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A Synthesizer's Parting Words: Ernst Mayr Reflects on Evolutionary Biology as Science

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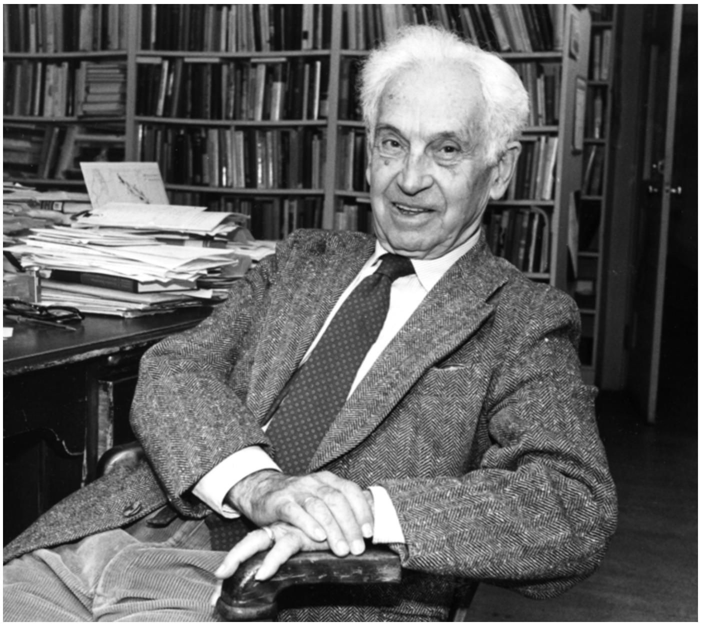

Photograph courtesy of Ernst Mayr Library, Harvard University.

We biologists rejoice in biological diversity, in all its complexity, unpredictability, and even messiness. To physicists and philosophers raised on physics as the paradigmatic science, it might sometimes look as though we are merely fumbling our way toward some deeper understanding that can ultimately be reached only through hard-nosed reductionism. Ernst Mayr's 25th book, *What Makes Biology Unique? Considerations on the Autonomy of a Scientific Discipline* (Mayr 2004a), addresses this gulf from the author's perspective as naturalist, evolutionary biologist, historian of science, and philosopher. Mayr died in February at the age of 100, so this is his final book.

Any biologist with even a passing interest in evolution knows Mayr for proposing the biological species concept, which emphasizes the importance of reproductive isolation in defining the boundaries between species. In *The Origin of Species* (1859), Charles Darwin showed that species have changed over time, and he explained how natural selection produced such change. But, to the modern reader steeped in Mayr's ideas, Darwin had surprisingly little to say about what species were and how new ones came into being. That's not to say that Darwin was silent on these matters. He had much to say about the extent of variation within and between species; about limits to successful reproduction between members of different species; and even about isolated areas, such as islands, as fertile grounds for new species to evolve. But unlike his clear explication of adaptation by natural selection, Darwin's discussions of species never pulled all his data and ideas together into an explicit theory about what species are and how new ones originate. This void had to be filled, and it was Mayr, more than anyone else, who did so.

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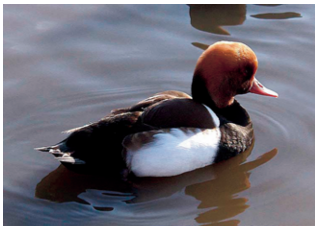
Ernst Mayr was born in Kempten, Bavaria, in 1904, only a few decades after Darwin had published *The Origin of Species.* Mayr was an avid naturalist as a teenager but, like Darwin, set out to become a medical doctor, at least partly to fulfill family expectations. But Mayr's love of natural history and adventure, also like Darwin's, would lead him, too, along a different path. While in medical school, Mayr spied two ducks of a species he had never seen before; after examining bird books, he concluded that they were red-crested pochards. However, this species had not been seen in that region for decades, and no one believed his sighting. But someone he met knew the leading ornithologist in Berlin, Erwin Stresemann, and Mayr ventured to speak with him. Stresemann was initially skeptical but, after speaking with Mayr, accepted the observation. More important, Stresemann invited Mayr to work on classifying tropical birds during his breaks from medical school, and within a couple of years Mayr had obtained a PhD in ornithology.

Before long, Mayr embarked on a voyage of discovery to collect specimens in New Guinea for Walter Rothschild, of the banking family, who was trying to build the most complete collection of birds in the world. Rothschild's previous man in New Guinea had died, and Mayr was to replace him. Before long, a report came back that Mayr, too, had died. Although Mayr suffered from malaria and other maladies, the rumors of his death were greatly exaggerated—and were off by about three-quarters of a century. His adventure in the Southern Hemisphere was extended by an invitation to lead a South Seas expedition, the fruits of which went to the American Museum of Natural History, where Mayr was appointed a curator after the expedition. Rothschild also sold his collection—more than a quarter-million specimens—to the museum when an illicit affair led to blackmail, and a cash-flow crisis, at the outset of the Great Depression.



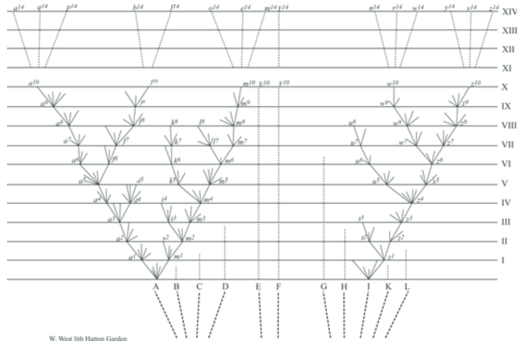
Observing red-crested pochards in an unexpected locale led Mayr toward his interest in natural history. Photograph: Adrian Pingstone.

Throughout the early and mid-1930s, Mayr devoted his work to this great collection, publishing numerous papers and species descriptions that helped launch his professional reputation and develop his expertise in the nature of species. As recently as 2001, Mayr cowrote a definitive treatise on the birds of northern Melanesia (Mayr and Diamond 2001). Mayr's coauthor, Jared Diamond, is another great synthesizer, having written the Pulitzer Prize–winning *Guns, Germs, and Steel: The Fates of Human Societies* (1997) and the recent *Collapse: How Societies Choose to Fail or Succeed* (2004). As a teenager, Diamond met Mayr and was encouraged to follow in his footsteps by studying the birds of New Guinea, during which time Diamond also became a keen observer of the human condition.

Back in the 1930s, Mayr was immersed in trying to make sense of the relationships among the species and subspecies of birds in his collections, including various examples of specimens from different islands that showed the importance of geographic isolation for speciation. Mayr was an evolutionist, and had been since he was a youth. But Mayr said he "belonged to a German school of evolutionary taxonomists that was unrepresented in the United States [that] accepted a Lamarckian inheritance of newly acquired characters but simultaneously accepted natural selection as facilitating gradual evolution" (Mayr 2004b). Meanwhile, the modern synthesis was getting under way, with population geneticists like R. A. Fisher, J. B. S. Haldane, and Sewall Wright combining mathematics with Mendelian genetics to explain how populations evolved and adapted by natural selection. Wright, with his multipeaked fitness landscapes and shifting-balance model, began to incorporate processes that might allow a single species to split into two incipient species, but for the most part the synthesis had not yet addressed how new species arose. According to Mayr, these geneticists were ignorant of systematics and had missed the evidence for the role of geographic isolation in the origin of species.

Historians of evolutionary biology often give Mayr all the credit for bringing the issues of species and speciation into the emerging synthesis, but Mayr gives priority to Theodosius Dobzhansky, whom he called the "one evolutionist who had the background to be able to resolve the conflict between the geneticists and naturalists" (Mayr 2004b). In his 1937 book *Genetics and the Origin of Species,* Dobzhansky gave numerous examples of intra- and interspecific variation in natural populations that illustrated the accumulation of genetic differences of the sort that could lead to reproductive isolation and the origin of new species. But Mayr felt that Dobzhansky had only touched on some of the issues and had confused others. Therein lay Mayr's opportunity, which he seized in a series of talks eventually culminating in his 1942 landmark book, *Systematics and the Origin of Species from the Viewpoint of a Zoologist.*

In that book, Mayr advanced a set of ideas on the nature of species and on how new species evolve that became a core part of the growing synthesis. Evolutionary theory needed to say what a biological species was in such a way that it would inform an understanding of how species originate. The definition of biological species had to be conceptual, not merely a rule book for solving each and every practical case. Mayr's biological species concept stated that "species are groups of actually or potentially interbreeding natural populations, which are reproductively isolated from other such groups" (Mayr 1942). Thus, his concept hinged on reproductive continuity among members of the same species, and reproductive barriers between different species. (The phrase "actually or potentially" was meant to address the problem that reproductive continuity is directly observable only when two species are sympatric; one must infer by some other means whether reproductive barriers would exist if allopatric species were to become sympatric.) Importantly, the extent of mor-



The single figure from* On the Origin of Species *illustrates Darwin's thinking about the evolution of species over time and demonstrates the focus of Mayr's lifework. Image courtesy of the British Library.

phological differentiation is irrelevant to the biological species concept, except to the extent that such differences constrain reproduction. Thus, in some taxa, two different species may be similar in outward appearance if subtle differences in behavior preclude them from breeding. In other taxa, certain varieties might be morphologically distinctive yet belong to the same species if they can successfully interbreed in regions of sympatry.

Given this emphasis on reproductive isolation, the next question was how such isolation evolved. For several decades, Mayr was adamant that such isolation could evolve only in allopatry, not in sympatry. The idea was that a population became disconnected from the rest of its species distribution by colonizing a distant area, or by changes in geology or climate that presented a barrier to movement. Over time, the separated populations would diverge from one another as they adapted to their different environments or as their gene pools drifted apart. Sympatric speciation was untenable to Mayr, owing both to its implausibility and to the paucity of evidence. The implausibility arose because it seemed to require that an incipient species must change both its ecological niche and its reproductive biology simultaneously, whereas neither change alone could become established. In recent decades, however, Guy Bush, along with others, gathered increasingly strong evidence for sympatric speciation in some insects and other groups. These researchers maintained that sympatric speciation was readily achieved in certain groups, such as insects that mated on the same plants on which they fed. In these cases, changes in ecological niche and reproductive behavior were manifestations of the same genetic changes, which overcame the objection that neither change alone could become established. Despite his earlier skepticism, Mayr conceded that "so many examples of sympatric speciation were found, particularly among fishes and insects, that there is now no longer any doubt about the frequency of sympatric speciation" (Mayr 2004a, p. 108).

Mayr also backtracked from his earlier emphasis on founder events in triggering so-called genetic revolutions. The idea was that incipient species often started as small populations whose gene pools were subject to rapid change because of random drift, inbreeding, and complex interactions among multiple loci. Absent much compelling support, the role of genetic revolutions in the origin of species shifted to the back burner and is not discussed in his final book. But despite these concessions and unresolved issues, Mayr's biological species concept, and especially his emphasis on how this concept relates to the process of speciation, was hugely influential in drawing attention to a core aspect of evolutionary theory that demanded careful analysis. There has been a resurgence of productive and important work on species and speciation in recent years. Readers interested in learning about the current state of knowledge and debate on species concepts and speciation will find excellent resources in two recent books: *Endless Forms: Species and Speciation,* a collection of papers edited by Daniel Howard and Stewart Berlocher (1998), and *Speciation,* a synthesis by Jerry Coyne and Allen Orr (2004).

Turning to Mayr's final book, most chapters are borrowed from his previous writings, but with several new ones to pull things together. Most chapters bear on the stated subject of the book—the autonomy of biology as a scientific discipline—but their integration into a cohesive whole is often more implicit than explicit. Hence, the book reads more like a collection of essays than like one long argument. Mayr also often refers to points he has made elsewhere, which may leave some readers feeling obliged to track down the other sources. Again, this makes the book feel less cohesive than it might have been. There are also some poorly edited sections. One particularly jarring passage has Mayr saying, out of the blue, "Yes, God was the creator of this world and either directly or through his laws he was responsible for everything that existed and occurred" (Mayr 2004a, p. 15). From what follows, it would seem he meant this statement to express an idea compatible with those of early physicists, like Galileo, who accepted a superior organizing force beyond their theories. Nonetheless, the transition is awkward. Some specialists will want to read this book, but other books by Mayr are probably better suited for most readers. For the general reader, I recommend his penultimate book, *What Evolution Is* (2001), or *One Long Argument* (1991), which examines Darwin's contributions to evolutionary theory. Historians and philosophers just getting interested in evolution should begin with Mayr's treatise *The Growth of Biological Thought* (1982).

Mayr begins his final book by arguing that the philosophical conceptualization of science has relied too heavily on the case of physics. Although some attributes are shared among all sciences, such as the organization of knowledge in terms of explanatory principles, he maintains that some other attributes are not necessarily shared. For example, Mayr argues that the precise mathematics that underlie physics are not applicable to biology, in which determinism, typological thinking, and reductionism have limited utility. In chapter 2, he builds on this point by splitting biology into two distinct domains, functional and historical. While functional biology may fit within a framework similar to that of physics, Mayr argues that the historical domain of biology—in essence, evolution—requires a different framework. My own view is that evolutionary history, like the history of the physical universe, reflects dynamical processes (e.g., mutation and natural selection) that can be described mathematically and tested experimentally (as indeed they often are), although evolving biological systems are more complicated than what physicists study. Mayr's distinction between the functional and historical domains of biological understanding may reflect his limited interest in evolutionary dynamics per se.

In chapter 3, Mayr contrasts the goal-directed behaviors exhibited by living organisms with teleology. The challenge of biology is to understand the existence of developmental and behavioral programs that enable organisms to achieve specific goals in the future. Natural selection provides a satisfactory explanation if organisms with the genes encoding these programs have had greater reproductive success than those without such programs under past circumstances similar to those that produce these goal-directed behaviors. Mayr calls these evolved organismal programs "teleonomic" to distinguish them from the metaphysical baggage associated with the word *teleology.* Continuing in a philosophical vein, chapter 4 contrasts the aims of reductionism and holism. Mayr emphasizes that the latter is essential in biology, owing to ubiquitous interactions that generate emergent properties. Mayr also rejects the adequacy of theory reduction, whereby one theory subsumes another. He argues that "no principle of historical evolutionary theory can ever be reduced to the laws of physics or chemistry. Contrary to the claims of some reductionists, this has nothing to do with any alleged immaturity of biology" (Mayr 2004a, p. 79).

Chapters 5 and 6 discuss the vast influence of Darwin on modern biological thought. Mayr counts five major theories among Darwin's contributions: evolutionary change per se, common ancestry, gradualism, speciation, and natural selection. While Mayr discusses some limitations of Darwin's ideas and certain ongoing debates, he says, "It strikes me as almost miraculous that Darwin in 1859 came so close to what would be considered valid 145 years later" (Mayr 2004a, p. 113). Mayr also emphasizes how Darwin and his theories overturned such deeply held concepts as teleology, typology, and determinism, replacing them with population-based concepts of selection acting on variation that arises by chance.

In fact, Darwin had misgivings about invoking chance as the source of variation. In his chapter on the laws of variation, Darwin wrote, "I have hitherto sometimes spoken as if the variations...had been due to chance. This, of course, is a wholly incorrect expression, but it serves to acknowledge plainly our ignorance of the cause of each particular variation" (Darwin 1859, p. 131). One of Darwin's key insights, in my view, was separating the origin and the fate of heritable variations. Only by looking past the mysterious source of variation was he able to develop the principle of natural selection to explain why certain variations persist and others perish. Of course, later discoveries about mutations and DNA clarified the origin and physical nature of heritable variations, while beautiful experiments by Salvador Luria and Max Delbrück, and by Joshua and Esther Lederberg, showed that mutations are indeed random insofar as they are independent of selection on the resulting phenotype.

In 1993, I corresponded with Mayr on the randomness of mutations following the publication of a review I wrote with John Mittler (Lenski and Mittler 1993). Several years earlier, John Cairns and colleagues (1988) had published a provocative paper suggesting that bacteria could produce beneficial mutations in response to their immediate needs. This phenomenon, known as "directed mutation," attracted much attention because it challenged the view that selection provides the direction in evolution while mutation is random. To make a long story short, alternative explanations were proposed and tested that did not require such a radical interpretation as directed mutation. However, the issue attracted Mayr's interest, and he wrote in a letter to me (21 January 1993) that "I could imagine that processes in prokaryotes could be of such immediate selective advantage that they would be incorporated into the variational mechanism of the genotype." He clarified this point in another letter (22 February 1993): "I did not imagine that my proposed mechanism consists of the induction of the needed mutation, but rather of an increase in the mutability of the relevant locus." In fact, he was remarkably prescient about the possibility that bacteria may have evolved ways to bias the production of mutations toward certain genetic loci, without mutations actually being directed by the immediate needs of an organism. At about the same time, bacterial geneticists Paul Rainey and Richard Moxon sent me their paper (published in 1993) citing evidence for the sort of process that Mayr had suggested. This episode shows Mayr's engagement with ongoing science even in his later years.

Returning to Mayr's most recent book, he dismisses the existence of evolutionary laws and maintains that the theory of evolution is based instead on concepts. However, it seems to me reasonable to view natural selection as a scientific law. Natural selection, like gravity, can be represented precisely using mathematics. Complications arise because natural selection interacts with various other processes, such as random drift in finite populations; but gravity also interacts with other forces, such as friction. Moreover, natural selection transcends biology and can be applied as an algorithmic process to generate useful new features in electrical circuits, software, robotics, and even art (Lenski 2004).

Mayr explains in chapter 7 that the maturation of Darwinism was not the single synthesis we sometimes imagine, in which everyone came together and worked things out. Instead, it spanned decades and encompassed August Weismann's refutation of the inheritance of acquired characters; the reconciliation of Mendelian genetics and natural selection, which concerned evolution within a species; and the development of ideas about how evolution produced new species. All this was followed by a period of great advances in molecular genetics, which split biology apart over the short run but eventually strengthened the Darwinian framework by its remarkable confirmation of the common ancestry of all life. Mayr then addresses some of the various meanings of selection in chapter 8. He gets off on the wrong foot, in my view, by suggesting important differences between "selection of the best" and "culling" the worst. I think this distinction is a matter of degree and semantics, rather than the important difference he implies. Mayr, like Darwin, had an aversion to mathematics, and this perhaps colored some of the ways in which he contrasts biology and physics as exemplars of science. I also found Mayr's discussion of levels of selection—gene, individual, kin, and group—to be rather weak, with too much emphasis on words rather than illuminating biological examples or mathematical theory. Elsewhere, Mayr criticizes philosophers of science for excess abstraction, and the same criticism can be made here.

In chapter 9, Mayr questions Thomas Kuhn's view of scientific revolutions, according to which there are long periods of normal science punctuated by revolutionary advances that overturn previous thinking. Mayr doesn't argue that science is necessarily gradual, but rather that there is a broad distribution of rates of progress. Moreover, some parts of a new theory may be revolutionary in their effects, while others require incremental science to become established. For example, Mayr points out that Darwin's theory of evolution per se was accepted immediately and had a revolutionary impact, while natural selection required a long period of investigation before becoming widely accepted. In particular, acceptance of natural selection required not only the discovery of genetics but also the further careful understanding that Mendelian genetics did not itself imply discontinuous evolution. Mayr also mentions the revolutionary advances in genetics after the discovery of DNA as the material basis of heredity, which led to "a new field, with new scientists, new problems, new experimental methods, new journals, new textbooks and new culture heroes" (Mayr 2004a, p. 164). Yet all this newness produced a transition that was entirely compatible with previous developments in genetics. Mayr argues that the "rise of molecular biology was revolutionary, but it was not a Kuhnian revolution" (Mayr 2004a, p. 164). He concludes that Kuhn's theory is overinfluenced by the dichotomous perspective of a physicist. Mayr favors an epistemology according to which science advances in a manner that is more evolutionary than revolutionary.

Chapter 10 addresses the "species problem" and thus goes to the heart of Mayr's lifelong interests and contributions. He downplays his own role by stating that "a number of recent historians have credited me with authorship of the [biological species concept]. This also is not correct. My merit was to propose a simple, concise definition" (Mayr 2004a, p. 179). And while he strongly emphasizes the value of conceptualization, he dismisses "armchair taxonomists" and notes his own credentials as a "practicing systematist" who described "26 new species and 473 new subspecies of birds" (Mayr 2004a, p. 172). He also rejects new species concepts that encompass asexual as well as sexual organisms; he asserts that any such concept is wrongheaded and "misses the basic characteristics of the biological species definition (the protection of harmonious gene pools)" (Mayr 2004a, p. 190).

Mayr ends with two chapters that reflect the intellectual vitality of an old man looking across the reaches of time and space. The penultimate chapter defends the importance of understanding human evolution, despite its difficulties, while the last chapter considers the search for extraterrestrial intelligence. He questions spending money on that search instead of "researching the rapidly dwindling diversity of the tropical rainforests on Earth" and asks, "Should we perhaps organize a search for terrestrial intelligence?" (Mayr 2004a, pp. 212–213). However, in the human quest for discovery, both terrestrial and extraterrestrial efforts seem highly worthwhile to me. Mayr also misrepresents the interests of many researchers when he says they "could not care less whether some bacteria-like very primitive organisms exist on other planets" (Mayr 2004a, p. 213). Be that as it may, this final chapter shows Ernst Mayr as someone quite content to make his home on Earth, and skeptical of the heavenly life.

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