



Ernst W. Mayr

1904–2005

BIOGRAPHICAL

*Memoirs*

*A Biographical Memoir by  
Walter J. Bock*

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# ERNST WALTER MAYER

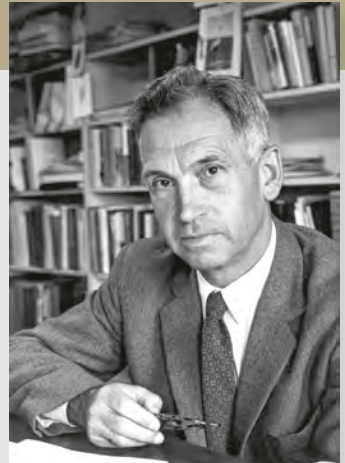
July 5, 1904–February 3, 2005

Elected to the NAS, 1954

Ernst Walter Mayr<sup>1,2</sup> was a man of the twentieth century, having missed only a few years at the beginning of that century and lived a few years into the twenty-first. He was by inclination a naturalist from youth onward, which established the foundation for his career as an evolutionary biologist. Often called the “Darwin of the twentieth century,” Ernst was one of the leading evolutionary biologists of his time, having been a major architect of that famous meeting of the minds known as the modern evolutionary synthesis of 1937-48 and the moving force behind the founding of the Society for the Study of Evolution.

Although he was born and educated in Germany, Ernst was a thoroughly American scientist, having worked at New York’s American Museum of Natural History (AMNH) and the Museum of Comparative Zoology at Harvard University for 74 of his 100 years. Despite his highly developed scientific mind, Ernst was truly a non-technical person and complained in his later years about libraries’ putting their catalogues in an electronic form because he did not know how to type—he did not even know the location of the keys on the keyboard—which delayed him greatly in finding books. The most advanced electronic device he ever used was a Dictaphone. Computers were out of the question.

Ernst was outgoing, sought out interesting people whether they were important or not, talked to them, listened to what they said, read intensively, and thought deeply about what he took in. He had an amazing memory, but, more importantly, he could readily put small pieces of knowledge together into new and significant ideas. He was a real teacher and simply could not bear to have someone leave his company with wrong notions. He had firmly held beliefs, hence many people considered him to be somewhat dogmatic. He was interested in what was correct, but not necessarily in who was correct. He would argue



Ernst Mayr

By Walter J. Bock

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strongly for his ideas, but he would change his position readily if he became persuaded of the rightness of the opposing point of view. One had to be certain of one's facts and logic in any discussion with Ernst, which prevented many students and co-workers from discussing controversial ideas with him, something that he regretted. I can recall his saying, "My bark is worse than my bite."

My first meeting with Ernst was in the summer of 1953, when I was an undergraduate student volunteer in the Department of Ornithology at the AMNH. He had just started his tenure as an Alexander Agassiz Professor of Zoology at Harvard's Museum of Comparative Zoology. We talked a bit about my educational aims. Late the following summer, when he was again at the AMNH, I was able to speak with him further about graduate studies, and to my complete surprise he suggested that I study with him at Harvard. I applied, was accepted, and received my degree in 1959.

From that time forward I maintained close contacts with Ernst as a mentor to me and as a close friend for the rest of his life. I visited him for the last time in late December 2004, a few weeks before his death, when he was in the nursing wing of his retirement home. During my visit, he walked down a long corridor to another room for physical therapy, which he did every day because he was anxious to return to his apartment. I also spoke with him by telephone several times the following month. His mind was remarkably clear until the very end, but he was slowing down and finally lost interest in his last project, which was on Darwin's attitude toward creationism (Bock, 2005).

Major treatments of Ernst's work in evolutionary biology and the history and philosophy of biology (Greene and Ruse, 1994) and in ornithology (Bock, 2004a; Bock and Lein, 2005) are available, as is a complete bibliography of his papers by Jürgen Haffer (2005). Haffer (2007) has also completed a full-length biography of Ernst Mayr.

### **Early life**

Ernst Mayr, the second son of three, was born on July 5, 1904, in Kempten, Bavaria. His father, Otto Mayr, was a jurist in the Bavarian court system; Otto died of kidney cancer in 1917 at just 49 years of age, shortly before he was to be appointed to the supreme court in Leipzig. Ernst's mother, Helene Pusinelli (1870–1952), was of a German family with Italian ancestry who had come to Germany in 1809. Ernst grew up in a tightly knit family, with the parents taking the three boys on long excursions on weekends, during which they placed great emphasis on the boys' learning natural history. By the time he was 10 years old, Ernst could identify the birds of the area by song as well as by sight.

Following a tradition in the Mayr family in which the boys went into either law or medicine, Ernst opted for medicine—though, considering where his life’s path would lead, perhaps with less than full enthusiasm.

After his father’s death, the family moved to Dresden, the hometown of his mother, where he attended the Gymnasium, graduating in 1923. Following a tradition in the Mayr family in which the boys went into either law or medicine, Ernst opted for medicine—though, considering where his life’s path would lead, perhaps with less than full enthusiasm.

In Dresden Ernst joined the Saxony Bird Society, a group of amateur birders. When he graduated from the Gymnasium in April, his mother gave him a new pair of binoculars as a present for earning his *Abitur*—a combination school-leaving and university enrollment eligibility certificate. He used his free time before starting his medical studies to do some intensive bird watching. One day in late March he bicycled to the ponds of Moritzburg, the former hunting palace of the kings of Saxony, where he observed a pair of ducks that were new to him and not mentioned in the guidebooks. These proved to be a pair of red-crested pochards (*Netta rufina*), a species that had not been reported in Germany since 1846 (1).<sup>3</sup>

This fortuitous event would have an impact on Ernst that he could hardly have imagined at the time. He was unable to show this pair of ducks to any of the older members of the Saxony Bird Club, because the birds had disappeared before the weekend, when some adult members were able to accompany him to Moritzburg. But one of the members was a former classmate of Dr. Erwin Stresemann, of the Zoological Museum in Berlin, and he provided Ernst with a letter of introduction to Stresemann.

For his medical studies Ernst chose the University of Greifswald, located near the southern coast of the Baltic Sea in the northeast part of Germany. He made this choice not on the basis of the university’s having any kind of reputation as a top medical school, but because it sat in one of the more ornithologically interesting regions of Germany. And by good fortune, the train he would be taking from Dresden to enroll at Greifswald made a stop in Berlin. Armed with his letter of introduction, Ernst got off the train in Berlin and called on Stresemann to report his sighting of the red-crested pochards. Stresemann read Ernst’s field notes carefully and then quizzed him on the identity of other species of ducks, using specimens from the museum’s collection. He was satisfied

3 Numbers in this form refer to the Selected Bibliography at the end of the text.

with the sighting and, impressed with the knowledge and enthusiasm shown by this young student, invited him to work as a volunteer at the museum during his university holidays. Ernst accepted immediately, exclaiming later, “It was as if someone had given me the key to paradise.”

Ernst worked at the museum several times during his university holidays. There he was introduced to a broad range of avian biology. Viewing the young man’s efforts and his unmistakable passion for this kind of work, Stresemann felt that his future belonged in the biological sciences, not medicine, and he set about persuading Ernst to change his field of study. Stresemann even offered him the promise of a birding expedition to a far-away site. Soon, Ernst gave in to Stresemann’s urging and his own preferences and in March 1925 changed his studies from medicine at Greifswald to zoology at the University of Berlin. Ernst completed his Ph.D. *summa cum laude* in 16 months (in June 1926) just before his 22nd birthday. He had to rush through the work because a position was opening up at the museum and the deadline for applying was July 1. He needed to have his doctorate in hand to be able to apply. He thus had to work day and night on his course work and thesis. There was very little time for anything else, including courses and books that were not directly applicable to finishing his degree. Hence during his student days in Berlin he did not learn more than the very basics about what would become a major focus of his work—evolutionary theory, including species concepts and speciation. He did, however, have a firm grounding in species systematics.

### **Expedition**

Having dangled the possibility of an expedition to an exotic land before the eyes of the youthful Ernst, Professor Stresemann now had the obligation to arrange such an expedition. As it happened, a collector working for the noted gentleman ornithologist Lord Walter Rothschild, F.R.S., was unable to undertake a planned expedition to Dutch New Guinea because of a stroke. Stresemann introduced Ernst to Lord Rothschild and the curator of his extensive bird collection, Ernst Hartert, at the International Congress of Zoology in Budapest in 1927 and suggested that the budding ornithologist would be a good substitute. The decision to send the inexperienced Ernst on an expedition to an unexplored section of New Guinea was very speculative and almost foolhardy. Ernst was in excellent physical shape, but he had never collected a bird in his life and had almost never had a shotgun in his hands; his knowledge of tropical lands came only from what he had read. Fortunately for him, the Natural History Museum in Buitenzorg, Dutch East Indies, became deeply involved in the expedition.

With all preparations completed, Ernst sailed on a German boat, the *Fulda*, from Genoa on February 7, 1928. During the voyage, he learned Malay from several younger Javanese passengers. The boat reached Batavia (now Jakarta, Indonesia) on March 4, and Ernst went to the Buitenzorg Museum, where Dr. Karel Willem Dammermann, the director, and Dr. Siebers received him graciously and instructed him for two weeks. They provided him with equipment and, most importantly, with three experienced indigenous museum assistants who knew how to collect and prepare birds and insects and how to camp and survive in the jungle. The three assistants trained Ernst to become a competent collector and explorer.

Ernst's expedition became tripartite; the first two parts were in New Guinea, where he collected for the Rothschild Museum, in Tring, England, and the AMNH, and later for the Berlin Museum (3, 6). Close to the end of this phase of the expedition, he received a telegram inviting him to take part in the Whitney South Sea Expedition (WSSE) of the AMNH as well as a message from Professor Stresemann advising him to accept, with the permission of the Berlin Museum to do so. Stresemann wrote Ernst that accepting this invitation could be good for his future career, advice that turned out to be prophetic.

The expedition visited several islands in the Solomons (13) and under Ernst's urging changed tactics from exploring the lowlands only to including also the interior uplands—an important move to ensure that endemic species living in the mountains were not overlooked. Although reaching and collecting in the elevated parts of each island was much harder, this effort increased the number of species obtained by the WSSE and became the standard procedure thereafter.

The expedition was a central turning point in Ernst's life. He started as a novice and ended as a seasoned field man. He was able to visit remote areas and people in New Guinea just before the major influx of Europeans into the interior. And he acquired enough stories to last for the rest of his life. But most importantly, it brought him into contact with several people who influenced the rest of his career. These included Lord Rothschild and Dr. Hartert of the Tring Museum, but more importantly, Dr. Leonard Sanford, a trustee of the AMNH and patron of its Ornithology Department, who would set the stage for Ernst's move to the United States.

Dr. Sanford was a wealthy surgeon in New Haven, Connecticut, a professor in the Medical College of Yale University, and an amateur ornithologist with a private collection of birds. He was in close touch with Rothschild and Stresemann, and he was a friend of many wealthy people and could readily raise funds for the museum. He was especially

successful in obtaining support from Harry Payne Whitney and his family of New York, who provided funds for the WSSE and much of the money needed for building a new wing of the AMNH that housed the Department of Ornithology and several exhibition halls of birds. His family later purchased the Rothschild ornithological collection for the AMNH and would provide Ernst's salary for most, if not all, of his tenure at the museum. Dr. Sanford and Ernst also became close friends, with Sanford becoming a mentor and, indeed, almost a surrogate father to Ernst, whose own father had died when Ernst was only 12 years old.

Ernst's move to the United States had nothing to do with the worsening political climate in Germany. It happened only because the position at the AMNH was by far the best one that he could have obtained in the early 1930s.

### Early years in New York

Some potential difficulties with the WSSE were developing back in New York in 1930, because little work had been done on the large and important collection of birds that was being amassed in the Ornithology Department. Dr. Sanford worried that if nothing was done to begin putting the collection in shape, the Whitneys would lose interest and cut off further funding of the expedition before its work was completed. To forestall such an event, he persuaded the Whitneys to fund the hiring of a temporary person to study this collection, and he already had a candidate in mind—Ernst Mayr. Ernst received an invitation to join the AMNH as a visiting research associate in October 1930. The Berlin Museum granted him a year's leave of absence, and Ernst accepted this position, leaving Germany early in 1931 and reporting for work at the AMNH on January 19.

Ernst's move to the United States had nothing to do with the worsening political climate in Germany. It happened only because the position at the AMNH was by far the best one that he could have obtained in the early 1930s. He would have available to him one of the best possible collections of birds to study questions of the species concept, speciation, and biogeography. Further, it would have been most difficult for him to obtain a university position in Germany after having worked at a natural history museum.

Once in New York, Ernst plunged right into work on the WSSE birds. He published his first paper on March 31 (4), just two months after he arrived, and by the end of the year he had published 12 papers describing 12 new species and 68 new subspecies. But his job with the AMNH was only for one year—until further events unfolded. Lord Rothschild



was being bled dry by a blackmailer, an infamous but still unnamed “titled lady,” so he could not continue his ornithological researches and was forced to sell his collection. The Rothschild collection came to New York in 1932, and Ernst was appointed the first, and only, Whitney-Rothschild curator (31). At this point he came to the momentous decision to make his home in the United States, and he resigned his position in Berlin.

In 1931 Ernst joined the Linnaean Society of New York, a group of amateur bird watchers who met in the museum; he established an informal monthly seminar to discuss current papers in field ornithology and encouraged members to concentrate on some project. In the 1940s he started another informal seminar in systematics that lasted into the 1970s, well after he had left for Harvard. He directed independent research projects for several students and served as a mentor for three younger members of the department. He liked teaching, and he interacted well with younger people interested in biology and systematics.

During Ernst’s first decade at the AMNH, his scientific work was focused mainly on avian systematics and biogeography (Bock, 1994; LeCroy, 2005; Schodde, 2005; Vuilleumier, 2005). The museum’s vast collection of birds from Australia, New Guinea, and the South Pacific provided him with the best possible material on which to study avian speciation and biogeography. His empirical work on the AMNH collections provided him with a firm foundation for his theoretical work in systematics and evolution and, later, in the history and philosophy of biology. While doing all this research, he was involved in moving the bird collection to its new quarters in the Whitney Wing, unpacking the Rothschild collection, integrating it into the existing collection of the AMNH, and cataloguing this immense body of material.

In the early 1940s he also supervised the Sanford Hall of the Biology of Birds (15), probably the first exhibition hall in an American natural history museum devoted to the biology of a single group of organisms (LeCroy, 2005). During this busy period Ernst completed his synopsis of New Guinea birds (11), which, more than 70 years later, is still the basic reference work on this avifauna. Some of his important ideas are hidden in papers with unexceptional titles, such as “The birds of Timor and Sumba” (14), the only paper that discussed in English the new approach by Stresemann for biogeographical analysis. He also published his first theoretical paper on the species concept and speciation (10).

Ernst had read the then-new book by Bernhard Rensch (1929) on species concepts and speciation after his return from the South Pacific, and was much impressed by it (25).



He always stated that Rensch's book provided the foundations for his later thinking about the species concept, species taxa, and speciation. Clearly, however, he formed most of his own ideas about evolutionary theory after arriving at the AMNH, when he was able to study the vast collections there. This empirical research, supplemented by his wide reading of the literature coming into the museum's library and conversations with recently trained biologists in fields from genetics to ecology, formed the foundation for his evolutionary thinking and later work in the philosophy of biology.

Although almost everyone thinks of Ernst as an evolutionary theorist, his first and last interest was biogeography (Vuilleumier, 2005). He analyzed in detail the spread in Europe of the serin (*Serinus canarius*) (2) and attempted to provide explanations for its remarkable geographical advance over a period of just 125 years. In all he published about 80 papers (almost 10 percent of his total output) on biogeography, treating diverse topics, from island biogeography to the origin of the North American avifauna to the definition of a fauna. Unfortunately, he never wrote a book on biogeography, but a careful analysis of all his papers on this subject provides an excellent account of his thinking. In his studies of the avifauna of New Guinea and the South Pacific, he knew at least as much about the biogeography of these birds as about their systematics and evolutionary history.

Biogeography was important in the earliest projects that Ernst chose when starting at the AMNH, such as his analysis of the birds of Randell Island (5), which was the second paper he published that was based on his research in the AMNH collections. In an almost unknown 1933 paper with the innocuous title "Die Vogelwelt Polynesiens" (7), he laid out the total set of ideas about island biogeography, a subject made famous much later by MacArthur and Wilson (1967). Ernst repeated his ideas in a subsequent set of papers (8, 9). His penultimate book (34) dealt with a very detailed analysis of the distributional history of the birds of Northern Melanesia, the region of the last part of his expedition 70 years earlier.

At the 1939 AAAS meeting in Columbus, Ohio, the American Society of Naturalists and the Genetics Society of America sponsored a joint symposium on speciation; Ernst was asked to speak on geographical variation in birds and its bearing on the process of speciation. His lecture was a great success. After the symposium, Professor L. C. Dunn of Columbia University invited Ernst to take part in the 1941 Jesup Lectures, together with Edgar Anderson. When Anderson stated that he would not provide his part of the

manuscript for the planned book based on the joint lectures, Ernst was asked to expand his manuscript, which became *Systematics and the Origin of Species* (12).

In this volume Ernst expressed his now-famous definition of the biological species concept (p. 120): “Species are groups of actually or potentially interbreeding natural populations, which are reproductively isolated from other such groups.” He also distinguished between physical isolating barriers, which were needed during the process of speciation, and intrinsic isolating mechanisms, which are attributes of species and prevent gene flow from one species to others. He argued against the widespread concept of sympatric speciation, in which new species evolve from a single ancestral species in the same location. He said that conceptual difficulties existed in the proposed mechanisms of external barriers keeping apart two sympatric populations of the same species during the speciation process.

### Later years in New York

Ernst had a very informal manner, a result of his years of living in the United States, and asked younger colleagues and his students, once they obtained their doctorate, to call him by his first name. He was fiercely loyal to his friends, with whom he corresponded throughout his life. He was generous in discussing research projects with younger workers and reading the resulting manuscripts. Many visitors stayed with Ernst and his wife Gretel in their home in Tenafly, New Jersey, and later in Cambridge, Massachusetts, as well as their rural retreat in New Hampshire. Ernst and Gretel were key figures in the American Ornithologists’ Union project of sending care packages to European ornithologists after World War II, as well as sending large numbers of packages independently of this cooperative ornithological effort.

After his Jesup Lectures and the publication of his *Systematics and the Origin of Species*, Ernst continued his work on birds but became more and more interested in evolutionary theory and in the formation of what became the Society for the Study of Evolution and its journal, *Evolution*, of which he was the founding editor (Cain, 1994; Smocovitis, 1994a, b). However, he became more and more reckless in his situation in New York City. He accepted a single-term appointment at the University of Minnesota in the spring of 1949 and another at the University of Washington in the autumn of 1952. Although Ernst had become an adjunct professor at Columbia University in the late 1940s and taught a course every winter, he was unable to direct graduate students there.

Ernst felt real and perceived obligations to Dr. Sanford, who had been responsible for a good part of the growth of the Department of Ornithology at the AMNH, including bringing Ernst there, and he turned down several offers of positions elsewhere. Ernst felt that he could not leave the museum during Sanford's life, because this would have been a great disappointment to the older man, who had been so central to his career. With Sanford's death in December 1950, Ernst felt free to consider offers from other institutes, and in the autumn of 1952 he received a telephone call from Professor Alfred S. Romer, director of the Museum of Comparative Zoology at Harvard University, inquiring whether he would be interested in a position as an Alexander Agassiz Professor of Zoology. Ernst accepted, because this was the best possible university position for him in the United States. As attractive as the offer from Harvard was, however, he left the AMNH with a sad heart because he had been there for 22-plus years and had accomplished much. Also, he was leaving behind the marvelous collection of the AMNH and, as a consequence, his own empirical research, which would continue to be the essential foundation for all of his theoretical work after he left the museum.

## **The Harvard years**

### **Evolutionary Biology**

Ernst's career after moving from New York to Cambridge, Massachusetts, can be divided roughly into three categories. These are not sharply separated, and all three started well before he arrived at Harvard. Moreover, his earlier interests in ornithology, systematics, and biogeography continued to the end of his life. The three parts were evolutionary theory, history of science, and philosophy of science.

The Mayrs were able to find an apartment in Cambridge located so that Ernst could walk to work. Later they bought a house even closer to the museum. And they started to look for a rural retreat, finding an old farm on a dirt road outside of Wilton, New Hampshire. The farm had been abandoned and the house was in poor condition, but with most of the property wooded and bordering on a pond, it was just what they were looking for. Always known thereafter just as "the Farm," it became the Mayrs' little piece of heaven. They spent almost all weekends there from spring until late autumn and all summers when they were not travelling. Students, friends, and visitors were taken there whenever possible, and were always given guided walks with extensive commentary on the local natural history. For Ernst, the naturalist, it was a place for quiet, reflection, observation, and work. He spent four to six hours a day in his room in one corner of the house, dictating papers and correcting manuscripts and proofs.

The move to Harvard basically ended Ernst's empirical research career, because he no longer had access to the bird collections he would have needed. His ornithological work, however, continued. He was asked by James Greenway, curator of ornithology, to join as his co-editor in the completion of the massive, and exhaustive, *Peters Check-List of Birds of the World*, which had been started in the late 1920s by the then-curator James Lee Peters and was less than half completed at the time of Peters' death in 1952. Although Romer assigned Greenway the task of completing this multi-volume project, Ernst took over the major role of organizing the work, assigning the treatment of diverse families to other ornithologists all over the world, obtaining the initial funds for completing the project, and editing most volumes.

Ernst oversaw the publication of volumes 8-15 and revised volume 1, which was far out of date; time and energy did not exist for him to revise any of the other early volumes. The decision was made to publish the remaining volumes in whatever order they reached completion. The last volume to come out was number 11, which appeared in 1986, 55 years after the publication of volume 1 and 23 years after Ernst took over the project. His inscription in the copy that he sent to me was, "At last the millstone is off my neck." The result was a complete list of all birds of the world down to the level of subspecies (Bock, 1990).

Ernst was one of the few people who had been present at both the 50th (1933) and the 100th anniversary meetings of the American Ornithologists' Union. He was president of the organization from 1956 to 1959 and also served as president of the International Ornithological Committee (1958-62) and hence of the 13th International Ornithological Congress, in Ithaca, New York, in 1962. He was elected to the National Academy of Sciences in 1954, shortly after moving to Harvard, and for the next decade he served on the National Science Foundation and on the Biology Council of the National Research Council. In these positions he pushed strongly for increased support for systematics and for natural history museums. For this work and for his contributions in systematics and evolutionary biology, Ernst received the prestigious National Medal of Science in 1969 from the President of the United States.

Ernst continued to work in systematics, but his main output on this subject was general papers. He also wrote three new editions of his textbook in systematics (16), publishing them either alone or with different co-authors. He became deeply involved with the work of the International Commission on Zoological Nomenclature, starting with the 1953 Copenhagen Zoological Congress, and was elected a commissioner in 1954, serving

until 1976. He was very active in the preparation of the first two editions of the Code of Zoological Nomenclature, arguing strongly for the conservation of established names in opposition to strict priority and writing the important preamble to the first edition of the code, which has been kept in all subsequent editions.

Beginning in his last years at the AMNH, Ernst had become increasingly involved with evolutionary theory and especially with details of the species concept and speciation. In his 1942 book, he discussed the “dumbbell model” of speciation. On further analysis, he felt that this model was not sufficient, and he formulated what he termed the “founder principle,” which was central to the “peripatric or the budding model” of speciation (17), in which a “genetic revolution” accompanies the speciation process. He was concerned with the size of the population that led to a new species in peripatric speciation—evolution of a new species physically isolated from a larger parent species—and concluded that most often it was very small, as in a founder population.

Ernst considered this idea to be one of his most important in evolutionary theory, but considerable controversy still surrounds the concept of a genetic revolution during speciation and whether most speciation events result from peripatric speciation. Ernst published two important papers in connection with the centenary of Darwin’s *On the Origin of Species*; one was “The emergence of evolutionary novelties,” in the major Chicago celebration (18), and the second was “Accident or design: the paradox of evolution,” in Melbourne, Australia (20), where he was on his first sabbatical from Harvard.

During his first decade at Harvard Ernst completed his enlarged treatment of the species concept and evolution in *Animal Species and Evolution* (21), which was his last major book on species and speciation, although *Populations, Species, and Evolution* (23) is not just an abridgement of his 1963 book but a considerable revision. He did not discuss sympatric speciation in the book because he felt that the subject had been sufficiently covered in his earlier works. In later years, however, he acknowledged that sympatric speciation may have occurred—for example, in the cichlid fishes in African lakes [see also (12), pp. 213-215]—but the nature of the essential external barriers during the speciation process in these cases is still unknown.

### **History of Biology**

As Ernst was completing the revised edition of his book on animal species, his interests turned more and more to the history of biology. This was not a new career direction for him but went back to papers he had written in the 1930s; now, however, he focused

more on this area. His first project was a historical analysis of the period of the evolutionary synthesis of 1937-1948. Ernst felt that it would still be possible to collect observations and interpretations directly from several of the important architects of this synthesis. He organized two conferences held in Cambridge in May and October 1974, and sent questionnaires to several workers. He summarized the results of the conferences and other contributed material in a book titled *The Evolutionary Synthesis* (25, 26), which provides many insights into what was and was not accomplished during this most interesting period of evolutionary biology since Darwin.

In connection with his evolutionary work, Ernst read Darwin's *On the Origin of Species* several times. It is not clear whether he read very much of Darwin's other publications, but he did know and greatly appreciate this one. He was disturbed that although many reprints of this book were available, in both the first and the sixth editions, most interested scientists did not have the exact first edition available. He therefore persuaded the Harvard University Press to publish a facsimile of this edition, for which he wrote an introduction (22). Later he presented a thorough analysis of Darwin and the beginnings of evolutionary thought (30).

Ernst's most important contribution to the history of biology started at the end of the 1960s, when he first had the thought of writing a book on the history of ideas in biology. He spent the years from 1970 to 1975 reading, organizing his notes, and preparing the first draft of his book. At that time it was clear to him that the coverage of all of biology was too vast a subject for a single volume and he decided to limit the book to what he called "ultimate (evolutionary) causations," the area that he knew best. Even with this restriction, it took seven more years until *The Growth of Biological Thought* (27) appeared—a volume of 980 pages, covering in detail systematics, evolution, and genetics, along with four general chapters. This book remains the standard treatment of these three subjects to this day.

Originally Ernst planned a second volume on "the biology of 'proximate' (functional) causations"—see (27: pp. vii-viii)—but this proved to be too large a task in an area of biology less known to him. At the same time, his thoughts were turning more and more to the philosophy of biology.

Ernst's most important paper on Darwin contained an argument stating that Darwin had presented in the *Origin* not merely one theory, as Darwin himself had claimed and almost everyone had accepted, but a bundle of five independent theories (28). According to Ernst, one of these theories—that common descent implies that all species or popu-

lations of organisms have descended with modification from common ancestors—is historical-narrative. The other four—evolution as such, gradualism, multiplication of species (splitting of phylogenetic lineages as well as transformational change within a lineage), and natural selection (Darwin’s mechanism for phyletic transformation)—are all nomological-deductive (Bock, 2004b). Ernst’s analysis of Darwin’s theories about evolution is significant in that it provides a better understanding of the history of Darwin’s ideas as well as permitting a clearer comprehension of the philosophy of evolutionary ideas.

### **Philosophy of Biology**

The major thrust in Ernst’s thinking during the last two decades of his life was the philosophy of biology and especially how it differed from the standard philosophy of science, which was based on physics. This interest was not new for him, but went back to his earliest work in evolutionary biology, which was centered on individual and other variation in species. He stressed population thinking in biology, in contrast to typology and stereotypes that dominated scientific thinking in all areas, including biology. He sketched the beginnings of his agenda in the philosophy of biology in the introductory chapter of *Growth of Biological Thought* (27). Although he published several papers dealing with diverse aspects of the philosophy of biology, and brought together many of these in his several collections of essays (24, 29, 33, 36), Ernst never published a book on the philosophy of biology. This was a great regret for him, as he expressed in a recorded interview that was made in November 2003 and published in DVD form (Bock and Lein, 2005). However, a careful reading of his papers on this subject, including those in evolutionary theory, will provide a good overview of Ernst’s thinking.

Most significantly, he argued that biology was autonomous from the physical sciences in that all explanations in biology depended on a dual causation (19, 27, 36), which he called proximal (=functional explanations) and ultimate (=evolutionary explanations) causations.

Ernst rejected typology and insisted that in biology all individuals were unique, so that one always had to use population thinking. Unfortunately a short and catchy term like typology has not been introduced for population thinking. He always emphasized the importance of population thinking in all theories about relationships between humans, and he stressed the incorrectness, as he saw it, of stereotypical approaches to thinking



about all human aspects—from growth to education to medicine. One wonders what he would have thought about mapping the human genome.

When reading Ernst's writings on the philosophy of biology, one must be aware of several idiosyncrasies in his thinking. Perhaps most important was that his concept of biology, when he considered the philosophy of science, was that biology was restricted to evolutionary biology and perhaps almost to historical evolutionary theory. He therefore did not believe in statements that were given the status of natural or scientific laws; he substituted the notion of concepts in their place. Other biological explanations that were strictly in the area of functional biology he dismissed as physics. He considered reductionism and holism as systems of explanations, and he favored holism in biological explanations. His holism, however, was not complete, because it seemed to go only to the level of the organism and fell short of the necessary holistic level of the organism in its full interaction with its environment. He rejected all forms of reductionism and therefore referred to any analysis that does confuse the issue as "methodological reductionism," because all scientific and technological investigations have to start as methodological reductionism.

Ernst rejected teleology, but included concepts of teleomatic, and of teleonomic, for goal-directed activities controlled by a program such as ontogenetic development and by many types of animal behavior. He stated, quite correctly, that evolutionary change was not teleological, because there was always an accidental cause for phyletic evolutionary change, thus evolution is always accidental, and it is difficult or impossible to label evolutionary change as progressive or having a goal.

Furthermore, Ernst quite correctly rejected both a Cartesian approach to science and a philosophy of science based strictly on the physical sciences, yet he was unable to develop a coherent philosophy of science that included all aspects of biology. He was sadly disappointed that the large amount of work done by philosophers of biology over the previous four decades had not achieved this important goal. His explanation was that most philosophers interested in the philosophy of biology were trained in physics or mathematics and thus lacked a sufficient understanding of biology, including an appreciation for dual causation in biology. Part of the reason why he was unable to write such a book himself is that he simply ran out of time. He became primarily interested in the philosophy of biology at an age when most of us cease scholarly work, and there were other projects that he wanted to complete.

## The last years

Gretel died in 1990. Ernst continued to work at his office in the Museum of Comparative Zoology, but more and more he went in only in the mornings. In the afternoons he worked at home in his small office and then took a long walk in the late afternoon. His daily walk was essential to him and was perhaps one of the reasons why he enjoyed good health throughout his long life. He also spent considerable time at the farm, as long as he was still able to manage alone or when one of his children or grandchildren stayed there with him. His birthday on July 5 was always celebrated at the farm in a ritual gathering for all of his family living in the area, and included his 100th birthday in 2004.

After Gretel's death, Ernst spent January to March in a warmer clime, first in Gamboa, Panama, as a guest of the Smithsonian Tropical Research Institute, and later in Florida as a Distinguished Scholar at Rollins College in Winter Park. Finally, in 1997, he gave up his house in Cambridge and moved to a full-care residential community, the Carleton-Willard Village in Bedford, Massachusetts, close to his younger daughter. Ernst still did his daily walks and was occasionally taken on short birding outings in the area. He still drove to the museum at least once a week until his 99th year, when his daughters persuaded him to give up driving.

The final decade of his life was a busy one. He published five books during this period (30, 32, 33, 36), including *The Birds of Northern Melanesia* (34), in which he returned to the avifauna he had first observed 70 years earlier in the last part of his South Seas expedition and studied in his years at the AMNH. His last book (36) appeared after his 100th birthday and dealt with his final ideas on the philosophy of science, including why he considered biology to be autonomous from the physical sciences. I was pleased to be involved in his last co-authored paper (35) on ordering systems in biology.

Ernst received many honorary degrees, memberships, awards, and recognitions. His first honorary doctorate was in 1957 from Uppsala University (Sweden) in systematics, in connection with the observation of the 250th birthday of Linnaeus. Of his awards, he was especially pleased to receive the Balzan Prize (Switzerland/Italy) in 1983, the International Prize in Biology (Japan) in 1994, and the Crafoord Prize (Sweden) in 1999. Characteristically, he donated the monetary awards associated with these prizes to various causes and funds. His last award came late in 2004: the Gold Medal from the Accademia dei Lincei (Italy). When I last visited him he was on the telephone in a complex discussion on how to arrange a time and place when a delegation from the Accademia dei Lincei could present the actual medal to him. Alas, this never happened because

of his illness and because of a major blizzard late in January 2005 that prevented the planned trip to Bedford of the director of the Museum of Comparative Zoology, who had received the medal and was to present it to him. But of all of the honors he received, the one that pleased him the most was the naming of the Museum of Comparative Zoology's library for him. Libraries were very special to him as the accumulation of human knowledge, and he once remarked to me that every time a scholar dies, a library of accumulated knowledge dies with him or her.

Ernst told me in the late summer of 2003 that the doctors had found secondary cancer lesions in his liver but that the primary site was not known. He became steadily weaker, although his mind was clear until the very end. Early in the morning of February 3, 2005, his two daughters received a telephone call that their father was not going to last very long. They came immediately and were at his bedside when he quietly slipped away. In 2005 Ernst's family gathered as usual on the July 4 weekend at the Farm; I was invited to join them. On Sunday morning, everyone gathered on the glacial esker bordering Burton Pond, which had been Ernst and Gretel's favorite spot. His ashes were scattered along this low ridge to join those of Gretel.

Ernst Mayr was surely one of the greatest ornithologists and evolutionists of the twentieth century as well as an outstanding biologist. He was a leader in the history of biology and one of the driving forces in the philosophy of biology since its emergence in the early 1960s. Because of his long life, he provided a connection to many workers in what most of us would consider the dim past. He was well known to scholars around the world and is missed by all.

### ACKNOWLEDGEMENTS

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**POSITIONS**

- 1926–32 Assistant Curator, Zoological Museum, University of Berlin  
 1931–32 Visiting Research Associate, Department of Ornithology, AMNH, New York  
 1932–44 Associate Curator, Whitney–Rothschild Collection, AMNH, New York  
 1944–53 Curator, Whitney–Rothschild Collection, AMNH, New York  
 1953–75 Alexander Agassiz Professor of Zoology, Harvard University  
 1961–70 Director, Museum of Comparative Zoology, Harvard University  
 1975–2005 Alexander Agassiz Professor of Zoology, Emeritus, Harvard University

**HONORARY DEGREES**

- 1957 PhD, Uppsala University (Sweden), systematics  
 1959 DSc, Yale University, systematics  
 DSc, University of Melbourne (Australia), evolution  
 1966 DSc, Oxford University (England), ornithology  
 1968 DPhil, University of Munich (Germany), evolution  
 1974 DPhil, University of Paris VI (Sorbonne), evolution  
 1979 DSc, Harvard University, evolution  
 1982 DSc, Cambridge University (England), evolution  
 DSc, Guelph University (Canada), philosophy of biology  
 1984 DSc, University of Vermont, evolution  
 1993 PhD, University of Massachusetts, Amherst, systematics  
 1994 DSc, University of Vienna (Austria), ornithology  
 DPhil, University of Konstanz (Germany), philosophy of biology  
 1995 DSc, University of Bologna (Italy), evolution  
 1996 DSc, Rollins College, Florida, philosophy of biology  
 1997 Degree honoris causa, Muséum National d’Histoire Naturelle, Paris, systematics  
 2000 DPhil, Humboldt University of Berlin (Germany), systematics

**AWARDS AND RECOGNITIONS**

- 1946 Leidy Medal, Academy of Natural Sciences, Philadelphia
- 1958 Wallace–Darwin Medal, Linnean Society of London
- 1965 Brewster Medal, American Ornithologists' Union
- 1966 Verrill Medal, Peabody Museum, Yale University
- 1967 Daniel Giraud Eliot Medal, National Academy of Sciences
- 1969 Centennial Medal, American Museum of Natural History, New York  
National Medal of Science
- 1971 Walker Prize, Museum of Science, Boston, Massachusetts
- 1972 Molina Prize, Accademia delle Scienze, Bologna, Italy
- 1977 Linnean Medal (Zoology), Linnean Society, London  
Coues Prize, American Ornithologists' Union
- 1978 Premio Jabuti, Brazil, CBL Medal, Collège de France
- 1980 Mendel Medal, Leopoldina Academy, Halle (Germany)
- 1983 E. Eisenmann Medal, Linnaean Society of New York  
Balzan Prize (Switzerland/Italy)
- 1984 Darwin Medal, Royal Society (England)
- 1986 Award for Service to the Systematics Community, Association of Systematics Collection  
Sarton Medal (History of Science)
- 1989 Alexander von Humboldt Stiftung, Medal
- 1991 Phi Beta Kappa Book Prize
- 1992 Naming of Ernst Mayr Dining Room at Cold Spring Harbor Laboratory
- 1994 Salvin–Godman Medal, British Ornithologists' Union  
International Prize for Biology, Japan Prize  
Dedication of the Ernst Mayr Library at the Museum of Comparative Zoology,  
Harvard University
- 1995 Walk of Fame, Rollins College  
Benjamin Franklin Medal (American Philosophical Society)
- 1996 George Gaylord Simpson Award (Society for the Study of Evolution)
- 1997 Establishment of the Ernst Mayr Lectureship at the Berlin-Brandenburgische Akademie
- 1998 Lewis Thomas Prize (Rockefeller University)

- 1999 Crafoord Prize, Stockholm (Sweden)
- 2000 Golden Plate Award (American Academy of Achievement)  
Biologist of the Year 2000 (Washington)
- 2004 Treviranus Medal (Verein deutscher Biologen)  
Gold Medal from the Accademia dei Lincei, Rome, Italy

**HONORARY SOCIETY MEMBERSHIPS**

- 1939 Royal Australian Ornithological Union, Corresponding Member
- 1941 Deutsche Ornithologen-Gesellschaft, Honorary Fellow
- 1943 American Society of Naturalists, Honorary Fellow
- 1944 New York Zoological Society, Fellow; 1987, Scientific Fellow
- 1945 Netherlands Ornithological Society, Corresponding Member; 1953, Honorary Fellow
- 1948 Société Ornithologique de France, Honorary Foreign Member  
Zoological Society of London, Corresponding Member
- 1949 Academy of Natural Sciences of Philadelphia, Correspondent
- 1950 Royal Society of New Zealand, Honorary Fellow
- 1951 Botanical Gardens of Indonesia, Honorary Fellow  
Ornithologische Gesellschaft in Bayern, Corresponding Member; 1976, Honorary Fellow
- 1952 Linnean Society of London, Foreign Member  
South African Ornithological Society, Corresponding Member
- 1954 National Academy of Sciences, Member  
American Academy of Arts and Sciences, Fellow
- 1955 Kongliga Vetenskaps-Societeten i Uppsala, Honorary Member  
Zoological Society of India, Corresponding Fellow; 1961, Honorary Member
- 1956 British Ornithologists' Union, Honorary Member  
Dansk Ornithologisk Forening, Honorary Member
- 1958 American Association for the Advancement of Science, Fellow
- 1962 Sociedad Venezolana de Ciencias Naturales, Corresponding Member  
Zoological Society of India (Calcutta), Honorary Member
- 1963 Asociacin Ornitológica del Plata (Buenos Aires), Honorary Member  
Societas Scientiarum Fennica (Helsingfors), Honorary Member
- 1965 American Philosophical Society, Member
- 1968 Sociedad Colombiana de Naturalistas, Honorary Member
- 1970 Zoologische Gesellschaft, Germany, Honorary Member
- 1971 Academia de Ciencias Físicas, Matemáticas y Naturales (Caracas, Venezuela), Foreign  
Corresponding Member



- 1972 Department of Ornithology, AMNH, Curator Emeritus  
Deutsche Akademie der Naturforscher Leopoldina, Halle (Germany)  
Société Zoologique de France, Honorary Member
- 1975 Sociedad Espanola de Ornitologia (Madrid), Honorary Member  
Nuttall Ornithological Club, Honorary Member
- 1976 Society of Systematic Zoology, Honorary Member  
Linnaean Society of New York, Honorary Member
- 1977 Senckenbergische Gesellschaft, Frankfurt, Corresponding Member  
Bayerische Akademie, Munich, Corresponding Member
- 1978 Académie des sciences, inscriptions et belles-lettres de Toulouse,  
Corresponding Member
- 1980 Accademia Nazionale dei Lincei, Foreign Member
- 1981 Italian Zoological Society, Foreign Member
- 1984 Zoological Society of London, Honorary Member
- 1986 American Society of Zoologists, Honorary Member
- 1988 Royal Society, Foreign Member
- 1989 Académie des Sciences, Paris, Associate
- 1993 Center for the Philosophy of Science, Pittsburgh, Honorary Fellow
- 1994 Russian Academy of Science, Moscow, Honorary Member  
Berlin-Brandenburgische Akademie, Honorary Member
- 1998 Gesellschaft Naturforschender Freunde zu Berlin, Corresponding Member
- 2002 Verband Deutscher Biologen und biowissenschaftlicher Fachgesellschaften,  
Honorary Member
- 2003 Gesellschaft für Biologische Systematik, Honorary Member  
Sociedade Fritz Müller de Ciencias Naturais, Brazil, Honorary Member  
Darwin-Gesellschaft, Honorary Member

**SOCIETY OFFICES HELD**

Linnaean Society of New York, Editor, Proceedings and Transactions, 1934–41  
American Ornithologists' Union, Vice President, 1953–56; President, 1956–59  
Nuttall Ornithological Club; Councillor, 1954–55; Vice President, 1955–57; President, 1957–59  
International Commission on Zoological Nomenclature, Commissioner, 1954–76  
American Society of Naturalists, President, 1962–63  
Society for the Study of Evolution, Secretary, 1946; Editor, 1947–49; President, 1950  
Society of Systematic Zoology, President, 1966  
11th International Zoological Congress, Vice President, 1958  
13th International Ornithological Congress, President, 1962  
International Society for the History, Philosophy, and Social Studies of Biology, Honorary  
President, 1990

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