From: P.L. Farber, Finding Order in Nature (JHUP: 2000)

8 New Synthesis

The Modern Theory of Evolution, 1900–1950

The Water Babies, published in 1863, delighted several generations of English-speaking children. Charles Kingsley, a close friend of Thomas Henry Huxley and a prominent Victorian clergyman, wrote the book as a fantasy to demonstrate a parallel between the natural and spiritual worlds. Fairies transformed children who had been mistreated or had died of preventable diseases into "water babies" (four-inch, humanlike creatures with external gills). Through moral evolution, they were able to grow up and become adult humans. Kingsley's charming story plays with ideas about what we can see and know and challenges children to question whether things they cannot see (water babies) actually exist.

In 1892 at the age of nearly five, Julian Huxley read Kingsley's book. Intrigued by an illustration of his grandfather, Thomas Henry Huxley, and Richard Owen examining a bottle that supposedly contained a water baby, he wrote to his grandfather to ask whether he had seen a water baby and whether he (Julian) might someday see one. The elderly Huxley (he died three years later) waffled on the issue of what he had actually seen but told his grandson: "There are some people who see a great deal and some who see very little in the same things. When you grow up I dare say you will be one of the great-deal seers and see things more wonderful than Water Babies where other folks can see nothing."*

Julian Huxley did just that. Admirers thought that he had vast synthetic—at times visionary—ability. His critics thought he saw more than actually existed. From an early age he found living things fascinating. In his autobiography he wrote that his first memory (which dated from age four) was of a toad that jumped out of a hawthorn hedge. Whether or not that event led to his career as a scientific naturalist, as Huxley claimed, he did develop a strong interest in natural history, and in the life sciences more generally. Bird watching at Eton led to a serious interest in ornithology, especially in the behavior of birds,

*Julian Huxley, *Memories* (London: George Allen and Unwin, 1970), 24–25.

and as a student at Oxford he explored the evolutionary foundations of bird behavior.

Huxley did not limit himself to the traditional subjects of natural history. A year's fellowship in 1909 at the Zoological Station in Naples allowed him to experience the excitement (and often the frustrations) of experimental biology. He experimented on sponges by separating the organisms into individual cells and then following how they regrouped and developed. Although he published the studies, he felt dissatisfied with his abilities in physiological research—but not enough to abandon them completely. He went on to do serious investigations of growth and development.

His first love, natural history, was the perspective that informed all his work, but it was deeply infused with knowledge from all branches of biology. This can be seen in the volume of essays he edited in 1937, *New Systematics.* The book reflected the work of the Association for the Study of Systematics in Relation to General Biology, one of several groups in different countries which focused on revitalizing taxonomy. During the third and fourth decades of the twentieth century, naturalists, particularly in the United States, Great Britain, and the Soviet Union, hoped that the pioneering work being done in cytology, ecology, and genetics might provide the basis for an "experimental taxonomy." In spite of initial enthusiasm, the new systematics proved to be problematic. The fields capable of illuminating taxonomy were themselves experiencing considerable flux, and the individuals involved in classification rarely had time to bring themselves fully up-to-date on the latest developments. Cytological or ecological knowledge applied to taxonomic questions allowed a broad range of interpretation, and by midcentury most naturalists realized it was unlikely that the new systematics would eliminate the conundrums of taxonomy. Experimental taxonomy, however, did provide many new techniques and tools for taxonomic work.

Theodosius Dobzhansky, a Ukrainian naturalist who in 1927, early in his career, came to the United States to work with the geneticist Thomas Hunt Morgan, made striking use of the new tools. Dobzhansky clarified the taxonomic relationship of what had been considered two major geographical races of a single species of fly (*Drosophila pseudoobscura*). By using staining techniques developed to study cells, he and his group identified structural rearrangements on the chromosomes (easily seen in the gigantic chromosomes of the fly's salivary glands) of the two races, and these rearrangements could be used to help differentiate the races. Although known to produce sterile offspring when interbred, the two races appeared morphologically identical and overlapped geographically. They differed, however, in a variety of physiological functions. Ultimately, it was the genetic and chromosomal differences that proved central in convincing Dobzhansky and others that the two races were actually separate species.

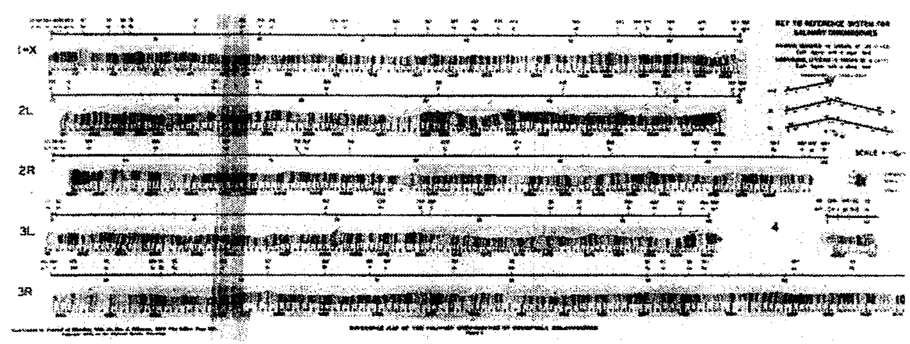
Not many species had chromosomes as easily seen as those of *Drosophila*, so Dobzhansky's techniques would not be generally applicable. But that was not the point. Taxonomists came to realize that the new biological specialties had tools and techniques that could be incorporated into an understanding of biological relationships. Because many of these relationships were evolutionary ones, the new systematics helped bring an even closer tie between taxonomy and research on evolution. It was no accident, then, that many researchers associated with the new systematics were important in the reformulation of the modern theory of evolution.

The Modern Synthesis

Life scientists in the late nineteenth century had come to general agreement that living organisms evolved over time, but by the dawn of the twentieth century there was little consensus on how that evolution occurred. Darwin's emphasis on natural selection seemed overly simplistic to many. Scientists proposed various alternatives that stressed either large-scale, sudden changes or general, progressive "tendencies."

The rediscovery of Mendel's Laws in 1900 would later be of central importance, but it initially distanced many of Darwin's supporters from the research done in heredity and from what ultimately came to be the specialty of *genetics*. Central to Mendelian genetics is the notion that hereditary traits are discrete units that come from parents and can recombine in the fertilized eggs that become offspring. Understanding how traits recombine appeared to many researchers the key to evolution. The leading figures in genetics criticized the "outdated" selectionist (i.e., Darwinian) approach, but that did not discourage a central core of naturalists. In particular, several of the leading figures of the new systematics movement, notably Julian Huxley and Ernst Mayr, remained fundamentally Darwinian in their orientation and brought that perspective to the entire body of their work. It was, however, the pioneering research done in population genetics by Soviet scientists, many of whom had naturalist backgrounds, which proved decisive in uniting evolution and modern genetics.

Theodosius Dobzhansky began his career in Kiev in 1918 studying the systematics of ladybird beetles. His move to the genetics institute in Leningrad shifted him to a different line of research, but his natural history background remained an important influence. Dobzhansky studied the genetics of popu-



Choice of Research Animals

Drosophila, the common fruit fly, played a special role in the Modern Synthesis. Its study helped establish modern genetics, and research on its distribution contributed vital knowledge in population genetics. Why fruit flies? In part, they are easy and inexpensive to maintain and study. They require two weeks to complete a generation; a single pair can produce hundreds of offspring. The laws governing the inheritance of their physical traits are simple. Equally important, they possess giant salivary gland chromosomes that can be easily stained to study their structure.

The *chromosome map* shown here demonstrates what geneticists could do in the 1930s. For example, Theodosius Dobzhansky made use of such maps to conduct research on *Drosophila* and to show important relationships among different populations.

■ From *Journal of Heredity* 26, no. 2 (1936); courtesy of Oxford University Press.

lations found in nature, and his classic *Genetics and the Origin of Species* (1937), which he wrote after moving to the United States, argued for a return to emphasizing Darwin's concept of natural selection in evolution.

Unlike the history of other great theoretical shifts, the emergence of the Modern Synthesis had several classic texts rather than one. The difference reflects the much larger nature of modern scientific communities, which are communal enterprises, in contrast to earlier times, when the scientific investigator was more isolated. Dobzhansky's book, the first of the seminal texts that defined the Modern Synthesis, sketched the outlines of the modern theory of evolution. Other texts quickly followed. Ernst Mayr (curator of birds at the American Museum of Natural History in New York and previously leader of three expeditions to New Guinea and the Solomon Islands from the Zoological Museum at the University of Berlin) wrote *Systematics and the Origin of Species* (1942) from a naturalist's perspective and stressed the importance of geographical variation. Julian Huxley's *Evolution: The Modern Synthesis,* published the same year, supplied the most popular name used for the modern theory of evolution. Like Mayr, he took his starting point from the natural history tradition. George Gaylord Simpson's study *Tempo and Mode in Evolution* (1944) used the fossil record to establish the compatibility of the Modern Synthesis with paleontology. Later, G. Ledyard Stebbins's *Variation and Evolution in Plants* (1950) brought plants fully into the story.

Several different lines of research converged in the Modern Synthesis. The naturalist tradition played a critical role by supplying a conception of species which expanded Darwin's insight and made clear a distinction central to Darwinian evolution. *Species* before Darwin had traditionally been defined in terms of physical characteristics. Occasionally naturalists used other criteria, for example, Buffon recommended successful interbreeding as a test of relatedness. Given the practice in natural history of relying on preserved museum specimens for classification, the use of anatomical features, usually external, had predominated. A *type specimen* referred to an individual specimen, usually in a known collection, that served as a physical model to define the species. *Type species,* similarly, referred to individual species that embodied the shared characters of a genus. Darwin's shift to a dynamic view of nature undermined the meaning of types because he considered species as groups of individuals; the composition of the group—due to variation and selection—changing in time. A species, therefore, needed to be thought of as a population, or more accurately, a set of populations. The ornithologists whom Mayr studied under in Germany had employed a version of this conception of species. Mayr, who had field experience as well as museum training, emphasized the need to reconceptualize older concepts of species, or what he called the *typological* concept of species which stressed a static plan, and to draw out the populational thinking implied by Darwin in light of new knowledge.

An understanding that species had isolating mechanisms that prevented successful cross-species reproduction lay at the heart of the new concept. Mayr's *Systematics and the Origin of Species* proposed that a new species develops if a population becomes geographically isolated from its parental species population and its members develop characteristics that make it impossible to successfully reproduce with individuals from the parent population should contact between the populations be renewed. The perspective reflected Mayr's geographical research on birds. Mayr proposed a new definition of species, which he called the *biological species concept.* Expressed in the simplest terms, biological species are "groups of actually or potentially interbreeding natural

populations, which are reproductively isolated from other such groups."* Even though Mayr's characterization underestimated other recognized methods of speciation that exist in plants and various lower organisms, it quickly caught on because it captured both the natural history background and the genetic underpinning of evolutionary thought.

Critical as Mayr's work was for the Modern Synthesis, historians more often cite Dobzhansky's *Genetics and the Origin of Species* as being of central importance, in part because it came out first. More important, the Modern Synthesis emphasized the genetics of population change. The collaboration of mathematical modelers, laboratory scientists, and field biologists brought the study of the genetics of natural populations, the genetics of specific traits in individuals, and the theoretical models of population dynamics together into a new discipline of *population genetics.* Pioneers in this field sought to demonstrate how natural selection operating on small characteristics could result in larger, stable evolutionary change.

Dobzhansky, who in his early research had been interested in the amount of variation in natural populations, took techniques from recent work in genetics and applied them to the study of natural populations of *Drosophila* to demonstrate the genetic variation within and between species. Dobzhansky also collaborated with the American mathematical geneticist Sewell Wright, who had done experimental and theoretical work in both a university setting and in the Animal Husbandry Division of the U.S. Department of Agriculture. Wright stressed the interaction of gene systems and, in what he termed *random genetic drift,* the chance fluctuation of gene frequencies in small populations. The rigor of the mathematical models and the tie to experimental results lent greater scientific respectability to the theory of evolution. Given that scientists had criticized earlier theories of evolution as too speculative, the field of genetics proved valuable by providing an impressive and rigorous material basis for a new theory of Darwinian evolution.

Unifying Strength of the Modern Synthesis

In the wake of the publicity surrounding the dramatic research being conducted today in molecular biology and in molecular genetics which has resulted in genetically engineered crops and the identification of the genes responsible for specific diseases, one could easily lose sight of the Modern Synthesis's tremendous intellectual importance. The modern theory of evolu-

*Ernst Mayr, *Systematics and the Origin of Species* (1942; New York: Dover, 1964), 120.

tion represents a unifying project more ambitious than Darwin's earlier synthesis. Late-nineteenth-century life scientists such as Haeckel had argued for a synthesis based on evolutionary principles, but the lack of a sufficiently coherent and accepted theory of evolution impeded the development of a unified biology. The architects of the Modern Synthesis deliberately set out in the 1930s and 1940s to construct a theory of evolution that would make sense of what they already knew of the living world. Their success rested on acceptance of a formulation of natural selection with population genetics as the driving force of evolution. Random mutation, recombination, and selection drove the evolutionary process, and everything in biology could be understood as a consequence. Dobzhansky's famous quip that nothing in biology made sense except in the light of evolution best sums up the enormous generalizing power the Modern Synthesis claimed for itself.

The early proponents of the Modern Synthesis also saw evolution in broad philosophic terms and thought that as a worldview it had social significance. Julian Huxley, perhaps more than any of the other creators of the modern theory of evolution, elaborated on the wider implications of evolution.

Huxley claimed in *Evolution: The Modern Synthesis* that biology had embarked on a phase of unification following a period in which emerging disciplines had developed in isolation. He held that in the study of evolution varied facets came together: ecology, genetics, paleontology, distribution, embryology, systematics, comparative physiology, and comparative anatomy found common ground in the study of evolution. The unification of biology held even more promises, however. Huxley claimed that the study of evolution revealed biological progress over time. But what of the future? Although he argued that the study of evolution did not reveal purpose in nature, it did show direction: toward an increase in control, independence, and knowledge, and toward the means of coordinating knowledge. Human evolution reflected those advances and stood as the latest stage of an ancient story.

Typical of a large segment of Western intellectuals at the time, Huxley sought a replacement for the crumbling Victorian worldview that had been undermined by the First World War. For him, natural science promised to be this replacement, and evolution, the science of origins, appeared the most likely to chart human destiny. Huxley argued that humankind had reached a stage of evolution where it created values and that future human evolution would entail the increase and advancement of aesthetic, intellectual, and spiritual experience. In numerous essays Huxley elaborated on a scientific humanism that he characterized as basically democratic and progressive and that stressed education and humanitarian concerns based on scientific knowledge.

Naturalists in the Field

Field biology has improved considerably since the heroic days when naturalists traveled off to distant lands without the protection of vaccinations or the lifelines of radios and cell phones. Many early naturalists of the late eighteenth and early nineteenth centuries did not survive their journeys. Collecting in the field is still hazardous, and naturalists must contend with medical, political, climatic, and logistical problems. But the attraction remains.

Ernst Mayr collected birds in Dutch New Guinea, Papua New Guinea, and the Solomon Islands between 1928 and 1930. His observations on the distributions of birds later proved critical in his evolutionary thinking. This photograph of Mayr and his Malay assistant was taken in Dutch New Guinea in June 1928.

■ Courtesy of Ernst Mayr.

Other architects of the Modern Synthesis explored the human implications of evolution with fairly similar conclusions, resulting in a liberal humanism that stressed the value of science and the mechanical and material basis of life. Like earlier naturalists who framed their vision of nature in terms of contemporary ideas, the modern evolutionists crafted a consistent and highly popular image that suited the political and intellectual concepts of the day. Just as Linnaeus located his taxonomic contributions in the context of a northern Christianity, and Buffon constructed a tableau that he offered as a cornerstone to the French Enlightenment's efforts to reform European thought, so, too, did Huxley and his associates envision their brilliant biological synthesis as part of a larger cultural construction. The strength of the biology, they held, lent support to their shared social and philosophical convictions. Although the architects of the Modern Synthesis regarded evolution as part of a wider worldview, we should not confuse, however, the vast unifying power of the theory with an acceptance of its alleged philosophical or social implications.

The modern theory of evolution unifies the life sciences in a way that early naturalists had hoped their science would. The naturalist tradition sought to describe the living world and to discern its order. Darwin's theory of evolution grew out of his attempt to understand how different species came into existence and their relationships to one another. In so doing, he fashioned a th ory that explained other regularities and made sense of why living organisr functioned as they did. Physiologists uncovered how organisms functioned ar showed the amazing complexity and integration of systems. Evolution, by r lating function to adaptation, showed how and why functions came into b ing. The Modern Synthesis used the fruits of decades of experimental biolog to help elucidate the material basis of evolution and to bring a deeper unde standing of its mechanisms. By its profoundly historical nature, the theor continues to demonstrate the importance of the naturalist tradition. Only b studying what has actually come into existence; only by uncovering the extan fossil record to determine which phylogenies have developed in the course o time; and only by documenting the distributions of contemporary and extinc species can we know life on Earth.

The life sciences have uncovered many general laws, such as Mendel's Laws of inheritance and the genetic code. But the theory of evolution goes beyond significant and interesting regularities common to living organisms by viewing all biological knowledge as the result of a long historical process. The Modern Synthesis, in an important way, fulfills the goal of earlier naturalists to describe and comprehend the order in nature. It is not what Linnaeus or Buffon would have expected—and, like all of our central unifying scientific theories, it remains to be seen how future generations will alter or regard it—but it currently stands as a major milestone in the naturalist tradition.