Ernst Mayr and evolutionary biology: Polemics and synthesis*

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Here, I attempt to explore the interactions between evolutionary biologist Ernst Mayr and other biologists in the process that has been called the professionalizing of evolutionary biology, and in the defence of organismal biology and of systematics. I will use the tool of quoting from original writings rather than paraphrasing them, since it is necessary to preserve the flavour of the arguments and controversies that Mayr was involved in, and that led to Mayr's role in helping to build the edifice of evolutionary biology as it is known today.

Keywords: Beanbag genetics, modern evolutionary synthesis, neutral evolution, organismal biology, species concepts.

A hundred years is but an instant in evolutionary time; however, during the life of Ernst Mayr (1904–2005) that spanned a century, significant progress was made in the understanding of the pattern and process of evolution. This article is a tour through the shifting contours of the intellectual landscape of evolutionary thought during Mayr's lifetime. It will, however, be a selective tour because it will only highlight concepts and controversies that Mayr was either involved in, or those that are necessary to visit in order to understand Mayr's contributions to the study of evolution and his interactions with the practitioners of the biological sciences. Ernst Mayr was an ornithologist and systematist by training; he embraced Darwinism and championed the cause of evolutionary biology throughout his long and highly productive career.

The conflict between biometry, Darwinism and Mendelism

We begin the tour in the period between 1900 and 1918, when the genetic basis of biological traits was being understood. Although Mendel made his discoveries in the 1860s, he remained unknown until his re-discovery by Hugo de Vries, Carl Correns and Erich von Tschermark around 1900. This re-discovery led to the rise of the Mendelians who recorded variation in discontinuous biological traits in populations, viz. the colours of flowers or the shape of seeds, what in statistics would be known as categorical variables. At around that time also, the field of biometry was being developed in the UK, mainly by Darwin's cousin Francis Galton (*Natural Inheritance*, 1889), and by Karl Pearson ('Contributions to the mathematical theory of evolution', *Journal of the Royal Statistical Society*, 1893). As the name suggests, biometry is the measurement of biological traits in populations, and thus the examination of the distribution of population variation in these traits. Naturally, biometricians were only able to measure traits that exhibited continuous variation in populations, viz. height, and were thus on a collision course with the Mendelians who recorded discontinuous traits. Biometricians did not believe that Mendel's laws of inheritance could be applied to continuous traits and thus they doubted the generality of Mendel's findings. While the controversy between the Mendelians and the biometricians was on-going, there was concomitantly a rejection of Darwinism by important founders of Mendelism such as William Bateson, Hugo de Vries and Wilhelm Johannsen. Why was this so? It was because Darwinism at that time meant gradual evolution, as annunciated by Darwin: 'nature does not make leaps'; modification by descent was via slow evolutionary change. The Mendelians who were observing discontinuous traits seemed to think that nature did indeed make leaps, and this formed the basis of the rejection of evolution by gradual steps. It thus appeared as if Darwinism and Mendelism were incompatible. According to the historian of science Sahotra Sarkar, this conflict was resolved by Ronald Aylmer Fisher, in an important paper in 1918. The paper[1] dealt with similarities between related individuals. Here, Fisher assumed that continuous traits were determined by a large number of Mendelian factors, which mostly acted independent of each other. According to Sarkar, by doing so, Fisher reduced biometry to Mendelism and thus broke the impasse between Mendelism and Darwinism[2]. Fisher's crucial assumption was empirically supported by work on *Drosophila* by researchers of the Morgan school who were also finding out, at about that

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time, that small variations could be caused by Mendelian factors. This meant that all biological traits could come under the purview of population genetics, which was an important development. This facilitated the synthesis of Darwinism, Mendelism and biometry[3].

The evolutionary synthesis begins

Beginning in the 1920s, the classical genetics of Morgan was being integrated with disciplines such as cytology and enzymology. Morgan's *The Theory of the Gene* (1926) also played an important interdisciplinary role in this process. Evolutionary biology was also being put on a strong theoretical foundation with the work of what has been called the 'triumvirate' – a set of three individuals whose contributions were quite different yet extremely significant. Fisher (1890–1962) believed that significant evolutionary change took place only in large populations, almost exclusively by natural selection on near-independent loci. He discussed this in his classic book *The Genetical Theory of Natural Selection* (1930). Sewall Wright (1889–1988) was more interested in the behaviour of genes in small populations or in small demes of larger populations. An important consequence of population substructure was the occurrence of random genetic drift in such small populations, which could result in non-adapted genotypes. Wright also formulated his famous shifting balance theory of evolution, which essentially provided a powerful heuristic tool to conceptualize the movement of populations over an adaptive landscape, from non-adapted valleys to more adapted peaks, a movement that could be brought about by a combination of mutation, migration and selection within and between populations. The third member of this select club was J.B.S. Haldane (1892–1964) who, among many other issues, was concerned specifically with examining the time available for evolution by natural selection to occur, given known mutation rates. *A satisfactory theory of natural selection . . . must show not only that it can cause a species to change, but that it can cause it to change at a rate which will account for present and past transmutations* ('A mathematical theory of natural and artificial selection', *Transactions of the Cambridge Philosophical Society*, 1924). It is often believed that the work of this troika was what was largely responsible for the modern evolutionary synthesis. However, contributions by non-Anglo-US researchers should not be forgotten. Mayr and Theodosius Dobzhansky were particularly careful later on to highlight the efforts of Russian naturalist-geneticists who, for example, studied variation in natural populations of *Drosophila*. Thus, they believed that the triumvirate should be extended to a quadrumvirate by the inclusion of Sergei Chetverikov (1880–1959), who proposed that mutations are not necessarily deleterious and that natural populations are a storehouse of mutations on which natural selection can act. *[A] species, like a sponge, soaks up heterozygous mutations, while remaining from first to last externally (phenotypically) homozygous* ('On several aspects of the evolutionary process from the view point of modern genetics', *Zhurnal Eksperimental'noi Biologii*, 1926). Chetverikov's student, Timofeeff-Ressovksy went on to found a vibrant school of genetics in Germany.

The public perception of natural selection and evolution: The response of evolutionary biologists

The period of the 1920s was also a time when there was considerable dispute in the popular press among popular figures such as the pro-Darwinian H. G. Wells and the anti-Darwinian writers Hilaire Belloc, George Bernard Shaw and G. K. Chesterton. Criticism was directed against Wells's *Outline of History* (1920) in which he depicted a materialistic progression of life on earth that also included the evolution of human culture and society. The criticism was not so much against evolution, which was generally, by that time, accepted as a fact, as against the process of natural selection. The palaeontologist, Arthur Keith went on to declare in the *Rationalist Annual* in 1922: *[The] very fact that Mr. Chesterton and Mr. Hilaire Belloc could confidently assure readers of the Sunday Press that Darwin's theory was dead, showed that those who are studying the evidence of our origin, and who are Darwinists to a man, had lost touch with public intelligence* (quoted in Sarkar[2]).

It was the clarion call sounded by Keith that was taken up by Haldane, according to Sarkar[2]. Haldane wrote an essay in the *Rationalist Annual* defending Darwinism in 1927. This was followed in 1932 by *The Causes of Evolution*[4] – one of the most important books on evolution for the intelligent layperson in which he said: *Darwinism has been a subject of embittered controversy ever since its inception. . . . The few really pertinent attacks were lost amid a jabber of ecclesiastical bombinations. The criticism was largely dictated by disgust or fear of this doctrine, and it was natural that the majority of scientific men rallied in Darwin's support. By the time of Darwin's death in 1882, Darwin had become orthodox in biological circles. The next generation saw the beginnings of a more critical attitude among biologists. It was possible to criticise Darwin without being supposed to be supporting the literal authenticity of the Book of Genesis . . . . The rising generation of biologists, to which I belong, may now perhaps claim to make its voice heard. We have this advantage at least over our predecessors, that we get no thrill from attacking either theological or biological orthodoxy; for eminent theologians have accepted evolution and eminent biologists denied natural selection.*

The Causes of Evolution is an extremely valuable book, not only because it explains lucidly the processes contributing to evolution, but in an Appendix at the end, it gathered together all the then known mathematical models of population genetics, providing a useful and scholarly source of reference. It was clear that Haldane's vision and concerns went much beyond the framework of population genetics and included all of evolution. This is why historians of science such as Sarkar, consider Haldane to be the most important member of the quadrumvirate and regard his efforts as resulting in the constitution of an evolutionary genetics rather than just population genetics[2]. This broad integrative approach was not taken by either Fisher or Wright. Others, such as, Carson[5] also believed that the evolutionary synthesis began in earnest with the approach of Haldane, that besides the work of Darwin, Mendel, Fisher and Wright, also brought in genetic phenomena such as inversions, translocations, polyploidy, hybridization, as well as disciplines such as palaeontology. Haldane's broad view of factors contributing to evolution and to its investigation was vital to the synthesis.

The modern evolutionary synthesis

Beginning in the 1930s, the Jesup lecture series at Columbia University was influential in focusing the efforts of key scientists who played an important role in professionalizing evolutionary biology. These scientists in America and the books which resulted from their lectures in the series were Theodosius Dobzhansky: *Genetics and the Origin of Species* (1937), Ernst Mayr: *Systematics and the Origin of Species from the Viewpoint of a Zoologist* (1942), George Gaylord Simpson: *Tempo and Mode in Evolution* (1944) and G. Ledyard Stebbins: *Variation and Evolution in Plants* (1950). Julian Huxley (the grandson of T. H. Huxley) in England also played an extremely important role in this process in three ways. Firstly, in 1930, he co-authored a book entitled *The Science of Life* along with H. G. Wells and his son G. P. Wells. This book was a sequel to Wells's earlier book, *The Outline of History*, which had caused much controversy because of its materialistic perspective. Secondly, in 1940, Huxley edited an important book entitled *The New Systematics* in which he said: *Even a quarter century ago it was possible to think of systematics as a specialized, rather narrow branch of biology, on the whole empirical and lacking in unifying principles, indispensable as a basis for all biological workers, but without much general interest or application to other branches of their science. Today, on the other hand, systematics has become one of the focal points of biology. Here we can check our theories concerning selection and gene-spread against concrete instances, find material for innumerable experiments, build up new inductions: the world is our laboratory, evolution itself is our guinea pig.* Thirdly, in 1942, he wrote *Evolution: The Modern Synthesis*, which was where, for the first time, he used the term 'modern synthesis' for the process that was occurring among the evolutionary biologists wherein conflicts between geneticists and naturalist-systematists were being resolved.

It is beyond the scope of this article for me to summarize the content of all these books. Since our focus is on Mayr, I will summarize the central idea of his 1942 book and thus of his intellectual contribution at that time. Although the title seems quite innocuous, Mayr's 1942 book is a powerful statement, as was Huxley's, in the cause of protecting the intellectual status of systematics as well as of systematists. It makes the point that, although Darwin's 1859 opus was called *On the Origin of Species*, Darwin himself did not have a species concept and neither adequately defined a species nor the process of species formation. For example, in 1859 Darwin said: *In determining whether a form should be ranked as a species or a variety, the opinion of naturalists having sound judgement and wide experience seems the only guide to follow.* And: *[T]he only distinction between species and well-marked varieties is, that the latter are known, or believed, to be connected at the present day by intermediate forms, whereas species were formerly thus connected.* Therefore, Mayr set out both to define a species as well as to bring together known mechanisms of speciation. The species concept that appealed most to Mayr was that of the biological species wherein species are defined as 'groups of actually or potentially interbreeding natural populations, which are reproductively isolated from other such groups'[6]. Furthermore, in this book he applauded Julian Huxley's use of the term 'New Systematics' in which 'the importance of the species as such is reduced, since most of the actual work is done with subdivisions of the species, such as subspecies and populations. The population or rather an adequate sample of it, . . . has become the basic taxonomic unit'[6]. The process of speciation that Mayr thought was most plausible was that of allopatric speciation wherein a once continuous population of a species may become split into two or more geographically isolated populations; these isolated populations may achieve reproductive isolation in allopatry such that when they later meet in sympatry, they are already separate species incapable of interbreeding. It is important to remember, however, that these ideas of sympatric and allopatric species, of the biological species concept, as well as of reproductive isolating mechanisms had already been articulated by the lepidopterist E. B. Poulton[7–9], in papers that date back to 1904. What Mayr, however, achieved in his remarkable book[6] was a synthesis of thought on species concepts and not much original work itself; he brought his vast experience on the systematics of birds to bear on the field of systematics and was able to successfully couple it with the various species concepts available at that time. Perhaps one original contribution of Mayr in this regard was a 1954 paper in which he proposed peripatric speciation[10]. Mayr[11] claims that in this paper he was the first to develop a detailed model of the connection between speciation, evolutionary rates and macroevolution. The 1954 paper was also apparently his favourite one[12]. In this paper, he proposed that founders from peripheral parts of the population of a species could, if isolated for a sufficiently long time, form separate species. However, the rate of evolution and probability of speciation in such peripheral isolates would also be determined by the size of the founding population.

The main features of the evolutionary synthesis thus came to be established. These were firstly, that gradual evolution (Darwinian evolution) could be explained by mutations and recombination; secondly, that natural selection was an important force that could influence the pattern of genetic variation, and thirdly, that macro-evolutionary processes, i.e. speciation, could be explained by known genetic mechanisms. Mayr was certainly an important contributor to the synthesis, and surely one of its principal architects. In an edited volume in 1980 entitled *The Evolutionary Synthesis: Perspectives on the Unification of Biology*, he had this to say about the intellectual process that was taking place during this period: *When I read what was written by both sides [experimental geneticists and population-naturalists] during the 1920s, I am appalled at the misunderstandings, the hostility, and the intolerance of the opponents . . . Just as in the case of warring nations, intermediaries were needed . . . [T]hese bridge builders were the real architects of the synthesis. What qualifications did an evolutionist require to be able to serve as a bridge builder? . . . None of the bridge builders was a narrow specialist. They all had, so to speak, a foot in several camps*.

Ernst Mayr and the Fisher–Wright debate

In the above quotation, Mayr was describing the role that he felt was played by scientists such as himself, Dobzhansky, Stebbins, Simpson, and Huxley, i.e. the 'inner circle' who would remain closely connected by their strong commitment to the cause of championing Darwinism. In the quote, Mayr mentions intolerance and misunderstanding, and it is therefore important, from a historical perspective also, to understand the role that Mayr played in an important debate that has been called the Fisher–Wright debate, because it involved a major argument between Fisher and Wright, a veritable clash of titans. The argument was basically over differences in perspective between Fisher and Wright, as to which was the most important evolutionary force: natural selection or random genetic drift. On one side was ranged Fisher and the ecological geneticist E. B. Ford, who wanted to use data on the moth *Panaxia dominula*, which was found in two small populations around Oxford, to demonstrate the importance of natural selection. Using the small *Panaxia* populations, Fisher and Ford wanted to show that natural selection could be an important force even in such small populations and that drift was not necessarily the major evolutionary force within small populations. They were upset by Wright's criticisms of natural selection in Huxley's 1940 book *The New Systematics*, and in 1947 wrote a paper using the *Panaxia* data to counter this viewpoint. Dobzhansky, who saw this paper in *Heredity*, wrote to Wright in 1948 and implored him to reply to what he saw as an attack against Wright's theory of genetic drift. *I think you should publish a retort, not for your own sake but for the sake of the multitude which Fisher deliberately leads astray. Perhaps a note in* Nature *will do the trick, or is a more extended statement desirable?* (quoted in Provine[13]). Stebbins also suggested that Wright publish his response to the Fisher–Ford paper in the journal *Evolution*. Why the journal *Evolution*? This was because Mayr had just been elected in 1947 as the first Editor of this newly established journal, which was supposed to be the mouthpiece of the Society for the Study of Evolution (SSE)[14]. [The founding of the SSE was also an important event in the professionalizing of evolutionary biology, as it arose as a merger of the Society for the Study of Speciation and the Committee on Common Problems in Genetics, Paleontology, and Systematics. Through his important organizational role in this society, which also included serving as the Society's Secretary and as Editor of *Evolution*, Mayr played a vital part in the 'confederation' of scientists working towards an integration of disciplines in evolutionary biology[15].] Wright accordingly did submit this paper to *Evolution*, and it was accepted by Mayr. On seeing this article, Ford wrote the following to Mayr in 1949 (quoted in Provine[13]): *I . . .have seen the article by S. Wright in* Evolution *in which he criticises a paper by Fisher and myself in* Heredity. *It is, I think, not normally worth replying to criticism. The only circumstances in which this should be done are if others are likely seriously to be misled, or in the rare event in which one's views are actually misrepresented. In respect of Wright's criticism, both reasons hold. Consequently, Fisher and I have drafted a note briefly exposing Wright's misrepresentation of our statements and we should be so grateful if you could publish it in* Evolution . . . .

This is what Mayr had to say in response (quoted in Provine[13]): *I entirely agree with you that misrepresentation of fact as well as misquotations should be corrected. The pages of* Evolution *will always be open to such objective correction. Consistent with this policy, I would be glad to publish your note if, as you state, it would prevent that 'others are . . . seriously . . . misled'. However, it seems to me that in its present form your note fails to achieve this object . . . With the same breath you say that random fixation occurs but that it is of no evolutionary significance. I have always considered it axiomatic that anything that leads to a deviation from the present generation is automatically of evolutionary significance. I fail to see any refutation of this point in your note . . . As editor, I am interested in any discussion that leads to a clarification of a scientific problem. On the other hand, I am sure that the Editorial Board would never endorse a communication that might lead to a polemic. My personal impression is that the note, submitted by you, was written in haste* *and perhaps under some emotional stress. I would do you a great disservice by publishing it in its present form. I am therefore returning it to you for consideration . . .* Fisher withdrew the paper from *Evolution* and submitted it to *Heredity*, where it was published as 'The Sewall Wright Effect' in 1950. In this paper, the dichotomy between those who accept and those who reject random genetic drift as a major force in evolution was clearly outlined. Wright wrote a counter-paper in *American Scientist* in 1952 entitled 'Fisher and Ford on "The Sewall Wright Effect"'[16]. However, he also added a note on selection in this paper (quoted in Provine[13]): *I do not, of course, wish to maintain that my views on evolution have stood entirely still since 1931 . . . Qualifications and additions have been made, beginning in 1932, and have continued up to the present time. The interplay of directed and random processes in populations of suitable structure has, however, continued to be the central theme.* Why did Mayr champion Wright's cause against the views of Fisher in this debate? According to Provine[13], if Fisher and Ford's conclusions on the importance of natural selection in the small *P. dominula* populations were found to be true, then it could undermine Mayr's central idea of the founder effect in speciation. This founder effect relied on small population effects such as random genetic drift as important factors in generating population differentiations that could result in speciation.

Mayr and the controversy over beanbag genetics

Another major controversy that Mayr was involved in was on the importance of 'classical' population genetics. Beginning in the 1950s, there appeared to be a disenchantment with the contributions of the troika of population geneticists consisting of Fisher–Wright–Haldane, and their relevance to 'real' evolution, viz. evolution as observed in nature. This disenchantment was largely the result of a conflict among experimental biologists, naturalist-systematists and theoreticians. For example, the developmental biologist C. H. Waddington had this to say on the matter in 1952, in a Society of Experimental Biology Symposium in Oxford (as quoted in Provine[13]): The mathematical theories of Fisher, Haldane and Wright '*[have] not, in the first place led to any noteworthy quantitative statements about evolution. The formulae involve parameters of selective advantage, effective population size, migration and mutation rates, etc., most of which are still too inaccurately known to enable quantitative predictions to be made or verified*'. Dobzhansky, on the other hand, seemed to understand the great value of theoretical formulations, even though, as we will see later, he apparently did not understand all of it fully. This is what Dobzhansky had to say about population genetics in the Cold Spring Harbor Symposium on Population Genetics in 1955 (quoted in Provine[13]): *Haldane, Wright, and Fisher are the pioneers of population genetics whose main research equipment was paper and ink rather than microscopes, experimental fields,* Drosophila *bottles, or mouse cages. This is theoretical biology at its best, and it has provided a guiding light for rigorous quantitative experiment and observation*. Mayr was, however, not convinced, and in the 1955 Cold Spring Harbor Symposium Session on Integration of Genotypes had this to say (quoted in Provine[13]): *The study of the integration of genotypes has shown that population genetics can no longer operate with the simplified concepts it started out with.* In this symposium, Mayr spoke strongly of the limitations of theoretical population genetics and praised the contributions of field naturalists who were doing the 'real' biology. This talk was the forerunner to the beanbag genetics controversy. In 1959, Mayr gave a plenary talk at the Cold Spring Harbor Symposium organized on the occasion of the celebration of 100 years after the publication of Darwin's *Origin of Species*. In this talk entitled '*Where are we*?', Mayr divided progress in evolution into the following periods[13]. There was first the Mendelian period (1900–20) dominated by the mutation theory of evolution. This was followed (1920–30s) by the period of classical population genetics à la Fisher-Wright–Haldane, which was largely characterized by the belief in natural selection by gradual incremental 'Darwinian' processes, but also by the extremely simplistic view that evolutionary change was essentially an input or output of genes, i.e. beanbag genetics. This led to the phase of the so-called newer population genetics (late 1930–59) guided by naturalist-population geneticists such as Dobzhansky, Bruce Wallace and Michael Lerner. In his plenary address, Mayr seemed to be saying that theoretical population genetics, especially of the 'classical' kind could go only so far and no more, and by terming it 'beanbag genetics', he appeared to be disparaging it and attempting to elevate the genetics of individuals such as Dobzhansky to a higher, more relevant status compared to that of the classicists. In this context, it is interesting to examine comments made by Dobzhansky on Wright's papers, as it provides insight into the conceptual divide between the naturalist-geneticists and the theoretical population geneticists. Here are some extracts from the Oral History Memoir of Dobzhansky (1962; quoted in Provine[13]): *Wright gave a splendid paper at the Genetics Congress in 1932* [the Shifting Balance Theory]. *In a sense, that is still his best paper. He is a remarkably difficult writer. In most cases, he writes with so much profound and esoteric mathematics that common mortals cannot read him anyhow. Even when he attempts to write without esoteric mathematics, he is often rather hard to follow. This 1932 paper is an exception . . . My way of reading Sewall Wright's papers, which I think is perfectly defensible, is to read the conclusions he arrives at, and hope to goodness that what comes in between is correct. 'Papa knows best' is a reasonable assumption, because if the mathematics were incorrect, some mathematician would have found it out.*

Dobzhansky was clearly in awe of Wright, and through most of his professional career collaborated actively with him, a situation that some believe began to become onerous to Wright in later years since it was rather one-sided[13]. Mayr, on the other hand, seemed to be clamouring for the recognition of naturalists, systematists and such ilk in the history of progress in evolutionary thought. In the Cold Spring Harbor Darwin Centennial in 1959, he said (quoted in Provine[13]): [Fisher, Wright and Haldane] *have worked out an impressive mathematical theory of genetical variation and evolutionary change. But what, precisely, has been the contribution of this mathematical school to evolutionary theory, if I may be permitted to ask such a provocative question? . . . However, I should perhaps leave it to Fisher, Wright, and Haldane to point out what they consider their major contributions.*

In defence of beanbag genetics

It was inconceivable that Mayr's remarks about beanbag genetics would remain unanswered. Wright reviewed the symposium volume that resulted from this Darwin Centennial at Cold Spring Harbor for the *American Journal of Human Genetics*, and spent almost the entire review criticizing Mayr's comments on beanbag geneticists. In this review, Wright, however, praised Dobzhansky as one who seemed to have truly understood the value of interaction between empiricism and theory. Mayr did not confine this attack against beanbag genetics to his plenary address, but also wrote about it in his 1963 book, *Animal Species and Evolution*. By this time, Haldane was in India and missed the 1959 Cold Spring Harbor Symposium, as he was denied a visa to visit the US because of his Communist beliefs (a relic of the McCarthy era). He had also read the remarks about beanbag genetics in Mayr's 1963 book which he was reviewing for the *Journal of Genetics*. In 1964, Haldane wrote his celebrated paper entitled '*A defense of beanbag genetics*'[17]. This classic paper is essential reading for students of evolution because in it Haldane proceeds to demolish the opposition, with characteristic wit and satire. I reproduce a few extracts from this paper to provide a flavour of Haldane's counter-attack: *Now, in the first place I deny that the mathematical theory of population genetics is at all impressive, at least to a mathematician. . . .Our mathematics may impress zoologists but do not greatly impress mathematicians . . . One of the most important functions of beanbag genetics is to show what kind of numerical data are needed. Their collection will be expensive. Insofar as Professor Mayr succeeds in convincing the politicians and business executives who control research grants that beanbag genetics are misleading, we shall not get the data . . . . Perhaps a future historian may write, 'If Fisher, Wright, Kimura, and Haldane had devoted more energy to exposition and less to algebraical acrobatics, American, British, and Japanese genetics would not have been eclipsed by those of Cambodia and Nigeria about AD 2000'. I have tried in this essay to ward off such a verdict.* Haldane passed away in 1964, the year this paper was published.

What might one make of all of this polemic? Did Mayr truly believe that population genetics was not terribly useful in the progress of evolutionary thought? Perhaps this quote[18] from Mayr's book *The Growth of Biological Thought* may provide some insight: *My tactic is to make sweeping categorical statements. Whether or not this is a fault, in the free world of the interchange of scientific ideas, is debatable. My own feeling is that it leads more quickly to the ultimate solution of scientific problems than a cautious sitting on the fence . . . histories should even be polemical. Such histories will arouse contradiction and they will challenge the reader to come up with a refutation. By a dialectical process this will speed up a synthesis of perspective.*

Ernst Mayr and the defence of organismal biology

Mayr played another important role in evolutionary biology, specifically in the defence of organismal biology. After the discovery of the structure of DNA in 1953, the 1950s and 1960s saw the rise of molecular biology. With the arrival of James Watson as a member of the Harvard faculty in 1956, the organismal or the non-molecular biologists were, in the words of E. O. Wilson 'forced by the threat [of molecular biology] to rethink our intellectual legitimacy' (quoted in Dietrich[19]). Statements such as 'all biology is molecular' made by the Nobel laureate and biochemist George Wald, seemed to reinforce the view that organismal biology was being perceived as not keeping up with the Watsons[19]. Mayr, Dobzhansky and Simpson began a counter-attack on molecular biology. They attempted to do so by speaking out for organismal biology at various forums and also by writing in important journals such as *Science*. Mayr wrote an impassioned piece entitled 'Cause and effect in biology. Kinds of causes, predictability, and teleology are viewed by a practising biologist' in *Science* in 1961. In this essay, he outlined the difference between proximate and ultimate causation in biology. Molecular biology may provide, for example, a proximate cause for biological phenomena; however, the ultimate and most important causation was provided by natural selection. In a similar vein, Dobzhansky wrote about Cartesian versus Darwinian science, with Cartesian science being defined as the mechanistic aspect of a science like biology, while the Darwinian approach to science was said to provide the *vera causa*. Simpson[20] also followed with a paper in the same style. The central goal of Mayr, Dobzhansky and Simpson was to establish that organismal biology was unique and autonomous, since it was neither deducible from nor reducible to molecular biology. Dobzhansky's well-known saying: *Nothing makes sense in biology except in the light of* *evolution*, appeared in his paper entitled 'Biology, molecular and organismic' in the *American Zoologist* in 1964. According to the philosopher and historian of science, Michael Ruse (in an on-line eulogy for Ernst Mayr, 5 February 2005)[21]: *When Dobzhansky said that nothing in biology makes sense except in the light of evolution, he was not just making an epistemological claim. He was making a political statement. A war cry to rally the troops.*

Mayr attempted to do even more. In 1963, he wrote an editorial in the journal *Science*[22], entitled *The new versus the classical in science*[1]. I provide some quotes from this paper to illustrate the tone and the type of points he was making; furthermore, although he was attacking molecular biology, the word molecular biology itself did not appear; yet all who read the paper knew the target of Mayr's attack. *There long has been a bandwagon tendency in American science, but today it seems particularly rampant . . . . In addition, there is an inclination to equate 'classical' with 'old-fashioned' and 'passé' . . . We Americans worship the new: . . . Somehow the word new has acquired the meaning of 'better' . . . [T]he Young Turks in the new areas . . . tend to regard the more classical branches of their science with unconcealed contempt. At worst, this intolerance leads them to attempt to cut-off funds from the more classical fields . . . .*

Dobzhansky and Mayr were also having difficulty in reconciling new findings of molecular biology with organismal biology. These finding seemed to indicate that the rate of change of molecules was much higher than the rate of change of morphology. Furthermore, the rate of evolution at the molecular level seemed to be constant, e.g. the work of Linus Pauling and Emile Zuckerkandl on haemoglobins and sickle cell anaemia was revealing that the rate of amino acid change in primates was constant[23]. This disjunction between molecules and morphology was hard to explain. To hold onto the view that organismal biology was an autonomous discipline which is not predictable from lower levels, Dobzhansky also wrote a paper in *Science* in 1963 entitled 'Evolutionary and population genetics: Active and intellectually stimulating research is going on in organismic as well as molecular genetics' in which he said: *Man is an organism, not a molecule, although some diseases which afflict his flesh are molecular diseases.*

Mayr and neutral evolution

The ensuing paradox between molecular and morphological evolution was resolved by the brilliant insight of Motoo Kimura[24] as well as by King and Jukes[25], who declared that 'non-Darwinian' evolution took place at the molecular level. By this was meant that neutral substitutions or neutral mutations could occur at the molecular level. These mutations had no impact on the functionality, for example, of the protein in whose gene they occurred. This could happen, for instance, by mutations occurring in non-coding sites of the gene or in non-functional parts of the protein. Kimura formalized these ideas in the neutral theory of evolution in 1968, and this theory has been hailed as one of the most important insights on evolution at the molecular level that the 20th century has seen. According to Zuckerkandl[19], Mayr, Dobzhansky and Simpson were more 'irritated' by molecular biologists than by molecular evolution. They were trying to forge a secure relationship between organismal biology and molecular biology, such that the two could be successfully integrated. Central to this position was the issue of natural selection: on what did natural selection act? According to these three advocates, natural selection acted only on the organismal level. This continual advocacy must have had some effect because Zuckerkandl[26] did admit that: *The further away we get in the series of integrated biological levels from the gene level, the more disturbance is caused by environmental effects with respect to the unambiguous expression of the structure of a given gene*. The issues of levels of selection and of reductionism in biology are still important topics of debate in biology. Thus even today, many decades after Mayr's initial advocacy, biologists still feel compelled to write papers entitled 'The return of the whole organism'[27].

On the matter of neutral evolution, Mayr was still extremely ambivalent, and in his 1971 book *Populations, Species, and Evolution*, he had this to say: *A random replacement of amino acids unquestionably occurs occasionally in evolution, but it appears at present that it does not anywhere near approach selection in importance as an evolutionary factor*. In his opinion, chance caused disorder, while selection caused order. The evolutionary biologist, Mark Ridley has remarked that in an essay Mayr wrote in 2004 in *Science* on the occasion of his 100th birthday, he summarized the importance of the neutral theory of evolution by failing to mention it. In this essay entitled '80 years of watching the evolutionary scenery', Mayr[28] goes on to say: *It would seem justified to assert that, so far, no revision of the Darwinian paradigm has become necessary as a consequence of the spectacular discoveries of molecular biology.*

Epilogue

Mayr has justifiably earned for himself the title 'Darwin of the 20th century'. He declared himself Darwin's champion, and often pointed out that a most important consequence of the Darwinian revolution was the destruction of typological thinking. Mayr repeatedly stressed that there were important differences between Darwinism and contemporary theories of evolution. Evolution as conceived by Darwin was not goal-directed, while contemporary theories were orthogenetic or aristogenetic in the sense that they believed in a pre-determined progression of lower to higher forms. Furthermore, by focusing on individuals, Darwin destroyed the tyranny of typological thinking, which was a relic of the essentialism of Plato, who believed that groups of organisms were constructed according to certain homogeneities[18]. By attacking the concept of essentialism, Darwin provided a mechanism by which individuals became both a focus and an essential ingredient in the evolutionary process. This was a paradigm shift, and according to Mayr[18], a conceptual leap, that constituted a true scientific revolution. Mayr's zeal in defending Darwin and in protecting organismal biology and evolution from the 'non-believers' has formed the subject of this entire review, but it can also be seen in the titles of some of his recent books, e.g. *One Long Argument. Charles Darwin and the Genesis of Modern Evolutionary Thought* (1991), *This is Biology – The Science of the Living World* (1997), and *What Evolution Is* (2002). In a eulogy for Ernst Mayr[21], Michael Ruse had this to say: *Those dreadful geneticists had ignored variation, the basis of Mayr's gradualism, and so a lot of the history [The Growth of Biological Thought, Mayr, 1982] was devoted to showing that that rotter Plato had illicitly introduced essentialism – the idea that groups have no variation – into biological thought. Only slowly and gradually, thanks primarily to Darwin and to a certain immigrant to the United States of America, had population thinking finally triumphed.*

On the occasion of Mayr's 90th birthday, Douglas Futuyma[29] wrote in the journal *Evolution* in a special section to honour Mayr: *He may be given to categorical assertions that provoke or irritate; he may fight battles we suppose were long since won, but which we can hardly appreciate (because he helped to win them for us); his interpretations of genetic theory and evidence are sometimes questionable; and no one will agree with all his positions, analyses, and opinions. But that his style demands counter-argument is itself one of the reasons to read him . . . . Anyone who has failed to read Mayr can hardly claim to be educated in evolutionary biology.*

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