

## Origins of the Modern Synthesis

**The Evolutionary Synthesis.** Perspectives on the Unification of Biology. ERNST MAYR and WILLIAM B. PROVINE, Eds. Harvard University Press, Cambridge, Mass., 1980. xiv, 488 pp. \$25.

It is well known that the publication of the *Origin of Species* was followed by years of bitter controversy, particularly over the central mechanism of natural selection. However, many automatically assume that as the years went by, as Darwin's ideas got more familiar, and (particularly) as the stranglehold of religion loosened, natural selection moved smoothly to the central position it occupies in much evolutionary theorizing today. In fact, this assumption is quite false. At the beginning of this century Mendelism was rediscovered, and in the next 30 years the classical theory of the gene was articulated and elaborated. For a number of reasons, one of the chief being that the geneticists understandably tended to concentrate on distinctive characters that involved sharp contrasts with other features, the new theory of heredity was seen as an alternative, rather than as a complement, to Darwinism. Many geneticists and sympathetic biologists saw evolutionary changes as discontinuous, saltationary, rather than smoothly brought about by natural selection. T. H. Morgan, for instance, although keenly interested in evolution, always had trouble with Darwin's mechanism. And at the other end of the biological spectrum, especially among paleontologists, there were many who rejected natural selection in favor of ideas that predated Darwin's work, particularly hypotheses about the inheritance of acquired characteristics, so-called "Lamarckism."

Then in the mid-1930's something dramatic happened. It was recognized by biologists that Darwinian selection and Mendelian genetics were not true rivals but pieces of the same picture. Small new variations transmitted according to Mendelian principles were recognized as the "raw stuff" of evolution, which is then shaped and fashioned by Darwinian natural selection. The next few years saw an incredibly fertile period for evolutionary studies, as these ideas were fleshed out and elaborated by a number of workers, several of whom had themselves previously subscribed to non-Dar-

winian principles. In America one was given Theodosius Dobzhansky's *Genetics and the Origin of Species* (1937), Ernst Mayr's *Systematics and the Origin of Species* (1942), George Gaylord Simpson's *Tempo and Mode in Evolution* (1944), and just a little later G. Ledyard Stebbins's *Variation and Evolution in Plants* (1950). Elsewhere similar ideas were developing. In England, for instance, one had Julian Huxley's *Evolution, the Modern Synthesis* (1942) and in Germany Bernhard Rensch's *Neuere Probleme der Abstammungslehre* (1947, but written a little earlier).

Now, what brought about the rise of this synthesis, the modern theory of evolution, which, though currently under challenge, is still widely held today? The usual historical account gives the credit to the theoretical population geneticists working in Britain and America in the 1920's and early '30's, in particular to J. B. S. Haldane and Ronald Fisher in Britain and to Sewall Wright in the United States. It is argued that it was these men who saw that selection and Mendelism could be combined and that then, following their insights, the more traditional kinds of evolutionists came along and put empirical flesh on the theoretical bones of population genetics, thus creating the fully fledged modern evolutionary synthesis.

But there have always been some who have felt that there was more to the story than this and that the usual history is misleading if not false. Was the modern synthesis really simply an outgrowth of theoretical work in genetics? One who has argued consistently against this view is Ernst Mayr, one of the architects of the modern synthesis, and there are others who back his opinion, explicitly or implicitly. For instance, in the volume under review R. C. Lewontin points out that most biologists simply could not (and would not very much want to) tackle and comprehend the mathematics of the theoretical geneticists. In Lewontin's words, they look upon it as a form of "mental masturbation." Hence, one simply has to revise the traditional story.

Fortunately for us all, Mayr did something about his minority beliefs. Supported by the American Academy of Arts and Sciences, he organized two workshops in 1974 devoted to the genesis of the modern theory (the "synthetic" the-

ory), inviting all of the leading workers still alive, together with a number of younger evolutionists and a smattering of professional historians of biology and philosophers of science. *The Evolutionary Synthesis: Perspectives on the Unification of Biology* is the result: reports of papers and talks given at the workshops, answers to questionnaires given to those unable to attend, personal reminiscences, and other items pertinent to the story, all carefully woven together, introduced, and commented on by the two editors, Mayr and William Provine, a historian.

The workshops came none too soon. Since 1974 Dobzhansky has died, as have some other participants and some of the correspondents, including Julian Huxley. Indeed, if anything the workshops came a little late, because the geneticist L. C. Dunn died before he could prepare his contribution and as a result the key area of genetics is somewhat underrepresented in the collection. But let us rejoice at what we do have: personal contributions by Mayr himself, Dobzhansky, Rensch, Simpson (in answer to questions), E. B. Ford, C. D. Darlington, Stebbins, Ernest Boesiger (from France, and since deceased), Alexander Weinstein (a student of T. H. Morgan's), and others. In addition we have some of today's younger evolutionists writing about their elders and teachers: for instance, Stephen Jay Gould analyzes Simpson's work. And we have also some first-class essays by historians of science: Camille Limoges on French thought, Frederick Churchill on pertinent aspects of embryology, Garland Allen on T. H. Morgan and evolution, and, especially good, Mark Adams on Russian biology.

What do we learn? Was Mayr right in downplaying the importance of theoretical population genetics? I think the answer, as is so often the case, must be "yes and no." In North America certainly it becomes clear that the crucial work above all others in the formation of the evolutionary synthesis was that of Theodosius Dobzhansky: *Genetics and the Origin of Species*. Time and again we find credit being paid to this work. Thus Simpson writes,

My own thinking along theoretical lines was nevertheless mostly along lines of historiography and organismal adaptation, in fossil and recent organisms, until the first edition of Dobzhansky's *Genetics and the Origin of Species* (1937). That book profoundly changed my whole outlook and started me thinking more definitely along the lines of an explanatory (causal) synthesis and less exclusively along lines more nearly traditional in paleontology [p. 456].

And Mayr himself writes, "When Dobzhansky gave the Jesup lectures at Columbia University in 1936 [on which *Genetics and the Origin of Species* was based], it was an intellectual honeymoon for me" (p. 419). Indeed, Mayr is quite explicit that it was Dobzhansky who really made genetics come alive for him as crucial for an evolutionist (this stimulation being augmented by genetics seminars organized by Dunn). The theoretical geneticists cannot have been the main (or even a minor) direct influence. Mayr did not know of Fisher before reading Dobzhansky, and Haldane's work was unknown until 1947. Mayr writes, "Mathematical population genetics affected me only indirectly through Dobzhansky's book" (p. 421).

To use a metaphor, it is clear that at most, instead of a broad path leading from Fisher, Haldane, and Wright down to Dobzhansky, Mayr, and Simpson, with many crisscrossing trails, we have a series of paths (with respect to genetics) converging in Dobzhansky's work and then stemming out again to others. But is it enough simply to say this? Are the traditionally recognized figures still the ultimate influences, even if only through Dobzhansky? This volume shows that probably the crucial influence from population genetics came from none of the traditionally named figures (although their ideas certainly do come into Dobzhansky's work) but rather from the Russian geneticist Sergei Chetverikov, working in Moscow in the 1920's. Although never a student of Chetverikov's, Dobzhansky was much impressed by his work, and some of Chetverikov's key ideas were the very ones Dobzhansky was himself later to champion. One thinks here particularly of the claim that species are not collections of genetically uniform individuals but contain much genetic variation held in place by selection: variation ever ready to provide the material for evolution on which natural selection can act.

One may think that this all does little to prove Mayr's claims about the importance of nongenetic factors in the creating of the modern synthesis. To the contrary, rather, the place of genetics (even for Mayr) seems solidified, even if the ultimate influences were not quite what people have thought they were. However, it also becomes apparent, both from Mayr's own contributions and from those of others, that there were other crucial influences. Mayr himself establishes beyond reasonable doubt that systematics played a vital role. The theory of geographic speciation—that new species occur only when popula-

tions are isolated under new conditions—which is so much a part of the modern synthesis and for which Mayr is famous, comes straight from the naturalist-systematist tradition. It was the orthodox geneticists who argued most strenuously against this theory. Nevertheless, once again proving that a quick reading of history is inadequate, the volume shows that one cannot simply infer a straight opposition between genetics and other biological fields. Chetverikov was himself an ardent naturalist, his interest in natural history influenced his thinking about the genetics of populations, and thus we get a line down to the later theorists. Mayr writes,

Dobzhansky's thinking was so acceptable to me because, of course, the Russian school of population geneticists had grown out of taxonomy and talked in terms of species and natural populations and their variation. In fact, the Russians were interested in exactly the same phenomena as the evolutionary taxonomists; they were geneticists who spoke the language of the taxonomists and had adopted population thinking [p. 422].

This collection is not, and does not pretend to be, the definitive history of the synthetic theory of evolution. But it is a very important start. We know now that population genetics was vital to the modern evolutionary synthesis, but probably not in quite the way people have usually believed. Moreover, we know also that there were many other factors that contributed to the synthesis. This being said, let me conclude with three rather random comments inspired by this collection.

First, though in the discussion above I have concentrated on the American side of the story, the collection makes clear that things occurred both in parallel and in series elsewhere, especially in Britain. Undoubtedly Fisher was of key importance in that land, particularly in influencing such creative evolutionists as E. B. Ford. It is obvious that before the full story can be told the similarities and differences that existed across the Atlantic must be clarified. There were certainly many connections and similarities. For instance, Haldane's left-wing beliefs led him to Russia and to the influence of Chetverikov. But conversely I wonder if there were not enough differences, for instance over such concepts as genetic drift, to suggest that the extent to which a universal evolutionary synthesis was really achieved in the 1930's may have been exaggerated. Philosophers of science today warn us against assuming that scientists all adopt one monolithic theory. I wonder just how monolithic evolutionary studies really were in (say)

1945. We see dispute in Darwin's time. We see dispute today. Was there really a time when evolutionists were more like a set of identical molecules and less like the varied members of a species? This collection leaves me uncertain about the degree of agreement between the early synthetic theorists.

Second, given the keen interest there is today in human evolution, I am surprised at the apparent lack of interest in the subject on the part of the 1930's evolutionists. Dobzhansky, for example, certainly developed a strong concern with human biology in later years. Did the "monkey question," as it was called in Darwin's time, never enter and influence the thinking of evolutionists at the time of the development of the modern synthesis? One interesting footnote is that many of the group around Chetverikov were women. I wonder how they would feel about today's sociobiological speculations.

Third, there is the dreadful story of the French, intellectual dinosaurs and proud of it. Even in 1974 Ernest Boesiger could write that about 95 percent of all French biologists were more or less against Darwinism. Does one laugh or cry? Apparently in part the reason for the opposition lay in the reluctance of the French to accept ideas that were not homegrown. However, another powerful reason lay in the French educational system—those who were not Frenchmen and who did not have French university degrees could not teach in France, and professorships were passed on to close colleagues and students. Hence it was nearly impossible for Darwinian ideas to break into the community. The little headway they did make occurred only because one Darwinian thinker, a communist and not biologically trained, was given a professorship in 1945 as a reward for Resistance work. Surely here we have a prime example of the value of the study of history. In the past ten years the governments of both Canada and the United States have made it much more difficult for non-nationals (especially those with foreign degrees) to work in their respective countries. The story of the French and evolution should serve as a warning of the folly to which policies like these can lead.

I start to stray from the subject, but that is to be expected with a volume as suggestive as this. Let me simply offer thanks to Mayr, Provine, and all their contributors for what they have given us.

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