

Ernst Mayr (1904–2005) and the new philosophy of biology

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1. Accident or design: the paradox of evolution

When Ernst Mayr died in Bedford, Massachusetts, on 3 February 2005 he had lived an outstanding rich and successful life. With unrelenting dedication, enthusiasm and talent he had pursued his cause—the growth of biological thought—for more than 8 decades. His last book *What Makes Biology Unique? Considerations on the Autonomy of a Scientific Discipline* had appeared right in time for the celebration of his hundredth birthday on 5 July 2004. It was the life of a scientist, with instinctive assurance he had circumvented the political turmoil and catastrophes of the 20th century that afflicted the lives of his fellow biologists so dramatically and sometimes tragically.

In his unpublished *Autobiographical Notes (AbN)*¹ written during the last decades of his life, Mayr remembered that he had “often marvelled how many times the entire course of my life was changed by accidental circumstances” (*AbN* p. 96). He continued that in retrospect these ‘circumstances’ turned out not just accidental, but fortunate. During the First World War he was too young to take part in the fighting. During the Second World War Mayr and his wife Gretel were considered ‘enemy aliens’ in the United States, but were protected by their American-born children. They had to report to the local police department and to the Department of Immigration and Naturalization, but besides these inconveniences Mayr never had any difficulties in pursuing his work at the *American Museum of Natural History (AMNH)* in New York or with his scientific publications. Because of his age and status as an ‘alien’ in the

¹ The *Autobiographical Notes* cover his personal recollections of his family, friends and many other personal as well as scientific details; the *Scientific Autobiography* (“Recollections on My Scientific Development”) gives detailed comments on the content and reception of many of his publications. Both manuscripts consist of approximately 200 pages. In addition he has recorded his recollections of 24 influential or interesting people he had met during his life (*Reminiscences*). These autobiographical notes have not been published, but he made them (and his *Travel Notes*) readily available to me and other interested friends.

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United States he was neither drafted into the American military—nor into the Wehrmacht as most of his friends and colleagues back in his old home country. After the Second World War when evolutionary biology in Germany was struggling with the economic and ideological aftermath of the Third Reich, Mayr was at the very centre of the rejuvenated science of the living world that had emerged as a result of the conceptual and empirical progress made possible by the new Darwinism (the so-called Synthetic theory of evolution) and molecular biology. How fortunate Mayr actually was to be able to enjoy the fascinating and challenging aspects of 20th century biology without being dragged into its sinister and depressing parts, becomes obvious, when we look at the lives of some of his former colleagues and friends (the following examples are from Junker, 2004a).

Walter Arndt (1891–1944) his colleague and friend at the *Natural History Museum* of Berlin was executed by the Nazi Regime on 26 June 1944 after he had privately spoken out against the regime and had been denounced by a person he had considered a friend. The young botanist Werner Zündorf (1911–1943) vanished in Stalingrad. The native Russian and eminent population geneticist Nikolai W. Timoféeff-Ressovsky (1900–1981) was imprisoned in 1945 by the Red Army, because he had not complied when he was ordered back to the Soviet Union in 1937. At this time geneticists were already persecuted when they criticised the official ideology of Lyssenkoism. Timoféeff-Ressovsky nearly died in a labour camp and spent the rest of this life with damaged health, isolated from international contact and under close observation by the state police in remote or isolated territories.

The renowned developmental geneticist Richard Goldschmidt (1878–1958), head of a department at the Kaiser–Wilhelm Institute for Biology, was forced to emigrate in 1936 because of the religious denomination of his grandparents, had a very poor reception in the United States and could never again hold a professional position that was comparable to his former status. Mayr on the other hand had the double advantage of being not only much younger than Goldschmidt, but of having actively chosen to make a career in the United States. And finally Mayr's close friend, the zoologist Bernhard Rensch (1900–1990) had to join the army in both World Wars and came under political pressure during the Third Reich, because his Lamarckian ideas were considered 'leftist' and 'Jewish'. After the war there was no positive environment for evolutionary biology in Germany due to a variety of circumstances ranging from economic shortages to political resentment. As Mayr observed during his first visit to Europe in 1954: "In Germany—now a clerical state—the anti-evol[utionary] movement is particularly strong [. . .]. Just like McCarthy synonymizes liberalism and communism, thus after the war evolution was synonymized with the most typological selectionism, and biology with Nazi racism" (*Travel Notes 1954*; see Note 1).

Was it "accident or design",¹ to borrow from the title of one of Mayr's papers (1962), that contributed more to the success of his life and professional career? Chance or necessity—this "paradox" is one of the philosophical questions that received a new and fuller meaning through the theory of evolution. The answer given by modern Darwinism is unequivocal. Both factors play an important role in evolution, because they together determine the actual characteristics of an individual (the so-called phenotype) and its fate: "evolution is neither merely a series of accidents nor a deterministic movement toward ever more perfect adapta-

¹ Recently the word 'design' has been widely used by religious critics of the modern theory of evolution. In the tradition of the natural theology of the 18th century creationists claim that the apparent design of organisms and their parts can only be explained by the existence of an 'intelligent designer', a presiding, creative mind. Mayr has always criticized this view as unfounded and fully endorsed the opposing Darwinian view: "The product of selection is adaptation, and the adaptedness of organisms [. . .] is improved from generation to generation until it appears as perfect as if it were the product of design. In short, the solution of Darwin's paradox is that natural selection itself turns accident into design" (Mayr 1962, p. 14).

tion. [...] Many authors seem to have a problem in comprehending the virtually simultaneous actions of two seemingly opposing causations, chance and necessity. But this is precisely the power of the Darwinian process” (Mayr 2001, p. 229).

But what do evolutionary biologists mean when they speak of ‘chance’? Since Darwin’s time the precise meaning of this concept in evolution has been misunderstood and it is still frequently misrepresented by critics of modern Darwinism. In the evolutionary context ‘chance’ does not suggest a breakdown of causality resulting, for example, from the sub-atomic indeterminism claimed by influential representatives of quantum physics. On the contrary: It is fully compatible with a deterministic interpretation. The word ‘chance’ is used in evolutionary biology to designate the fact that the differences in the genetic constitutions of the individuals of a population or of an asexual lineage (the genotype of the individual) and many environmental circumstances are *fortuitous with regards to the needs of the organism*. An organism is confronted with the same kind of ‘chance’ a gambler encounters—when playing roulette the course of the ball and its final halt are determined by the laws of physics, but not by the needs of the gambler. With regards to his or her wishes the winning number is pure chance. On the other hand survival and reproduction—the kind of ‘winning’ that is relevant in the process of evolution—are *not pure chance events*, but depend on the inherited traits of the organism: “survival, the ability to contribute to the genetic content of the next generation, is not at all a matter of accident, but a statistically predictable property of the genotype” (Mayr 1964, p. [xvi]). The differences between the genotypes however are, as we have seen, due to the random effects of recombination and mutation.

I have included this short digression into the theory of evolution not only to explain a phenomenon that at first sight seems to be of a different kind—the professional life of a scientist—but to demonstrate one of the fundamental characteristics of Mayr’s way of thinking. He was convinced that biology and Darwinian evolution in particular have provided us with new concepts that constitute a whole new way of thinking about the world. This revolutionary *Weltanschauung* is not “limited to evolution and the consequences of evolutionary thinking”, but has “wide-reaching importance also outside of biology”: “Almost every component in modern human’s belief system is somehow affected by one or another of Darwin’s conceptual innovations” (Mayr 2004, pp. 85, 95).

On the occasion of Ernst Mayr’s ninetieth and hundredth birthday and after his death numerous accounts of his life and scientific work were published that focus on different aspect of his long career.² Most of them were written by former colleagues and students and directly or indirectly reflect his own views. This situation will not change fundamentally in the near future, as Mary P. Winsor has recently observed: “Historians who try to evaluate Mayr’s contributions will face a peculiarly subtle task, not only because they will have to build upon Mayr’s own historical work, but because many of these historians will be students of historians whom he directly influenced” (Winsor 2005, p. 416). Readers of the literature on Mayr should be aware of this situation, and my following account is no exception. After finishing my dissertation on the *Reception of Darwinism by German Botanists in the 19th Century* (Junker 1989) I had sent Mayr a copy. He answered with a very encouraging letter and reviewed the book for the *Journal of the History of Biology*. In the summer of 1992 he invited me as a post-doc in the history of science to Harvard University and thanks to a Feodor-Lynen-grant of the Alexander-von-Humboldt-Foundation I was able to take this marvellous opportunity. All in all I stayed with Mayr for eighteen months during the years 1993–1995. During this time I saw him at least once a week in his office, at his home or at

² The best concise biographical accounts are those by Walter Bock (1994, 2004). Jürgen Haffer is currently preparing a comprehensive biography that is scheduled for publication in 2007.

the ‘farm’ and we had long discussions. After I had returned to Cambridge, England, and then moved to Tübingen we had regular and frequent correspondence and I met him a couple of times in person.

I consider it one of the lucky circumstances of my life that I had the chance to get to know Mayr and to have intensive scientific as well as personal contact with him. Looking at the published reminiscences of his colleagues and friends I realize that in a similar way Mayr has shaped the careers of many scientists. He influenced them through his ideas—in his publications as well as his letters—his steady assistance, example, encouragement, and friendship. I am sure biographers will find abundant evidence in his published letters and in the unpublished correspondence at the Harvard Archive for the extensive amount of time and care he devoted to encouraging young scientist, historians and philosophers of biology (cf. Haffer 1997, 2007).

Of course, Mayr’s support was not disinterested, but has been characterized as “mutual exploitation” (Hull 1994, p. 376). I would rather speak of ‘reciprocal altruism’ or ‘mutual cooperation’, as the phenomenon is called by sociobiologists (for a theoretical analysis of altruistic behavior in humans cf. Mayr 1997, pp. 248–270). During my time as a post-doc I began to work on a project that was of personal as well as historical interest for Mayr. He repeatedly pointed out to me that according to his memories a scientifically sound evolutionary biology had existed in Germany during the years of the Third Reich and that an “evolutionary synthesis took place in the 1930s in Germany, largely independent of the synthesis in the English-speaking countries” (Mayr 1988, p. 549). I was able to confirm his impression to a large extent and even strengthen it: There was an evolutionary synthesis in Germany, but it was not ‘independent’. A considerable number of biologists in Germany were willing and able to maintain close ties with their colleagues in other countries and together they participated in an *international movement* with the explicit intention to forge a modernized Darwinism (Junker 2004a; Junker and Hossfeld 2002).

2. A life in science

Ernst Mayr was born in Kempten, a small town in Southern Germany, on 5 July 1904. In the following years his family moved to Würzburg and Munich, where his father was a district prosecuting attorney and finally an associate justice at the supreme court of Bavaria. Ernst was the second of three brothers, Otto was three years older, Hans a year and three-quarters younger. The family background was upper middle class and academic (*Bildungsbürgertum*). Both his parents were avid readers and particularly interested in history and philosophy. Their private library contained several thousand volumes. Mayr later commented that “in the upper class families of Germany an almost exaggerated emphasis was placed on Bildung. Not only was the humanistic gymnasium considered the best possible school but one was constantly encouraged to read good books and a couple of good books were usually what one got on one’s birthdays” (*AbN* p. 43).

When Mayr was 12 years old his father died of cancer of the kidney and the family moved to Dresden (1917). So far their financial situation had been quite comfortable, but now—toward the end of the war and during the years of inflation—they suffered considerable hardship. Nevertheless Ernst was able to begin studying medicine at Greifswald University in 1923. Medicine, however, was not his first choice, rather the reasonable thing to do, and whenever possible he spent his free hours in the field, observing birds. One of these observations—he had spotted a rare bird (*Netta rufina*) in the neighbourhood of Dresden—brought him into contact with the famous ornithologist Erwin Stresemann from the *Natural History Museum*

in Berlin. Stresemann noticed Ernst's talent for natural history and succeeded in recruiting him to zoology by promising that he could go on an expedition once his doctoral thesis was completed. This convinced Ernst who knew that as a physician he wouldn't have the opportunity "to be sent to foreign countries and see something of the world" (*AbN* p. 51).

But first he completed his premedical examination ('Physicum'), which meant that he could return to medical studies if his plan to become a zoologist would not be feasible. Having changed his studies from medicine at Greifswald to biology at Berlin, Mayr finished his biogeographic dissertation on the spread of the Serin finch (*Serinus canaria serinus*) in Europe in less than 2 years (June 1926). Now he could start making arrangements for an expedition. Two opportunities (Peru and Africa) did not materialize, but in the late summer of 1927 Stresemann introduced him to Lord Rothschild at the International Zoological Congress in Budapest. Rothschild was particularly interested in the so-called 'rare' birds of paradise known only from specimens collected by natives but never collected in the wild by an ornithologist. This was the task he engaged Mayr for: To go to New Guinea and find the 'rare' birds of paradise.

In February 1928 Mayr left Berlin. The difficulties he encountered on his one-man-expedition are hard to imagine in our days when bird explorers can rely on modern means of transportation and communication, antibiotics and are not at acute risk of being murdered by natives. Nevertheless, Mayr brought back a tremendous amount of bird specimens, material that not only helped Stresemann to resolve some of the puzzles concerning species diversity in birds of paradise but also provided the foundation for Mayr's own research in systematics and ornithology. Perhaps the most important direct result was a negative one. Despite the thoroughness of his collection, he had not found a single one of the mysterious 'rare' birds of paradise. This astonishing negative result provided Stresemann with the decisive clue: They were hybrids between known species of birds of paradise, which explained their rarity.

Just before Mayr was to return from New Guinea in 1929, he received a telegram asking him to join the Whitney South Sea Expedition to the Solomon Islands for approximately a year. When he eventually returned to Berlin in April 1930 the chances for a scientific career for an ambitious young ornithologist looked rather bleak. In the meantime however the *American Museum of Natural History* (*AMNH*) in New York had realized that they had this marvellous material from the Whitney South Sea Expedition, but no one qualified to working it up properly. In October 1930 they sent Mayr an offer for a 1 year position, which he accepted immediately. After completing the essential work in Berlin he arrived in New York on 19 January 1931. His appointment was renewed for a second year, and then a chance occurrence changed everything. The *AMNH* was able to acquire the private ornithological collection of Lord Rothschild in England of nearly 300,000 bird skins. This however meant that they needed a new curator and since the focus of the Rothschild collection was the Australian region, it was decided that no one would be better qualified for this appointment than Mayr. And so the one year appointment became a 23-year position.

In these years Mayr was responsible for the bird collection; in particular he had to integrate the Rothschild material into the collection of the *AMNH*. This included "estimating how much case space was needed for each family, arranging families in the various collection rooms, supervising the cataloging of the collection, and attending to all of the other details of curating a collection" (Bock 2004, p. 644). This work could be tedious, but he found the time to describe 26 new bird species and about 450 new subspecies. And it provided him not only with extraordinary experience in biogeography and systematics but with an empirical foundation for his concepts in evolutionary biology and in the philosophy of biology. In 1935 he married Margarete Simon (1912–1990); they had two daughters (Christa and Susanne).

In the early 1950's Mayr became more and more frustrated with his lack of contact with students. He accepted two single term visiting professor positions (University of Minnesota and University of Washington). And his interests shifted from systematic and biogeographic studies of birds to evolutionary biology. But although he increasingly moved away from ornithology, he never abandoned his original field completely. As late as 2001 he published a book on *The Birds of Northern Melanesia: Speciation, Ecology, and Biogeography* together with Jared Diamond (Mayr and Diamond 2001).

When Mayr was invited to join the *Museum of Comparative Zoology (MCZ)* at Harvard University as an Alexander Agassiz Professor of Zoology in 1953 he immediately accepted. He had to leave the outstanding collection of the *AMNH* behind, on which so much of his empirical work over the past two decades had depended, but he was finally acknowledged as one of the leading evolutionary biologists of his time. In 1975 he retired from Harvard, but kept his office at the *MCZ* until 1997, when he moved to a comfortable housing development for the elderly in Bedford, about 30km northwest of Cambridge. After his 'retirement' his output of scientific articles and books in the history and philosophy of biology even increased, and most of his major books were written in the last decades.

3. The second Darwinian revolution

Mayr saw the world through the eyes of a naturalist. His training as a biologist and the years he spent working on practical problems of ornithology, biogeography and systematics have further strengthened this perspective. For him 'nature' was the material world that can only be understood through observation *and* logic, but never without observation: "What I do not understand is why most philosophers of science believe the problems of the philosophy of science can be solved by logic. [...] An empirical approach [...] seems to be a better way" (Mayr 2004, p. IX). If this notion is correct we should expect that his theoretical ideas in the history and philosophy of science directly stem from his experiences as a naturalist or were at least strongly influenced by them (Bock 1994; Junker 2003).

"It all started with birds, and birds indeed were my almost exclusive interest early in my career" (*AbN*, p. 68). This, however, is only half of the answer. An organism can be analysed from a variety of perspectives and by different biological disciplines—from physiology and ethology to morphology and paleontology. Mayr has later discriminated between studies that focus on the proximate (functional) aspects and those that look at the evolutionary origin of traits. Mayr himself had been interested primarily in the geographical distribution of birds. And since the biogeography of a species can be analysed in a meaningful way only when its phylogeny is taken into account, there was only a short step toward evolutionary biology (Beatty 1994).

But evolution as such has two fundamental aspects: adaptation and the origin of diversity. Through his expedition to New Guinea and the subsequent work on the collections of the *AMNH* the problem of diversity nearly inevitably became his next major interest (and to some extent remained for the rest of his life). On the other hand, the population geneticists of the 1920s and 1930s had been interested almost exclusively in the process of adaptation. Since they dealt with closed populations, they had no ready access to the problem of how a species splits into two or more species under natural circumstances (speciation). The systematists on the other hand already had an explanation for the process of speciation in the late 1920s. They assumed that a species splits when two or more of its populations are mechanically separated from each other and during this geographic isolation become reproductively isolated. This can either be caused by sterility barriers or through behavioral incompatibilities. Races

were seen as incipient species. These ideas about speciation were ignored by the majority of evolutionary geneticists who attempted to explain speciation through special mutations. Many naturalists, on the other hand, had strong sympathies with Lamarckian or other non-Darwinian mechanisms.

The two authors who did more than anyone else to bring the question of biological diversity into the new Darwinian theory of evolution were Theodosius Dobzhansky (1900–1975) and Mayr. Dobzhansky, in his *Genetics and the Origin of Species* (1937), discussed genetics, selection and evolution, he had, however, not included a detailed analysis of speciation. Mayr's *Systematics and the Origin of Species* (1942) filled this gap. It demonstrated how the origin of a species can be explained as the result of a gradual, continuous process: "A new species develops if a population which has become geographically isolated from its parental species acquires during this period of isolation characters which promote or guarantee reproductive isolation when the external barriers break down" (Mayr 1942, p. 155). *Systematics and the Origin of Species* convinced the evolutionists that discontinuities can arise gradually and that they can be explained by studying geographic variation:

The real objective of my volume was to explain a whole set of phenomena,—such as species and speciation, as the effects of selection on populations, as the role of geography at the level of species and populations, and as the role of species in macroevolution,—that were omitted in the accounts of the geneticists or that were based on the findings of the systematists, such as in the volumes of Dobzhansky, Timoféeff-Ressovsky and Huxley. This is why *Systematics and the Origin of Species* was such an important contribution to the synthesis. It provided a vast area of evolutionary theory, which the geneticists were not competent to fill (*Scientific Autobiography*, p. 66; see Note 1).

Mayr's participation in what was later called the evolutionary synthesis was the starting point of his reputation as one of the leading evolutionists of the 20th century (Futuyma 1994; Hölldobler 2004). This 'second Darwinian revolution' of the 1930s and 1940s resulted in what became one of the most successful scientific theories of our time—the Synthetic theory of evolution (Synthetic Darwinism). Synthetic Darwinism has dominated evolutionary biology since the early 1950s (Junker 2004a; Ruse 1996; Smocovitis 1996). With its acceptance many of the controversies that had shaped the discussions about evolution since Darwin's *Origin of Species* came to an end. The unification of evolutionary biology was achieved on a Darwinian basis. Selection was regarded as the only causal factor leading to adaptation; mutation and recombination were identified as the sources of genetic variability. The importance of population size was stressed, in particular for small populations, where chance effects limit the power of selection. In addition geographic isolation was seen as a prerequisite for the splitting of a species.

In later years Mayr continued to make major conceptual advances to the problem of speciation. In 1954 he published "Change of genetic environment and evolution", which he considers the most important paper of his whole scientific career. He reasoned that "the selective value of many genes will change drastically on the altered background ('genetic environment') of a newly founded peripherally isolated population. This will lead to a rapid change of gene-frequencies simultaneously at many loci ('genetic revolution'), assisted by the selective effects of the change in the physical and biotic environment of the isolated area" (Mayr 1954, p. 178). Such a 'founder population' may, in the extreme, consist of only one inseminated female and carry only a small portion of the genetic variety present in the gene pool of the original population. In most cases these small founder populations will become

extinct, but under favourable circumstances they may go through a period of rapid evolutionary change resulting in the origin of evolutionary novelties. This concept of ‘peripatric speciation’ is an important addition to the gradualist Darwinian model, because it helps to explain rapid shifts in adaptation and the scarcity of fossil evidence for decisive phylogenetic episodes. Because the changes occur in rather small, isolated populations they appear in the fossil record as saltations, but in fact they are due to a gradual populational process.

For nearly two decades the paper did not draw much attention until Niles Eldredge and Stephen Jay Gould based their theory of punctuated equilibria on Mayr’s theory (Eldredge and Gould 1972). In 1963 Mayr presented his theory of speciation and the origin of biodiversity in the massive volume *Animal Species and Evolution* (Mayr 1963), which became a classic of modern Darwinism. As late as 2001 he published the general overview *What Evolution Is*, which gives a good impression of his interpretation of current evolutionary theory.

Not all of Mayr’s theoretical concepts were successful. It saddened him greatly that he was not able to gain acceptance for the ‘evolutionary classification’ in his own original field, systematics. Instead the so-called cladistic classification that had originally been worked out by the entomologist Willi Hennig under the name ‘phylogenetic systematics’ became the dominant approach. Hennig had demanded that a classification should be based exclusively on the branching pattern of phylogeny. Without much success Mayr criticized this idea and suggested that in addition a classification should reflect the degree of divergence of the various branches.

4. The history of biology as ‘Autobiology’

In the late 1950s and then again beginning in the middle of the 1970s, i.e. shortly before his retirement from Harvard, Mayr started to publish in the history of biology. More than 150 of his publications (out of a total number of roughly 700) deal at least in part with historical topics (Junker 1996). His major contribution to the history of biology is *The Growth of Biological Thought* (1982), an opus magnum of 974 pages. It is not a descriptive history of biology, but an analysis of the development of some of the ideas that dominate modern biology. And it does not cover the entire field of biology, but focuses on systematics, genetics, and evolutionary biology. Other significant books by him in the history of biology were *The Evolutionary Synthesis* (with William Provine 1980) and *One Long Argument: Charles Darwin and the Genesis of Modern Evolutionary Thought* (1991).

Mayr had always been interested in history, perhaps influenced by the numerous history courses in school, as well as by his family background. Mayr himself noted his interest in the history of biology as having arisen in connection with his reading of Arthur O. Lovejoy’s *The Great Chain of Being*. In particular he was intrigued by Lovejoy’s historiographic methodology that aims at the ‘biography’ of an idea (Lovejoy 1936, p. 22). This closely resembles what Mayr had in mind, when he argued for a ‘phylogenetic’ treatment of scientific problems: “In the case of the history of science, the focal points are problems rather than ideas, but the approach of the historian of science is not much different from that of a historian of ideas such as Lovejoy. Like Lovejoy, he attempts to trace the problem back to its beginning and to follow up its fate and its ramifications from such a beginning either to its solution or to the present time” (Mayr 1982, p. 18). His first paper strictly devoted to the history of biology was the one he wrote in 1959 on Louis Agassiz.

The immediate cause for Mayr’s historical interest was the Darwin centennial in 1959. Most of his early writings in the history of biology deal with Darwin, his forerunners

(Lamarck), successors (Weismann), and opponents (Agassiz), i.e. with a period he later called the “first Darwinian revolution” (Mayr 1991). The centennial of the publication of Darwin’s *Origin of Species* in 1859 became so important, because the representatives of Synthetic Darwinism saw and claimed Darwin as the founder of their research program: “If we celebrate the centennial of the publication of the theory of evolution through natural selection, we do this not merely for historical reasons. We do it because natural selection has remained, since Darwin, the most important component of the theory of evolution and has become the cornerstone of the modern, synthetic theory of evolution” (Mayr 1959, p. 10).

Mayr’s later historical writings focussed on three related topics: The “first Darwinian revolution,” the “second Darwinian revolution” of the 1930s and 1940s (the evolutionary synthesis), and the importance of the classical biological disciplines in opposition to mathematical and experimental approaches. Actually most, if not all of Mayr’s historical publications deal directly or indirectly with his biological work and its origins. This marked link between his own history and its interpretation has been noticed, and sometimes criticised by a number of reviewers. His former colleague, the paleontologist George Gaylord Simpson, even characterized *The Growth of Biological Thought* as ‘Autobiography’: “This book is in an unconventional and highly unusual way an autobiography. In it Mayr is seeking out, cleverly and successfully, the roots of his own accomplishments and opinions. It is an intellectual, psychological, and conceptual autobiography” (Simpson 1982, p. 438).

Why did Mayr emphasize the historical approach rather than a functional (‘philosophical’) analysis? His basic observation is that organisms and species evolve during a long historical process and that we can, as a consequence, only understand many of their features if we study them as historical phenomena. The same can be said about science: “Anything that changes in time has, by definition, a history—the universe, countries, dynasties, art and philosophy, and ideas. Science also [...] has experienced a steady historical change and is thus a legitimate subject for the historian” (Mayr 1982, p. 1). I.e. Mayr was interested in the history of biology, because it helps to understand scientific problems and the persistence of controversies in *current biology*: “Because the great controversies of the past often reach into modern science, many current arguments cannot be fully understood unless one understands their history” (ib.).

5. A new philosophy of biology?

In the 1960s Mayr became increasingly interested in the philosophy of biology and during the last two decades of his life he devoted most of his time and energy to solve the central philosophical problems that emerge in connection with the phenomena of life. At first sight this theoretical interest is hardly surprising and arises from his empirical work in systematics and evolutionary biology. But there is more to it. From his first philosophical paper (1961) to his last book *What Makes Biology Unique?* (2004) a persistent motivation is present—the feeling of dissatisfaction and annoyance with the traditional answers to the most fundamental question of biology: ‘What is life?’ The “unfortunate rift,” however, “that seems to exist nowadays between natural science, especially biology, and philosophy, can be bridged, if both camps are getting acquainted with the conceptual world of the other camp” (Mayr 1984, p. IX). To clarify his own point of view and to sketch the route toward a genuine philosophy of biology Mayr confronts it with a pair of opposite interpretations that both originated in the 17th century and still exert a formative influence on current debates.

On the one hand there is the mechanistic position of Descartes and his followers, which claims that an organism is “nothing but a machine” (Mayr 2004, p. 2). This view of life had

various historical manifestations and is introduced under different names by Mayr: Cartesianism, physicalism, mechanism, and reductionism. He defines it as the attempt “to explain all biological processes in terms of movements and forces”. It is a world-view where ‘everything is mechanistic, everything is deterministic, and there is no unexplained residue’ (Mayr 1988, p. 9). The machine theory of life is applied by biologists and philosophers of biology to understand biological phenomena with the methodologies of the physical sciences, i.e. as if they were inanimate objects. For Mayr this approach resulted in a neglect of the specifically biological subjects and left a painful gap. He has emphasized time after time that he rebelled against the philosophy of science because it was in fact a philosophy of physics and ignored the special characteristics of living organisms: “What annoyed me particularly was that philosophy of science in the 1950s and 1960s meant philosophy of physics” (AbN p. 71).

Where else could he turn? The historical alternatives to the machine theory of life have been subsumed under the name of ‘vitalism’. One of its precursors was Georg Ernst Stahl’s 17th century ‘animism’ that had originated as a reaction to Descartes’ mechanism. Until the early 20th century different versions of vitalism had gained considerable influence in biology as well as philosophy. Its representatives claimed that living organisms are fundamentally different from inanimate objects because they are controlled by a special force, a soul (*anima*), a *Lebenskraft* or a *vis vitalis*. After reading the books of the leading vitalists of his time, Henri Bergson and Hans Driesch, as a young man, Mayr concluded that he “had no use for a philosophy based on such an occult force as the *vis vitalis*” (Mayr 2004, p. 2; cf. Bergson 1921; Driesch 1928). He would not accept any principles or causes that were in conflict with the physical sciences. To be a genuine science these erroneous assumptions had to be eliminated from biology. For Mayr invalid ‘occult’ and metaphysical concepts in biology ranged from the *anima* and *vis vitalis* to teleological causations (*causa finalis*) and supernatural (religious) explanations. These ideas have in common that they cannot be proven scientifically and are in conflict with the laws of the physical sciences.

Modern biologists reject teleological causations, but at the same time they frequently use the so-called teleological language. Sentences such as ‘the migratory bird flies to warmer climates in order to escape the winter’ are common in biology. This seeming contradiction has confused and irritated many philosophers and Mayr has made great efforts to clarify the misunderstanding: Goal-directed (‘teleological’) behavior and processes are the most conspicuous and typical phenomena of organisms, but they can be explained through a strictly causal and mechanistic process. To mark this difference to the traditional teleological view (*causa finalis*) Mayr spoke of ‘teleonomic processes’ (Mayr 1974). The problem is the same that is encountered when the apparent design (the adapted features) of organisms and their parts are analyzed. The form and function of an organism have a common purpose that has its origin in their genetic program: It is the preservation and propagation of the very genes that constitute the genetic program, which explains why organisms have such a keen interest in their reproduction and survival. The answer, why and how the genetic program and this ultimate goal of all living organisms originated, was given by Darwin: They are products of natural selection and there is no need for an ‘intelligent designer’ or an ‘evolutionary planner’, for a vitalistic or a theistic explanation (Mayr 2004, pp. 59–61).

Since the 18th century biologists had struggled to find a third way that combines the valid elements of both the machine theory and vitalism. And at the end of the 20th century? In Mayr’s opinion this situation still persists: “Those who were looking for a philosophy of biology had the choice between a volume that was either vitalistic in its basic spirit or Cartesian” (Mayr 2004, p. 3). His philosophy of biology is motivated by the dissatisfaction with either approach. It is an attempt to initiate a third way that evades the traps of ‘physicalism’

and ‘occultism’ and at the same time guarantees the status of biology as an autonomous and genuine science.

Is Mayr’s third way forward-looking and successful or will he join the long line of famous or forgotten failed attempts to solve the riddle of life? Throughout his work he stressed again and again that there is a fundamental difference between living organisms and inanimate objects and, as a result, any attempt to unify the two sciences of biology and physics is misleading. The nature of life, the special characteristics of living organisms, has always been a puzzle for scientists and philosophers. Mayr praised the vitalists for their view that the machine theory of life is insufficient to solve the problem, because it has no answer for some of the most basic questions: How can a machine regenerate lost parts, how can it replicate itself? Even if this criticism should be valid, the efforts of the vitalists to find a better explanation for the phenomena of life were failures, and the “complexities of biological causality do not justify embracing nonscientific ideologies, such as vitalism or finalism, but should encourage all those who have been trying to give a broader basis to the concept of causality” (Mayr 1961, p. 1506). So, what is his solution?

His first, widely accepted conclusion is that two types of natural things can be differentiated: inanimate objects and living organisms. The latter display a specific set of characteristics that are found only sporadically and in rudimentary form in inanimate objects. He emphasized that these peculiar traits of living organisms are not in contradiction with physicochemical and strictly naturalistic explanations. They do, however, show much higher levels of complexity and because they act as integrated, functional wholes, qualitatively new traits emerge. To understand these emergent characteristics, their function, interaction and origin, a special, ‘autonomous’ science with specific concepts is necessary—biology. Laws, f.e. are of much less importance in biology because of the greater role played by chance, uniqueness and the historical nature of many phenomena in living systems. As a consequence most generalizations in evolutionary biology will be probabilistic and cannot be tested by applying Popper’s method of falsification (Mayr 1997, pp. 45–78; Mayr 2004, pp. 21–38).

Mayr has identified and discussed a number of characteristics that are typically found only in organisms—reproduction, metabolism, replication, regulation, adaptedness, growth, hierarchical organization and many others: “There are no inanimate systems [...] that are even anywhere near as complex as the biological systems of the macromolecules and cells. These systems are rich in emergent properties because forever new groups of properties emerge at every level of integration”. His key concept to explain the unique traits of living organisms is ‘emergence’. This term, Mayr admits, has a long history and was particularly popular among vitalists, who introduced it as a supernatural principle. But ‘emergence’ can and should be regarded as an empirical principle, defined as “the occurrence of unexpected characteristics in complex systems” (Mayr 2004, pp. 29, 74). Emergent properties originate through the interaction of previously unconnected components and can be observed on all levels, from molecules (as in the case of the formation of water from gaseous hydrogen and oxygen) and simple tools (when handle and head together form a hammer) to complex machines and organisms. Defined in this way, emergence is a daily encountered fact, an “immanent property of nature;” as he points out (Mayr 2004, p. 75). And its acceptance eliminates the need to invoke occult principles. The characteristics of living organisms that had seemed to be in conflict with the mechanistic explanation can thus be explained and vitalism or supernatural principles become superfluous. In modern scientific biology the naturalistic position is uncontroversial; insofar it has become a genuine science.

But Mayr’s rejection of vitalism is only one side of the coin: He equally stresses the differences between his view and the machine theory of life. Has he actually found a ‘third way’ between vitalism and physicalism? My impression is that in this respect his argument

is much less convincing and that its validity depends on a statement that must be described as a gross misrepresentation. But let me first clarify two problematic wordings.

First, Mayr's use of the word 'physicalism' is ambiguous insofar as it confers the impression that its representatives were predominately physicists. This, however, was not the case, but what he describes as 'physicalism' was and is a research program *within biology*, promoted by leading biologists (cf. Junker 2004b, pp. 47–57). Famous exponents were the students of Johannes Müller, the physiologists Emil Du Bois-Reymond, Ernst Brücke, Hermann von Helmholtz and Carl Ludwig. Even August Weismann, who Mayr regards as the greatest evolutionist after Darwin, was persuaded by this approach and “glibly spoke of certain biological processes as being due to the ‘movement of molecules’”. I.e. the word 'physicalism' stands for the “strictly physicalist” (Cartesian) endeavours of biologists, who accepted the idea that organisms must be understood as machines (Mayr 2004, pp. 68, 17).

This approach has been extremely widespread in biology since the 17th century. Weismann, f.e. emphasized the “extreme complexity of the machines [...], which we call organisms,” and discriminated the “living machines” from other machines insofar as they are able to build themselves from a single cell. But nevertheless he saw them as machines (Weismann 1913, vol. 1, pp. 330–331). To quote just one other, more recent example: For Richard Dawkins organisms “are survival machines—robot vehicles blindly programmed to preserve the selfish molecules known as genes.” At the same time (and in the same spirit as Weismann) he cherished their unique characteristics and complexity: “We animals are the most complicated and perfectly-designed pieces of machinery in the known universe” (Dawkins [1976] 1989, pp. v, vi).

Second, Mayr's understanding of the word 'machine' is unduly narrow. When criticizing the machine theory of life as 'completely dissatisfying' and inadequate to solve the basic problems of biology, he obviously has historic or current man-made machines in mind. Certainly neither the favourite example of the 17th and 18th century, the mechanical watch, nor a modern machine is able to regenerate lost parts or to replicate itself. But a machine that would be able to perform these tasks would still be a machine. A machine is defined as a device that consists of interacting parts, uses or modifies energy to perform a specific task and functions as an integrated whole. It is a complex system with emergent properties that is nevertheless completely determined by physicochemical causes. This definition perfectly fits living organisms, with the difference that they are much more complicated than the man-made machines of our time, are built of organic molecules and are able to perform additional tasks like growth and reproduction.

But if (1) the word 'physicalism' stands for the machine theory of life, (2) its representatives subscribe to the obvious fact that all machines have emergent properties, and (3) 'reductionism' is defined as the denial of the existence of emergent properties, then his statement that “reductionism is the declared philosophy of the physicalists” is obviously wrong (Mayr 2004, p. 34). Actually, if emergence is a daily encountered fact and a simple tool like a hammer has emergent properties, it would be more than surprising if this phenomenon should have been overlooked by 'physicalists' like Weismann and Dawkins who emphasize the complexity of the organismic machine. And in fact they don't. Dawkins, f.e. speaks of “emergent properties” of an organism, takes great pains to explain their origin, and dismisses the reductionism Mayr criticizes as a nonexistent myth: “It goes without saying [...] that the kind of explanations which are suitable at high levels in the hierarchy are quite different from the kinds of explanations which are suitable at lower levels” (Dawkins 1986, pp. 177, 13).

The important point is that the existence of emergent properties is no refutation of the machine theory of life, because machines—as Mayr himself demonstrates—exhibit emergence.

His whole argument against reductionism and in favor of holism is completely valid, but it does not constitute a third way, because it is equally compatible with Cartesian ‘physicalism’. Does this mean Mayr himself promoted a ‘physicalist’ view of life and there is no third way?

If my analysis of Mayr’s attempt to initiate a new philosophy of biology between vitalism and the machine theory of life is correct, he was not successful in this regard. What he actually achieved was: (1) To refute vitalistic and supernatural concepts and strengthen the “naturalistic explanation of life.” (2) To help convince biologists and philosophers alike that “emergence is an empirical phenomenon without any metaphysical foundations” that helps to “explain phenomena that previously had seemed to be in conflict with a mechanistic explanation of the evolutionary process” (Mayr 2004, pp. 90, 77)

But if Mayr himself was an unconscious ‘physicalist’, why did he argue so forcefully against the machine theory of life? In part his dissatisfaction with this approach can be explained as a residue of earlier experiences. When he started to argue for the autonomy of biology in the early 1960s, the unique, emergent characteristics of organisms were ignored by the philosophy of science which was dominated by physics (Greene 1994; Hull 1994). In this situation Mayr not only criticised this particular neglect as reductionism, but questioned the usefulness of the physicalist approach for biology in general. In recent decades this situation has clearly changed and this was also due to Mayr’s relentless fight for the recognition of the unique aspects of biology. Nevertheless he stuck to his broad rejection and ignored developments toward a more sophisticated view (cf. Emmeche, Kjøppe and Stjernfelt 1997). But there is probably more to it. His second motivation is an emotional aversion against connotations and implications of the word ‘machine’. The view that organisms—including humans!—are ‘survival machines’, ‘robot vehicles’ programmed to preserve their genes conveys a deterministic and mechanistic view that is perceived by many persons as a gross ‘narcissistic insult’ (Freud 1917, pp. 6, 7). It is a view that Mayr definitely did not appreciate.

But why should organisms be considered as machines? The answer is that this view has been extremely valuable in biology from a heuristic perspective. And it still is, as can be demonstrated when we look at Mayr’s examples of unique characteristics of life. He has given a rather comprehensive list of such differences, but the one that is said to provide an unequivocal demarcation is the existence of a ‘genetic program’. The term is commonly used to designate the information in the genome of an organism (DNA), specifically the set of instructions that controls its development, function, behavior and other traits. Most biologists probably agree that it is the most important characteristic of life: On the one hand not a single phenomenon in the living world is not in part controlled by the genetic program; on the other hand there is nothing comparable in the inanimate world.

The genetic program is clearly an emergent property characteristic of living organisms. As such, Mayr argues, it provides a “second set of causal factors”, which means that organisms are “controlled not only by natural laws but also by genetic programs” (Mayr 2004, pp. 90, 30). But where does the genetic program come from when “anything and everything that happens in the physical world is exclusively controlled by the natural laws, gravitation, the thermal laws, and the scores of other natural laws discovered by the physical sciences” (Mayr 2004, p. 89)? Genetic programs evolved through the completely mechanistic and natural Darwinian process of replication, variation and selection, as “an *a posteriori* product of natural selection” (Mayr 1961, p. 1506). I.e. the genetic program, the ‘second set of causal factors’, is completely controlled by the ‘first set of causal factors’, the natural laws. Of course in biology it is often useful to start with the genetic program of an organism as if it constituted a ‘second causality’. But it has to be kept in mind that it is just a matter of convenience to ignore the causal origin of the genetic program and that its existence does not produce a break in the chain of natural causations.

And there is a strong historical link between the machine theory of life and the concept of a genetic program. The term was originally coined in analogy to computer programs, i.e. it is a concept from the world of machines. Since the 1960s the similarities between the two programs have been a steady source of inspiration for biologists. As François Jacob wrote in his famous book *La logique du vivant*: “Everything then leads one to regard the sequence contained in genetic material as a series of instructions [. . .], to consider the plan of an organism as a message transmitted from generation to generation [. . .]. In short, everything urges one to compare the logic of heredity to that of a computer. Rarely has a model [. . .] proved to be more faithful” (Jacob 1970, pp. 264, 265). Genetic programs have evolved through variation and selection, they are stored in form of chemical molecules (DNA) and (together with the environment) they control all aspects of the individual organism, in the same way the operations of a machine are determined by a computer program. Should we stop calling a robot that is controlled by a computer program a machine? Probably not.

Why is it important to view organisms as machines? Historically the machine theory of life, the analogy between man-made and organismic machines, was of immense heuristic value, because it forced biologists to search for natural (physicochemical) causal explanations instead of relying on ‘occult’ forces or miraculous events. It provided a naturalistic starting point for the analysis of the *functioning* of organisms and their characteristics in the same way Darwin’s theory of evolution by natural selection provided an explanation for their *origin and adaptive value*. Together the ‘revolutionary proposals’ of the machine theory and of Darwin’s theory of selection have replaced “the divinely controlled world by a strictly secular world, run according to the natural laws” (Mayr 2004, p. 86). If the preceding analysis is correct, Mayr was not successful in his attempt to initiate a ‘new’ philosophy of biology that is a third way between vitalism and physicalism. But it failed in an interesting way and I want to emphasize that this effort was an important, but only one of many interesting suggestions in his philosophical books and articles.

6. Epilogue

Was Ernst Mayr the ‘Darwin of the 20th century’? This honorary title (cf. Curio 2004/05) refers to his participation in the ‘second Darwinian revolution’ of the 1930s and 1940s, i.e. in the formulation of the modernized Darwinian theory of evolution. Mayr himself has always stressed that one of the most defining characteristics of the evolutionary synthesis was that it could only be carried out because biologists from different fields collaborated. Within this group of “ten to twelve people most active in the synthesis” he particularly mentioned Dobzhansky: “There is complete agreement among the participants of the evolutionary synthesis as well as among historians that it was one particular publication that heralded the beginning of the synthesis, and in fact was more responsible for it than any other, Dobzhansky’s *Genetics and the Origin of Species* (1937)” (Mayr 1982, pp. 568, 569). Or, as George Gaylord Simpson, one of the other so-called ‘architects’ of the evolutionary synthesis, wrote: “The synthetic theory has no Darwin, being in its nature the work of many different hands” (Simpson 1949, p. 277).

Mayr has published more than 700 scientific papers and more than 20 books. He has received many honorary degrees from some of the most prestigious universities in the world, and was an elected member of many distinguished academies. Among the prizes he was awarded are the National Medal of Science of the USA, the Balzan Prize, the International Prize for Biology from the Japan Society for the Promotion of Science, and the Crafoord Prize given by the Royal Swedish Academy.

In personal conversation and his letters Mayr was unpretentious, full of humour, self irony and warmth. In scientific discussions, however, he stubbornly insisted on arguments and on unambiguous statements. Sometimes he preferred categorical, almost one-sided statements, because he thought that such an approach would challenge the readers to come up with a refutation: “My own feeling is that it leads more quickly to the ultimate solution of scientific problems than a cautious sitting on the fence” (Mayr 1982, p. 9). But he was tolerant of other points of view when they could be substantiated and never took criticism personally. From time to time he could be persuaded of another position, and he was proud that he had changed his mind on a number of controversial topics during his life. When he was confronted with pointless chattering or dishonesty he could be brusque and uncompromising. Most of all he wanted to see progress in biology, in history, and in philosophy and he detested ‘pink fog’, as he called it.

Mayr was one of the leading evolutionary biologists of the 20th century, he was an eminent ornithologist and systematist, one of the most influential historians of biology and a forceful advocate of a new philosophy of biology. His numerous articles and books became the point of reference for a whole generation of biologists, as well as for historians and philosophers of biology. For many he was an admired example, for others he became the prototype of obsolete traditions that had to be overcome. Whatever the particular reaction was he provoked, he could not be ignored. I am convinced that many of his ideas will survive. Far away from cursory fashions they already have become classics and will inspire future generations of biologist, historians and philosophers in one way or the other.

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