

## 80 years of watching the evolutionary scenery

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Having reached the rare age of 100 years, I find myself in a unique position: I'm the last survivor of the golden age of the Evolutionary Synthesis. That status encourages me to present a personal account of what I experienced in the years (1920s to the 1950s) that were so crucial in the history of evolutionary biology.

Evolutionary biology in its first 90 years (1859 to the 1940s) consisted of two widely divergent fields: evolutionary change in populations and biodiversity, the domains of geneticists and naturalists (systematicists), respectively. Histories covering this period were usually written by geneticists, who often neglected the evolution of biodiversity. As I am a naturalist, I consider this neglect to be a grave deficiency of most historical treatments.

Curiously, I cannot pinpoint the age at which I became an evolutionist. I received all of my education in Germany, where evolution was not really controversial. In the gymnasium (equivalent to a U.S. high school), my biology teacher took evolution for granted. So, I am quite certain, did my parents—who, to interest their three teenage sons, subscribed to a popular natural history journal that accepted evolution as a fact. Indeed, in Germany at that time there was no Protestant fundamentalism. And after I had entered university, no one raised any questions about evolution, either in my medical curriculum or in my preparations for the Ph.D. Those who were unable to adopt creation as a plausible solution for biological diversity concluded that evolution was the only rational explanation for the living world.

Even though creationism was not a major issue, evolutionary biology was nonetheless badly split by controversies. The disagreements concerned the causation of evolutionary change and the validity of various theories of evolution. I was a beneficiary of the furor, a bystander during the numerous clashes between supporters of the opposing theories favored during the first decades of the 20th century.

There are a multitude of reasons why so many controversies about evolution emerged during that period. For instance, the philosophy of science at that time was totally dominated by physics and by typology (essentialism). This philosophy was appropriate for the physical sciences but entirely unsuitable as a foundation for theories dealing with biological populations (see below). Perhaps more important was the fact that the paradigm of Darwinian evolution was not a single theory, as Darwin always insisted, but was actually composed of five quite independent theories.\* Two of these were readily accepted by the Darwinians: the simple fact of evolution (the “non-constancy of species” as Darwin called it) and the branching theory of common descent. The other three—gradual evolution, the multiplication of species, and natural selection—were accepted by only a minority of Darwin's followers. Indeed, these three theories were not universally accepted until the so-called Evolutionary Synthesis of the 1940s.

Superimposed on these conceptual differences were others that arose because of the preferences of evolutionists in different countries. The evolutionary theories considered



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valid in England or in France were rejected in Germany or the United States. One powerful author in a particular country often could determine the thinking of all his fellow scientists. Finally, different evolutionary theories were often favored by scholars in different branches of biology—say, genetics, or developmental biology, or natural history. To understand what happened during the Evolutionary Synthesis, one must be aware of the sources of disagreement during that earlier period. It was my good fortune that I became acquainted with most of the major schools of evolutionary thought of the first third of the 20th century and was therefore able to compare their claims.

In 1925–26, I prepared for my Ph.D. at the Natural History Museum of Berlin. Even though it was part of Berlin's Humboldt University, this museum had its own faculty and student body. This separation resulted in the development of two branches of evolutionary biology. The laboratory (experimental) geneticists in the University studied the processes taking place in a single population—in a single gene pool. Their emphasis was on gradual evolutionary change in a phyletic sequence of populations. The museum naturalists, including myself, were much more interested in a different aspect of evolution, the origin of biodiversity, and particularly the origin of new species and higher taxa. We studied the process of speciation and the transition from species level evolution to macroevolution—in other words, the origin of new types of organisms and the evolution of higher taxa.

We naturalists thought that evolution was indeed a gradual process, as Darwin had always insisted. Our material provided hundreds of illustrations of widespread species that gradually changed throughout their geographic range. By contrast, most early Mendelians, impressed by the discontinuous nature of genetic changes (“mutations”), thought that these mutations provided evidence for a saltational origin of new species.

When Mendel's laws were rediscovered in 1900, there was widespread hope that they would lead to a unification of the conflicting theories on speciation. Unfortunately, it turned out that the three geneticists most interested in evolution—Bateson, DeVries, and Johannsen—were typologists and opted for a mutational origin (by saltation) of new species. Worse, they rejected gradual evolution through the natural selection of small variants. For their part, the naturalists erroneously thought that the geneticists had achieved a consensus based on saltational speciation, and this led to a longlasting controversy between the naturalists and the early Mendelians.

The naturalists were unaware that there were other geneticists—like East, Castle, Baur, and Chetverikov—who may have been a majority. Their interpretation of small mutations and gradual evolution was completely compatible with the theories of the naturalists. Beginning in 1910, the work of the Columbia University group in New York under T. H. Morgan led to a refutation of the

theories of the saltational Mendelians, and established the basis for the origin of a rigorous school of mathematical population genetics, culminating in the work of R. A. Fisher, J. B. S. Haldane, and Sewall Wright. Most important, this new school of population geneticists fully accepted natural selection—and that permitted a synthesis.

Several historians have mistakenly thought that this synthesis within genetics had solved all the problems of Darwinism. That assumption, however, failed to take account of an important gap. One of the two major branches of evolutionary biology, the study of the origin of biodiversity, had been left out of the major treatises of Fisher, Haldane, and Wright. Actually, unknown to these geneticists, the problems of the origin of biodiversity had already been solved in the 1920s by several European naturalists, most important among them, Moritz Wagner,\* Karl Jordan,\* Edward Poulton,\* Chetverikov and Erwin Stresemann.

Thus, evolutionary biology around 1930 found itself in a curious position. It faced two major seemingly unsolved problems: the adaptive changes of populations and the origin of biodiversity. Two large and very active groups of evolutionists worked on these problems. One of these groups consisted of the population geneticists. As summarized in the works of Fisher, Haldane, and Wright, this group had solved the problem of gradual evolution of populations through natural selection. But they had not made any contribution to the problem of how species arise (speciation)—that is, to the problem of the origin of biodiversity. The other group of evolutionists consisted of the naturalists (taxonomists). Although unaware of the solution to the problem of gradual adaptive evolution, they had solved the open problems of the evolution of biodiversity through the contributions of the European naturalists Wagner, Jordan, Poulton, Stresemann and Chetverikov. Thus, by 1930, the two great problems of evolutionary biology had been solved, but by different groups whose accomplishments were unknown to one another.

As a student in Germany in the 1920s, I belonged to a German school of evolutionary taxonomists that was unrepresented in the United States. Our tradition placed great stress on geographic variation within species, and particularly on the importance of geographic isolation and its role in leading to the origin of new species. It accepted a Lamarckian inheritance of newly acquired characters but simultaneously accepted natural selection as facilitating gradual evolution. We decisively rejected any saltational origin of new species, as had been postulated by DeVries.

Fortunately, there was one evolutionist who had the background to be able to resolve the conflict between the geneticists and the naturalists. It was Theodosius Dobzhansky.\* He had grown up in Russia as a naturalist and beetle taxonomist, but, in 1927, he joined Morgan's laboratory in America where he became thoroughly familiar with population genetics. He was ideally suited to show that the findings of the population geneticists and those of the

European naturalists were fully compatible and that a synthesis of the theories of the two groups would provide a modern Darwinian paradigm, subsequently referred to as the "Evolutionary Synthesis".

What is particularly remarkable about this new paradigm is its stability. Dobzhansky's first approach was elaborated and modified in the ensuing years in the publications of Ernst Mayr,\* Julian Huxley,\* and Bernhard Rensch.\* I owe it to Dobzhansky that I played such an important role in the Synthesis. He knew that his own treatment of the evolution of biodiversity was insufficient. It was my task to fill the gaps in his 1937 account. Dobzhansky even provided the inspiration for the title of my book, *Systematics and the Origin of Species*—a title chosen deliberately as an equivalent to his *Genetics and the Origin of Species*. Curiously, there is no chapter on speciation in Dobzhansky's book. His description of the isolating mechanisms was erroneous. Isolating mechanisms are genetic properties of individuals, yet he included geographic barriers among them. In addition, his putative species definition refers to the stage of a process, but is not the description of a (species) population. I was able to correct this in my 1942 book.

At a meeting in Princeton in 1947, the new paradigm was fully acknowledged and it was confirmed again and again in the next 60 years. Whenever an author claimed to have found an error in the Synthesis, his claim was rapidly refuted. The two belief systems had only one inconsistency—the object of natural selection. For the geneticists the object of selection had been the gene since the 1920s, but for most naturalists it was the individual.

Elliot Sober\* showed how one could resolve this conflict. He pointed out that one must discriminate between selection of an object and selection for an object. The answer to the question of what is being selected for specifies the particular properties for which a given object of selection is favored. However, a particular gene can favor an individual without being the object of selection because it gives properties to the individual that favor its selection. It is a selection for these properties.

By the end of the 1940s the work of the evolutionists was considered to be largely completed, as indicated by the robustness of the Evolutionary Synthesis. But in the ensuing decades, all sorts of things happened that might

have had a major impact on the Darwinian paradigm. First came Avery's demonstration that nucleic acids and not proteins are the genetic material. Then in 1953, the discovery of the double helix by Watson and Crick increased the analytical capacity of the geneticists by at least an order of magnitude. Unexpectedly, however, none of these molecular findings necessitated a revision of the Darwinian paradigm—nor did the even more drastic genomic revolution that has permitted the analysis of genes down to the last base pair.

It would seem justified to assert that, so far, no revision of the Darwinian paradigm has become necessary as a consequence of the spectacular discoveries of molecular biology. But there is something else that has indeed affected our understanding of the living world: that is its immense diversity. Most of the enormous variation of kinds of organisms has so far been totally ignored by the students of speciation. We have studied the origin of new species in birds, mammals, and certain genera of fishes, lepidopterans, and molluscs, and speciation has been observed to be allopatric (geographical) in most of the studied groups. Admittedly, there have been a few exceptions, particularly in certain families, but no exceptions have been found in birds and mammals where we find good biological species, and speciation in these groups is always allopatric. However, numerous other modes of speciation have also been discovered that are unorthodox in that they differ from allopatric speciation in various ways. Among these other modes are sympatric speciation, speciation by hybridization, by polyploidy and other chromosome rearrangements, by lateral gene transfer, and by symbiogenesis. Some of these nonallopatric modes are quite frequent in certain genera of cold-blooded vertebrates, but they may be only the tip of the iceberg. There are all the other phyla of multicellular eukaryotes, the speciation of most of them still quite unexplored. This is even truer for the 70-plus phyla of unicellular protists and for the prokaryotes. There are whole new worlds to be discovered with, perhaps, new modes of speciation among the forthcoming discoveries.

The new research has one most encouraging message for the active evolutionist: it is that evolutionary biology is an endless frontier and there is still plenty to be discovered. I only regret that I won't be present to enjoy these future developments.