Ornithology and the genesis of the Synthetic Theory of Evolution

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During the 1930s and 1940s many of the controversies that had shaped discussions about evolution for more than a century came to an end. This unification of evolutionary biology was achieved on a Darwinian basis. Together with selection, which was regarded as the only causal factor leading to adaptation, further evolutionary factors were integrated (mutation, recombination, drift, geographic isolation). This Synthetic Theory of Evolution or Synthetic Darwinism has dominated evolutionary biology since the early 1950s. In contrast to the situation during the nineteenth century, when leading ornithologists opposed Darwinian evolution, ornithologists played a central part in the formulation of the new model. Both Bernhard Rensch and Ernst Mayr based much of their evolutionary theorising on ornithological data. The British zoologist Julian Huxley did intense research on the ethology of birds. On the other hand the leading ornithologist Erwin Stresemann, teacher of both Rensch and Mayr, never really accepted Synthetic Darwinism. By comparing the theoretical views of Stresemann, Rensch, and Mayr, I will discuss in which respect ornithologists were especially prepared to appreciate the new genetical theory of evolution.
Key words: History of ornithology, history of evolution, Erwin Stresemann, Bernhard Rensch, Ernst Mayr.

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'I took much pleasure in watching the habits of birds, and even made notes on the subject. In my simplicity I remember wondering why every gentleman did not become an ornithologist'. With these words Charles Darwin remembered one of his favourite childhood hobbies (Darwin 1958: 45). The enthusiasm of the founder of the modern theory of evolution for birds, however, was not matched by most ornithologists of his time and it was only in the 1930s that ornithologists actively participated in the development of the theory of evolution.

What was the relationship between ornithology and the theory of evolution? Did the majority or the leading ornithologists of the time accept evolution, did they actively support it, or can we observe strong opposition? From the viewpoint of the evolutionists on the other hand, we might ask if they were interested in ornithological data to verify their ideas, or did both fields exist in isolation? The answers to these questions, of course, vary with time and place. Not only ornithology has experienced fundamental change, but the theory of evolution itself was greatly modified during the nearly two hundred years since it was first formulated by Lamarck, and later Darwin.

Ornithology and evolution in the nineteenth century

In the nineteenth century not one of the major evolutionists can be regarded as an ornithologist. Jean-Baptiste de Lamarck, the author of the first comprehensive theory of evolution (Philosophie zoologique, 1809), mainly worked with molluscs. Darwin did most of his original research on barnacles (Cirripedia) and later on botany. Birds, however, became very important for Darwin in several respects.

First there is the famous case of the Galapagos birds. In March 1837 the ornithologists John Gould informed Darwin that the mockingbirds he had collected on three different islands in the Galapagos should be regarded as different species, and not as varieties as Darwin had originally suspected. Species and varieties it seemed were only quantitatively differing stages in a continuous process. As he remembered in *Origin of Species*: 'Many years ago, when comparing, and seeing others compare, the birds from the separate islands of the Galapagos Archipelago, both one with another, and with those from the American mainland, I was much struck how entirely vague and arbitrary is the distinction between species and varieties' (Darwin 1859: 48). The Galapagos finches were particularly remarkable, because gradual stages could be observed: 'a nearly perfect gradation of the structure in this one group can be traced in the form of the beak, from one exceeding in dimensions that of the largest gros-beak, to another differing but little from that of a warbler' (Darwin 1839: 462).

Another bird species became equally important for Darwin – his famous pigeons (*Columba livia*). The domesticated rock-pigeons were his favourite model organism to demonstrate the power of selection. They supplied him with a test-case for rapid evolution under artificial selection: 'when I first kept pigeons and watched the several kinds, knowing well how true they bred, I felt fully as much difficulty in believing that they could ever have descended from a common parent, as any naturalist could in coming to a similar conclusion in regard to the many species of finches, or other large groups of birds, in nature' (Darwin 1859: 28). Although the breeding of pigeons is only a narrow aspect of ornithology it gives an impression of the immense diversity and lavishness of forms that can be observed under natural conditions.

And finally birds provided Darwin with beautiful examples of traits acquired by sexual selection: 'Secondary sexual characters are more diversified and conspicuous in birds […] than in any other class of animals. On the whole, birds appear to be the most aesthetic of all animals, excepting of course man, and they have nearly the same taste for the beautiful as we have' (Darwin 1871, 2: 38).

Although birds were very important for Darwin and the emergence of his theories of evolution and selection, he had no special interest in ornithology as such. A very similar picture arises when we look at Darwin's supporters. The most important proponents of the theory of evolution came from other biological disciplines (Mayr 1982, Junker 1998, Junker & Hoßfeld 2001). Ernst Haeckel and Thomas Henry Huxley were morphologists working originally with marine invertebrates, Joseph Dalton Hooker and Asa Gray were botanists, August Weismann worked with butterflies and crustaceans, to mention just a few of Darwin's influential followers. Like Darwin, however, they were interested in the evolution of birds and their traits from different perspectives: Haeckel, for example, published a first provisional phylogeny of birds as early as 1866, tracing them back to the archaeopteryx and reptiles.

On the other hand leading ornithologists of the time were among the most outspoken critics of Darwin's theories. In Germany a significant number of them were not only opponents of the theory of selection, but even of evolution as such. As Erwin Stresemann has remarked in his history of ornithology, 'among the leading ornithologists in Germany the opponents of Darwinism still [in the early 1870s] were in the majority: J[ean] Cabanis, H[ermann] Schlegel, Th[eodor] von Heuglin, E[ugen] F[erdinand] von Homeyer, B[ernard] Altum, W[ilhelm] von Nathusius formed a mixed-coloured coalition that attempted to prevent the advance of the 'world-shaking' doctrine' (Stresemann 1951: 237). According to Stresemann this opposition can be explained in part by the fear that the acceptance of evolution would destroy the species concept and, as a consequence, be detrimental for taxonomy in general. Even those ornithologists who accepted evolution, such as Joel Asaph Allen, Henry Seebohm, and Ernst Hartert, rejected selection as the major causal factor and endorsed Lamarckian or orthogenetic explanations.

Although a similar picture emerges when we look at other biological disciplines, such as botany, anthropology or paleontology, the leading ornithologists seem to have been particularly hostile to Darwin's theories. Nineteenth century evolutionists, on the other hand, used ornithological data to support their theory, but they had no special interest in ornithology. This situation changed fundamentally during the first decades of the twentieth century. The anti-Darwinian tradition in ornithology that had prevailed in the nineteenth century still had its adherents. The creationist Otto Kleinschmidt, for example, was one of its most extreme representatives. But, and this was the great difference, a school of evolutionists within ornithology had emerged. Before I discuss these new developments with special reference to Stresemann and his pupils Bernhard Rensch and Ernst Mayr, it is necessary to look at the fundamental changes the theory of evolution encountered during the first decades of the twentieth century.

Twentieth century: The origin of Synthetic Darwinism

In *Origin of Species* and other publications Darwin had presented his theory as a unified concept and spoke of it in the singular. Very soon, however, single elements were isolated, criticised and accepted independently. For example many biologists of the nineteenth century accepted the idea of evolution, i.e. the gradual change of species over time, but rejected Darwin's mechanism, natural selection. Ernst Mayr has identified five major theories in Darwin's work: '(1) evolution as such, (2) common descent, (3) gradualism, (4) multiplication of species, and (5) natural selection' (Mayr 1985: 757). A sixth theory has to be added: Darwin's understanding of the origin of hereditary variation. Variation is an absolutely crucial prerequisite for the theory of selection – without variation there can be no selection. Darwin, who was well aware of this problem, devoted three chapters of *Origin of Species* to the origin of variation: The first two chapters deal with 'Variation under Domestication' and 'Variation under Nature', and in chapter 5 'Laws of Variation' are analysed. In addition he published a two volume book *The Variation of Animals and Plants under Domestication* (1868) comprising nearly 900 pages.

There is probably no other problem to which Darwin devoted more energy and at the same time was as unsuccessful as to the origin of variation. The reason for this disappointing result is that before 1900 the laws of inheritance were largely unknown and Darwin, like most of his contemporaries, accepted the inheritance of acquired characteristics (Lamarckism). According to this original Darwinism of the 1860s and 70s selection is the most important factor in evolution and explains the origin of most adaptations. At the same time Lamarckian effects were acknowledged for a number of cases. In 1883 August Weismann rejected the inheritance of acquired characteristics. His theory, based on a purely selectionist mechanism was called neo-Darwinism. As the major source of variation he identified recombination in sexual reproduction. Weismann, however, had no clear understanding of the laws of inheritance and no mechanism for the production of new heritable traits.

When modern genetics originated during the first decades of the twentieth century its main representatives – Hugo de Vries, William Bateson, Wilhelm Johannsen – believed that genetics would not only provide a correct understanding of the laws of inheritance, but of evolution as well. They assumed that evolution was driven by rare and large mutations. Genetics and Darwinism were considered incompatible. This seeming contradiction was overcome in the 1920s when several authors showed how the findings of genetics can be combined with selection. It could be empirically demonstrated that mutations are much more frequent and less conspicuous than the early geneticists had assumed, i.e. mutations together with recombination are a source of abundant hereditary variation. The new mutation-selection-theory of evolution was based on Darwin's ideas of evolution, common descent and selection. At the same time Darwin's erroneous Lamarckian theory of inheritance was replaced by the genetical theory of hard, particulate inheritance. The most important protagonists of the new model were Sergej S. Chetverikov, Erwin Baur, Ronald A. Fisher and J. B. S. Haldane among others and they considered themselves Darwinians (Provine 1971). Some historians and biologists equated this 'Mendelised 'neo-Darwinism' (Gayon 1998: 320) with the modern 'Synthetic theory of evolution''. The philosopher John Beatty, for example, wrote: 'According to the simplest such characterization of the [evolutionary] synthesis, Mendelian genetic theory and Darwinian evolutionary theory – once considered irreconcilable – were eventually reconciled in the theory of population genetics, which is the core of the synthetic theory' (Beatty 1986: 125).

If this characterisation is correct, the role of ornithology and other naturalists' disciplines was purely receptive. They had to accept the new theory and apply it to their field. This actually happened, but it is not the whole story. As long as evolution is understood as a process taking place within a single interbreeding population, genetics, population genetics and selection explain most of the observable changes. This, however, is only one aspect of evolution and one of the most conspicuous phenomena of organic nature is ignored: the origin of diversity. Species do not only evolve in time, but they also multiply. On the other hand, a population does not have to produce new species in order to stay adapted, i.e., a theory about the mechanisms that sustain adaptedness does not automatically entail an explanation about the multiplication of species.

Darwin also had a theory about the multiplication of species. In *Origin of Species* and his later works he assumed that selection would favour the splitting of species, because the struggle for existence between the most divergent variants is less severe (principle of divergence). The 'more diversified the descendants from any one species become in structure, constitution, and habits, by so much will they be better enabled to seize on many and widely diversified places in the polity of nature, and so be enabled to increase in numbers' (Darwin 1859: 112).

This mechanism was criticised by the geographer Moritz Wagner in 1868. He argued that isolation between two groups of individuals was necessary for the splitting of species. The situation is the same if we look at the breeding of animals or at evolution under natural conditions: free crossing has to be prevented, because it destroys the emergence of new races. Wagner, however, could not convince his contemporaries. One of the reasons for his failure was that he presented isolation as a alternative to selection. It took more than half a century until Wagner was vindicated and geographic isolation was integrated into the modern theory of evolution. The elaboration of a sophisticated theory of the multiplication of species was probably the most important contribution of ornithology to modern Synthetic Darwinism. The way was prepared by Stresemann and systematically elaborated by Rensch and especially Mayr in the 1930s and 40s.

The modern theory of evolution is Darwinian in the sense that it is based on evolution, common descent and selection. Two of Darwin's notions have been replaced by new concepts: his Lamarckian theory of inheritance was replaced by the genetical understanding of inheritance and mutations, and divergence as the mechanism of species splitting was replaced by geographic isolation. Despite these changes twentieth century Darwinism is very close to Darwin's original ideas. Theodosius Dobzhansky, for example, had not only given his 1937 book, which is considered the most influential document of the emerging theory, the title *Genetics and the Origin of Species* but this is also more than a superficial allusion, because Dobzhansky directly reproduced the structure of Darwin's argument in *Origin of Species*.

In the United States the theory is usually called 'synthetic theory of evolution', in England biologist prefer to speak of 'Darwinism' or 'Neo-Darwinism' and on the European continent both names are common. The theory is called synthetic, because it originated through a synthesis of theories, methods and data from various biological disciplines, in particular genetics, systematics, and palaeontology. The name 'Darwinian' derives from the fact that its evolutionary mechanism is built around Darwin's theory of selection (Mayr & Provine 1980, Junker 2003).

To sum up: Synthetic Darwinism as it was formulated in the 1930s and 40s does not only claim to stand in the Darwinian tradition, but its argument is actually structured in the same way as Darwin's. Together with selection, which is regarded as the only causal factor leading to adaptation, further evolutionary factors are integrated. Mutation and recombination were identified as the sources of genetic variability. The important effects of population size were stressed, in particular for small populations, where chance effects limit the power of selection. Geographic isolation was seen as an important requirement for the splitting of a species into two separate species. This modern theory of evolution evolved not only through the collaboration of biologists from a variety of disciplines, but also through the synthesis of different national traditions. It was a joint venture of Soviet, German, American and British biologists (Junker 2003, Junker & Hoßfeld 2002; see Table 1).

Next to entomologists, who constitute the majority of the naturalists among the architects of the synthetic theory of evolution, we find a number of botanists and ornithologists. Both Rensch and Mayr based much of their evolutionary theorising on ornithological data. The British zoologist Julian Huxley did intense research on the ecology of birds.

Ornithology and the genetical theory of selection: Stresemann, Rensch and Mayr

The role of ornithology in the origin of modern synthetic Darwinism can only be properly understood when we distinguish between two consecutive periods: the years 1924 to 1930, when a synthesis between genetics and Darwinism was achieved, and a second period from 1930 to 1947. While the first dealt with evolution within populations, i.e. anagenesis, the second also included cladogenesis, the multiplication of species. What is the

Table 1. The national origin of the major architects of modern Darwinism, the year of their early publications and their main fields of research. Italics indicate which authors contributed to the predominately genetical in contrast to the synthetic phase of the emergence of modern Darwinism.

Nationality	Author	Year	Fields of research
Soviet Union	*Chetverikov*	*1926*	*entomology, genetics*
	Dobzhansky	1937	entomology, genetics
	Timoféeff-Ressovsky	1939	entomology, genetics
Germany	*Erwin Baur*	*1924*	*botany, genetics*
	Zimmermann	1930, 1938	botany, systematics
	Rensch	1943, 1947	zoology, systematics
	Heberer, ed.	1943	
	Mayr	1942	ornithology, systematics
England	*Fisher*	*1930*	*mathematical population genetics*
	Haldane	*1932*	*mathematical population genetics*
	Huxley	1942	zoology
United States	*Wright*	*1931*	*mathematical population genetics*
	Simpson	1944	paleontology
	Stebbins	1950	botany

reason for the strong position of ornithologists in the second synthesis, was it more or less accidental, or was ornithology especially suited to fill in a gap in this synthesis? When I asked Ernst Mayr this question his answer was 'yes and no'. He continued: 'In the 1930s–40s no other group of organisms was better known taxonomically than the birds. Therefore the understanding of geogr[aphical] speciation was documented better than for any other higher taxon. However, the work of Karl Jordan and Ed[ward Bagnall] Poulton on selected groups of insects led to the same results. So it is not completely restricted to birds' (Ernst Mayr to the author, 2 August 2003).

The sophisticated status of ornithological systematics as such, however, did not necessarily lead to the acceptance of the mutation-selection theory. Even though systematics in the hands of Stresemann and Rensch had become a branch of evolutionary biology this did not mean it could only be combined with a Darwinian theory of evolution. A comparison of the evolutionary ideas of Stresemann, Rensch and Mayr will show the possible connections between evolution and the new systematics (Junker 2003).

Erwin Stresemann

Erwin Stresemann (1889–1972) was one of the most influential ornithologists of the first half of the twentieth century (Haffer et al. 2000). From 1921 to 1924 he was assistant curator of ornithology, from 1924–1961 curator of ornithology at the Zoological Museum in Berlin. From 1922 until 1944 he was the General Secretary of the *Deutsche Ornithologische Gesellschaft*, from 1949 to 1967 president of the *Deutsche Ornithologen-Gesellschaft*. During four decades, from 1922 to 1961, he edited the *Journal für Ornithologie*. Stresemann emphasised a populational approach to systematics and he was an early advocate of the biological species concept as well as of geographic speciation. For example as early as 1921 Stresemann asserted that mutations alone will usually not produce a new species, but that geographic isolation is required: 'I am not inclined to believe that 'sports', mutations, will establish good species, if they arise in the midst of normally coloured individuals. [...] Only a very long and complete geographical separation of the descendants from the same ancestors may have caused the rise of such important differences [...] – or perhaps, in some rare cases, a certain physiological mutation accompanied or not accompanied by mutation of external characters' (Draft of a

Figure 1. Erwin Stresemann and Ernst Mayr, 1954.

letter by Stresemann to R. Meinertzhagen, December 1921; from Haffer 1997: 927–28). These concepts were central tenets of the new systematics. Species were seen as groups of populations which vary geographically and are isolated from other species genetically.

Recently Mayr has emphasised that it 'is important to realize the great influence of Stresemann in these developments [i.e. origin of Synthetic Darwinism], for Stresemann was the teacher both of Rensch and of Mayr. Virtually everything in Mayr's 1942 book was somewhat based on Stresemann's earlier publications' (Mayr 1999: 23). On the other hand Stresemann was never really convinced that the Darwinian mechanism was sufficient to explain evolution. Instead he sympathised with a variety of other models – Lamarckism, mutation pressure and orthogenesis. So Mayr came to the conclusion: 'As progressive as Stresemann was in practicing population systematics and in his concepts of species and speciation, he was rather backward in his understanding of the mechanisms of evolution. He probably would have called himself an orthodox Darwinian, but he felt quite strongly that there were severe limits to the power of natural selection' (Mayr 1980: 415).

Bernhard Rensch

Bernhard Rensch (1900–1990) was a zoologist with very broad interests (Dücker 2000). In the summer of 1922 he worked as a volunteer for Stresemann at the Zoological Museum in Berlin. In 1925 he joined the Zoological Museum as an assistant and later became curator at the department of molluscs with close contacts to Stresemann's department of ornithology. In his 21 books and more than 200 papers Rensch discussed a variety of topics, ranging from evolution, animal psychology, biophilosophy, sensory and brain physiology, to biogeography, ecology and systematics. Roughly 20 % of this publications dealt specifically with birds. He was especially interested in the geographical variation of songbirds and attempted to find borderline cases between races and species to support the notion that species originate from isolated geographic races.

As early as 1929 Rensch had maintained that geographic isolation precedes physiological isolating mechanisms in the process of speciation. Later he established various ecological rules that demonstrated the adaptive nature of geographic variation (Rensch 1933). However, until the middle of the 1930s Rensch combined both the geographic model of speciation and the ecological rules with a Lamarckian mechanism and explicitly rejected a purely selectionist theory. Under the influence of the Berlin geneticist N. W. Timoféeff-Ressovsky Rensch was slowly convinced that the mutation-selection-theory was valid. Interestingly, this change did not require major changes of his systematic theory, which was equally adaptable to a Lamarckian and a selectionist model.

As we have seen, in the late 1920s systematists already had an explanation for the gradual origin of species through geographic isolation, i.e. for the origin of biological diversity. They assumed that species split when 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 synthetic Darwinism were Dobzhansky and Mayr. Dobzhansky, in his *Genetics and the Origin of Species* (1937), discussed genetics, selection and evolution, but had not included a detailed analysis of speciation. Mayr's *Systematics and the Origin of Species* (1942) filled this gap.

Ernst Mayr

In 1926 Ernst Mayr (b. 1904) was invited by Stresemann to come as an assistant to the Zoological Museum in Berlin. After his expedition to New Guinea and the Solomon Islands (1928–1930) Mayr accepted an assignment at the American Museum of Natural History in New York. In 1932 he became associate curator, and in 1944 curator at the Whitney-Rothschild Collection of the American Museum. Originally he worked on bird collections of the Whitney South Sea Expedition. When the Rothschild bird collection of 280,000 specimens was bought by the American Museum in 1932, Mayr was in charge of ordering, cataloguing and integrating it with the Whitney collections and other material of the American Museum. Until 1953, when Mayr became Alexander Agassiz Professor of Zoology at Harvard University, he was first of all an ornithologist.

In *Systematics and the Origin of Species* Mayr integrated the progressive ideas of European systematics on populations and speciation with the mutation-selection theory. In the tradition of the new systematics Mayr showed that the origin of distinct 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: 155). Like Stresemann and Rensch he demonstrated the potential of systematics for the study of evolution, but unlike Stresemann and the early Rensch (until 1935) he based his inferences on the mutation-selection theory, developed by Dobzhansky and his predecessors. He convinced the evolutionists that discontinuities could gradually arise and can be explained by studying geographic variation. The vertical dimension of evolution was thus supplemented by the horizontal dimension.

Conclusion

Birds played a very important role in the history of the theory of evolution. They provided Darwin with two important test cases: the Galapagos birds convinced him of the continuous transition from varieties to species, the breeding of pigeons demonstrated the power of selection. Nineteenth century ornithologists, however, were overwhelmingly reluctant to accept the new dynamic theory.

This changed in the second third of the twentieth century. Museum ornithologists were among the most progressive systematists of their time. Important proponents like Stresemann and Rensch were also very much interested in basing systematics on evolution. They did not, however, accept the new mutation-selection-theory of the geneticists, but preferred other evolutionary mechanisms.

Two phases in the development of the modern Darwinian theory of evolution have to be distinguished: the synthesis of the genetical theory of inheritance and selection (anagenesis) during the 1920s and the integration of a theory explaining the splitting of species through geographic isolation (cladogenesis) in the 1930s and 40s. Mayr and Rensch (after 1938) demonstrated that systematics could play an central role in Synthetic Darwinism by providing a theory for the horizontal component of evolution, i.e. cladogenesis.

Figure 2. Ernst Mayr (the first man on the right) at a meeting of the Saxony Ornithologists' Association (about 1925).

References

Bateson, W. 1914. Presidential Address. Pp 276–296 in Bateson, B. 1928. William Bateson, F. R. S. Naturalist. His essays & addresses together with a short account of his life. Cambridge University Press, Cambridge.

Baur, E. 1924. Untersuchungen über das Wesen, die Entstehung und die Vererbung von Rassenunterschieden bei *Antirrhinum majus*. Bibliotheca Genetica 4: 1–170.

Beatty, J. 1986. The synthesis and the synthetic theory. Pp 125–135 in Bechtel, W. (ed.). Integrating scientific disciplines. Martinus Nijhoff, Dordrecht.

Chetverikov, S. S. 1961. On certain aspects of the evolutionary process from the standpoint of modern genetics [1926]. Proc. Am. Phil. Soc. 105: 167–195.

Darwin, C. 1839. Journal of researches. Henry Colburn, London.

Darwin, C. 1859. On the origin of species by means of natural selection, or the preservation of favoured races in the struggle for life. John Murray, London.

Darwin, C. 1868. The variation of animals and plants under domestication. 2 vols. John Murray, London.

Darwin, C. 1871. The descent of man, and selection in relation to sex. 2 vols. John Murray, London.

Darwin, C. 1958. The autobiography of Charles Darwin 1809–1882. (Ed. N. Barlow). Collins, London.

Dobzhansky, T. 1937. Genetics and the origin of species. Columbia University Press, New York.

Dücker, G. (ed.). 2000. 100 Jahre Bernhard Rensch. Biologe – Philosoph – Künstler. LIT, Münster.

Fisher, R. A. 1930. The genetical theory of natural selection. Oxford University Press, Oxford.

Gayon, J. 1998. Darwinism's struggle for survival: Heredity and the hypothesis of natural selection. Cambridge University Press, Cambridge.

Haeckel, E. 1866. Generelle Morphologie der Organismen. 2 vols. Georg Reimer, Berlin.

Haffer, J. 1997. 'We must lead the way on new paths'. The work and correspondence of Hartert, Stresemann, Ernst Mayr – international ornithologists. Ökologie der Vögel, vol. 19. Ludwigsburg.

Haffer, J., Rutschke, E. & Wunderlich, K. 2000. Erwin Stresemann (1889–1972) – Leben und Werk eines Pioniers der wissenschaftlichen Ornithologie. Deutsche Akademie der Naturforscher Leopoldina, Halle (Saale).

Haldane, J. B. S. 1932. The causes of evolution. Longmans, Green, London.

Heberer, G. (ed.). 1943. Die Evolution der Organismen, Ergebnisse und Probleme der Abstammungslehre. Gustav Fischer, Jena.

Huxley, J. 1942. Evolution: The modern synthesis. Allen & Unwin, London.

Johannsen, W. 1915. Experimentelle Grundlagen der Deszendenzlehre; Variabilität, Vererbung, Kreuzung, Mutation. Pp 597–660 in Hinneberg, P. (ed.). Die Kultur der Gegenwart. 3. Teil, 4. Abteilung, Bd. 1, Allgemeine Biologie. Teubner, Leipzig/Berlin.

Junker, T. 1998. Charles Darwin und die Evolutionstheorien des 19. Jahrhunderts. Pp 356–385 in Jahn, I. (ed.). Geschichte der Biologie. 3d ed. Gustav Fischer, Jena/Stuttgart.

Junker, T. & Engels, E.-M. (eds). 1999. Die Entstehung der Synthetischen Theorie: Beiträge zur Geschichte der Evolutionsbiologie in Deutschland 1930–1950. Verlag für Wissenschaft und Bildung, Berlin.

Junker, T. & Hoßfeld, U. 2001. Die Entdeckung der Evolution. Eine revolutionäre Theorie und ihre Geschichte. Wissenschaftliche Buchgesellschaft, Darmstadt.

Junker, T. & Hoßfeld, U. 2002. The architects of the evolutionary synthesis in National Socialist Germany: Science and politics. Biology and Philosophy 17: 223–249.

Junker, T. 2004. Die zweite Darwinsche Revolution: Geschichte des synthetischen Darwinismus in Deutschland 1924 bis 1950. Basilisken-Presse, Marburg.

Junker, T. 2004. Geschichte der Biologie. Beck, München.

Lamarck, J.-B. de. 1809. Philosophie zoologique. 2 vols. Dentu, Paris.

Mayr, E. & Provine, W. B. (eds). 1980. The evolutionary synthesis. Perspectives on the unification of biology. Harvard University Press, Cambridge, Mass.

Mayr, E. 1942. Systematics and the origin of species from the viewpoint of a zoologist. Columbia University Press, New York.

Mayr, E. 1980. How I became a Darwinian. Pp 413–423 in Mayr, E. & Provine, W. B. (eds). The evolutionary synthesis. Perspectives on the unification of biology. Harvard University Press, Cambridge, Mass.

Mayr, E. 1982. The growth of biological thought. The Belknap Press of Harvard University Press, Cam-

bridge, Mass.
Mayr, E. 1985. Darwin's five theories of evolution. Pp 755–772 in Kohn, D. (ed.). The Darwinian heritage. Princeton University Press, Princeton.
Mayr, E. 1999. Thoughts on the evolutionary synthesis in Germany. Pp 19–30 in Junker, T. & Engels, E.-M. (eds). Die Entstehung der Synthetischen Theorie: Beiträge zur Geschichte der Evolutionsbiologie in Deutschland 1930–1950. Verlag für Wissenschaft und Bildung, Berlin.
Provine, W. B. 1971. The origins of theoretical population genetics. University of Chicago Press, Chicago.
Reif, W.-E., Junker, T. & Hoßfeld, U. 2000. The synthetic theory of evolution: general problems and the German contribution to the synthesis. Theory in Biosciences 119: 41–91.
Rensch, B. 1929. Das Prinzip geographischer Rassenkreise und das Problem der Artbildung. Borntraeger, Berlin.
Rensch, B. 1933. Zoologische Systematik und Artbildungsproblem. Akademische Verlagsgesellschaft, Leipzig.
Rensch, B. 1943. Die paläontologischen Evolutionsregeln in zoologischer Betrachtung. Biologia Generalis 17: 1–55.
Rensch, B. 1947. Neuere Probleme der Abstammungslehre. Die Transspezifische Evolution. Ferdinand Enke, Stuttgart. [English edn. 1960. Evolution above the Species Level. Columbia University Press, New York.]
Simpson, G. G. 1944. Tempo and mode in evolution. Columbia University Press, New York.
Stebbins, G. L. 1950. Variation and evolution in plants. Columbia University Press, New York.
Stresemann, E. 1951. Die Entwicklung der Ornithologie. F. W. Peters, Berlin. [English edn. 1975. Ornithology: From Aristotle to the Present. Harvard University Press, Cambridge, Mass.]
Timoféeff-Ressovsky, N. W. 1939. Genetik und Evolution. Z. f. ind. Abstammungs- und Vererbungslehre 76: 158–218.
Vries, H. de. 1901–03. Die Mutationstheorie. Versuche und Beobachtungen über die Entstehung von Arten im Pflanzenreich. 2 vols. Veit & Comp, Leipzig.
Wagner, M. 1868. Die Darwin'sche Theorie und das Migrationsgesetz der Organismen. Duncker & Humblot, Leipzig.
Weismann, A. 1883. Über die Vererbung. Gustav Fischer, Jena.
Wright, S. 1931. Evolution in Mendelian populations. Genetics 16: 97–159.
Zimmermann, W. 1930. Die Phylogenie der Pflanzen. Gustav Fischer, Jena.
Zimmermann, W. 1938. Vererbung 'erworbener Eigenschaften' und Auslese. Gustav Fischer, Jena.