sequence of cross sections through the entirety of developments in all branches of biology. This is not only a legitimate but indeed a most revealing approach. It creates a feeling for the zeitgeist and the totality of contemporary influences. It permits one to investigate how developments in other branches of science have influenced biology, and how even within biology advances made by the experimentalists have affected the thinking of the naturalists, and vice versa. The understanding of many problems in the development of biology is greatly facilitated by this chronological approach. However, it suffers from the drawback that each major scientific problem is atomized.

Biographical Histories

The endeavor in these volumes is to portray the progress of science through the lives of leading scientists. This approach is also legitimate, since science is made by people and the impact of individual scientists like Newton, Darwin, and Mendel has often been of quasi-revolutionary nature. However, this approach shares

with the purely chronological approach one very serious weakness: it atomizes each major scientific problem. The species problem, for example, will have to be discussed under Plato, Aristotle, Cesalpino and the herbalists, Buffon, Linnaeus, Cuvier, Darwin, Weismann, Nägeli, de Vries, Jordan, Morgan, Huxley, Mayr, Simpson, and so on. All of these discussions of the same problem are separated from each other by many pages, if not chapters.

Cultural and Sociological Histories

This approach stresses the point that science is a form of human endeavor and is therefore inseparable from the intellectual and institutional milieu of the period. This view is particularly fascinating to those who come to the history of science from the field of general history. They might ask such questions as why was British science from 1700 to 1850 so strongly experimental and mechanical while contemporary French science tended to be mathematical and rationalistic? Why did natural theology dominate science for 75 years longer in Britain than on the continent? To what extent was Darwin's theory of natural selection a child of the industrial revolution?

Even if the historian of biology chooses not to adopt this approach, he must carefully study the cultural and intellectual milieu of a scientist if he wants to determine the causes for the rise of new concepts. This is of evident importance in the present work, since one of the major objectives of my treatment is to investigate the reasons for the changes in biological theories. What enabled one investigator to make a discovery that has escaped his contemporaries? Why did he reject the traditional interpretations and advance a new one? From where did he get the inspiration for his new approach? These are the kind of questions that need to be asked.

Most early histories of science, particularly those of special scientific disciplines, were written by working scientists, who took it for granted that the intellectual impetus for scientific change came from within the field itself ("internal" influences). Later on, when the history of science became more professionalized and historians and sociologists began to analyze the progress of scientific thought, they tended to stress the influence of the general intellectual, cultural, and social milieu of the period ("external" influences). No one would want to doubt that both kinds of influences exist, but there is a great deal of disagreement on their rel-

ative importance, particularly with reference to specific developments, such as Darwin's theory of natural selection.

Often it is rather difficult even to distinguish external from internal factors. The Great Chain of Being (scala naturae) was a philosophical concept which clearly had an impact on concept formation in the case of Lamarck and other early evolutionists. Yet, Aristotle had developed this concept on the basis of empirical observations of organisms. On the other hand, universally adopted ideologies are among the most uncontroversial of external factors. The Christian dogma of creationism and the argument from design coming from natural theology dominated biological thinking for centuries. Essentialism (from Plato) is another all-powerful ideology. Interestingly, its displacement by Darwin was largely due to the observations of animal breeders and taxonomists—that is, to internal factors.

External factors do not necessarily originate in religion, philosophy, cultural life or politics, but—as far as biology is concerned—they may originate in a different science. The extreme physicalism (including determinism and extreme reductionism) that was prevalent in Western thinking after the scientific revolution strongly influenced theory formation in biology for several centuries, often quite adversely as is now evident. Scholastic logic, to cite another example, dominated taxonomic method from Cesalpino to Linnaeus. These examples, to which many others could be added, document without doubt the importance of external influences on theory formation in biology. They will be analyzed in full detail in the relevant chapters.

It is important to realize that external factors influence science in two entirely different ways: They may either affect the overall level of scientific activity at a given place at a given time, or they may affect or even give rise to a particular scientific theory. All too often in the past these two aspects have been lumped together, resulting in much controversy over the relative importance of external versus internal factors.

The effect of environmental conditions on the *level* of scientific activities has been appreciated as long as there has been a history of science. It has been speculated endlessly as to why the Greeks had such an interest in scientific questions and why there was a revival of science during the Renaissance. What was the effect of Protestantism on science (Merton, 1938)? Why did science during the nineteenth century flourish to such an extent in Germany? Sometimes important external factors can be specified,

for instance (as Merz, 1896–1914, has pointed out), the replacement in 1694 of Latin by German at Halle University, and the founding in 1737 of a University at Göttingen in which "Wissenschaft" played an important role. Institutional changes of all sorts, including the founding of the Royal Society, political events such as wars and the launching of Sputnick, as well as technological needs have had either a stimulating or a depressing effect on the level of scientific activity. Yet, this still leaves open the highly controversial question of to what extent such external factors have favored or inhibited specific scientific theories.

In recent years Marxist historiographers in particular have voiced the thesis that social ideologies influence the ideas of a scientist, and that the history of science as practiced until now has totally neglected the social context. The result, they believe, has been a bourgeois history of science, which is quite different from what a proletarian history of science would be. What is needed instead, they say, is "radical" history. This demand ultimately goes back to Marx's claim that ruling ideas cannot be separated from ruling classes. Therefore, bourgeois history of science will be quite different from proletarian history of science.

However, the thesis that there is a proletarian way to write the history of science is in conflict with three sets of facts: First, the masses do not establish scientific theories that are different from those of the scientific class. If there is any difference, it is that the "common man" often retains ideas long after they have been discarded by scientists. Second, there is high social mobility among scientists, with from one quarter to one third of each new crop of scientists coming from the lower socioeconomic classes. Third, birth order within a social class tends to be far more important in determining those who originate rebellious new ideas than does membership in a particular class (Sulloway, MS). All of this is in conflict with the thesis that the socioeconomic environment has a dominant impact on the birth of particular new scientific ideas and concepts. The burden of proof is clearly on those who make such claims, and so far they have failed to supply any concrete evidence whatsoever (see Chapter 11). http://email.org/

Of course no one lives in a vacuum, and anyone who reads voraciously, as for example Darwin did after his return from the voyage of the *Beagle*, is bound to be influenced by his reading (Schweber, 1977). Darwin's notebooks are ample evidence for the correctness of this inference. But, as Hodge (1974) points out, this by itself does not prove the thesis of the Marxists that "Darwin

and Wallace were extending the laissez-faire capitalist ethos from society to all nature." Up to now it appears that the influence of social factors on the development of specific biological advances has been negligible. The reverse, of course, is not true. But the study of the impact of science on social theory, social institutions, and politics belongs to the domains of history, sociology, and political science, and not to that of the history of science. I agree with Alexander Koyré (1965: 856) that it is futile to "deduce the existence" of certain scientists and sciences from their environment. "Athens does not explain Plato anymore than Syracuse explains Archimedes or Florence Galileo. To look for explanations along these lines is an entirely futile enterprise, as futile as trying to predict the future evolution of science or of the sciences as a function of the structure of the social context." Thomas Kuhn (1971: 280) has likewise observed that the historian seems invariably to give "excessive emphasis to the role of the surrounding climate of extra-scientific ideas" (see also Passmore, 1965).

Problematic Histories

More than one hundred years ago Lord Acton advised historians, "Study problems, not periods." This advice is particularly appropriate for the history of biology, which is characterized by the longevity of its scientific problems. Most of the great controversies of the nineteenth and early twentieth centuries relate to problems already known to Aristotle. Such controversies endure from generation to generation, and from century to century. They are processes, not events, and can be fully understood only through a historical treatment. As R. G. Collingwood said of history (1939: 98), it "is concerned not with events but with processes. Processes are things which do not begin and end but turn into one another." This must be stressed particularly in the face of the static views of the logical positivists who thought that logical structure was the real problem of science: "The philosophy of science is conceived [by them] primarily as a careful and detailed analysis of the logical structure and the conceptual problems of contemporary science" (Laudan, 1968). Actually most scientific problems are far better understood by studying their history than their logic. However, it must be remembered that problematic history does not replace chronological history. The two approaches are complementary.

In the problematic approach the chief emphasis is placed on the history of attempts to solve problems—for instance, the nature of fertilization or the direction-giving factor in evolution. The history not only of the successful but also of the unsuccessful attempts to solve these problems is presented. In the treatment of the major controversies in the field, an endeavor is made to analyze the ideologies (or dogmas) as well as the particular evidence by which the adversaries supported their opposing theories. In problematic history the emphasis is on the working scientist and his conceptual world. What were the scientific problems of his time? What were the conceptual and technical tools available to him in his quest for a solution? What were the methods he could employ? What prevalent ideas of his period directed his research and influenced his decisions? Questions of this nature dominate the approach in problematic history.

I have chosen this approach for the present book. The reader should be aware of the fact that this is not a traditional history of science. Owing to its concentration on the history of scientific problems and concepts, it slights by necessity the biographical and sociological aspects of the history of biology. It should therefore be used in conjunction with a general history of biology (like Nordenskiöld, 1926), with the *Dictionary of Scientific Biography*, and with available histories of special areas of biology. Since I am a biologist, I am better qualified to write a history of the problems and concepts of biology than a biographical or sociological history.

It is the essence of problematic history to ask why. Why was it in England that the theory of natural selection was developed. in fact independently four times? Why did genuine population genetics arise in Russia? Why were Bateson's explanatory attempts in genetics almost uniformly wrong? Why did Correns get distracted into all sorts of peripheral problems and therefore contributed so little to major advances in genetics after 1900? Why did the Morgan school devote their efforts for so many years to reinforcing the already well-established chromosome theory of inheritance, instead of opening up new frontiers? Why were de Vries and Johannsen so much less successful in the evolutionary application of their findings than in their straight genetic work? Attempts to answer such questions require the collecting and scrutiny of much evidence, and this almost invariably leads to new insights even if the respective question turns out to have been invalid. Answers to why-questions are inevitably somewhat speculative and subjective, but they force one into the ordering of observations and into the constant testing of one's conclusions consistent with the hypothetico-deductive method. Now that the

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legitimacy of why-questions has been established even for scientific research, particularly in evolutionary biology, there should be even less question about the legitimacy of such questions in the writing of history. At the worst, the detailed analysis necessitated by such a question may establish that the assumptions underlying the question were wrong. Even this would advance our understanding.

Throughout this volume I have endeavored to carry the analysis of each problem as far as possible and to dissect heterogeneous theories and concepts into their individual components. Not all historians have been aware how complex many biological concepts are—in fact, how complex the structure of biology as a whole is. As a consequence, some exceedingly confused accounts of the history of biology have been published by authors who did not understand that there are two biologies, that of functional and that of evolutionary causations. Similarly, anyone who writes about "Darwin's theory of evolution" in the singular, without segregating the theories of gradual evolution, common descent, speciation, and the mechanism of natural selection, will be quite unable to discuss the subject competently. Most major theories of biology were, when first proposed, such composites. Their history and their impact cannot be understood unless the various components are separated and studied independently. They often belong to very different conceptual lineages. Susmoleong to surskie oil it if

It is my conviction that one cannot understand the growth of biological thought unless one understands the thought-structure of biology. For this reason I have attempted to present the insights and concepts of biology in considerable detail. This was particularly necessary in the treatment of diversity (Part I) because no other adequate treatment or conceptual framework of the science of diversity is available. I am aware of the danger that some critic might exclaim, "But this is a textbook of biology, historically arranged!" Perhaps this is what a problematical history of biology ought to be. Perhaps the greatest difficulty any conceptual history of biology must cope with is the longevity of the controversies. Many of the current controversies had their origin generations or even centuries ago, some indeed going all the way back to the Greeks. A more or less "timeless" presentation of the issues is more constructive in such cases than a chronological one.

I have tried to make each of the major sections of this volume (Diversity, Evolution, Inheritance) a self-contained unit. A similar separation is attempted for each separate problem within these

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