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# Genetics and the causes of evolution: 150 years of progress since Darwin

### Citation for published version:

Bonsall, M & Charlesworth, B 2010, 'Genetics and the causes of evolution: 150 years of progress since Darwin', *Philosophical Transactions of the Royal Society B: Biological Sciences*, vol. 365, no. 1552, pp. 2427-2429. <https://doi.org/10.1098/rstb.2010.0109>

### Digital Object Identifier (DOI):

[10.1098/rstb.2010.0109](https://doi.org/10.1098/rstb.2010.0109)

### Link:

[Link to publication record in Edinburgh Research Explorer](#)

### Document Version:

Publisher's PDF, also known as Version of record

### Published In:

*Philosophical Transactions of the Royal Society B: Biological Sciences*

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*Introduction*

## **Genetics and the causes of evolution: 150 years of progress since Darwin**

The publication of *The Origin of Species* in 1859 represents an unsurpassed landmark in the history of biology. Charles Darwin had been thinking about evolution since 1836, and accumulating evidence both that it had occurred and that it was caused primarily (but not exclusively, as he was always careful to emphasize) by natural selection. By 1844, he had the preliminary ideas on evolution by natural selection committed to paper. While engaged in writing a much bigger book, Darwin was stimulated into publishing his ‘Abstract’ by Alfred Russel Wallace’s letter of 1858, describing Wallace’s independent discovery of the principle of natural selection. Most of Darwin’s subsequent publications, including a long series of weighty books, were devoted to documenting the evidence for evolution by natural selection. While the idea of selection had in fact been proposed several times previously (including by James Hutton, the founder of uniformitarian geology: Pearson 2005), no-one before Darwin and Wallace had developed it into a mature theory of the cause of evolution, supported by a wide-ranging body of evidence from the natural history of their time.

The finding that living organisms, including human beings, are the product of an immensely long historical process, whose causes are entirely impersonal, represented the natural extension to biology of the scientific revolution that had already taken place in astronomy, physics, chemistry and geology. While Darwin’s work revolutionized biology, it simply represented the application of ‘normal’ scientific methods to biology. As Darwin’s writings made clear, this entails a materialistic view of biological phenomena, including mental activities, and of course undermines the Argument from Design for the existence of God. For this reason, Darwin’s dual anniversary is being celebrated well beyond the venues of professional biologists (and is not being celebrated at all in some parts of the world).

The purpose of the Discussion Meeting *Genetics and the causes of evolution: 150 years of progress since Darwin*, organized jointly by the Genetics Society and the Royal Society, was to bring out both how much we owe to the insights of Darwin and Wallace, and how subsequent research into the basis of inheritance has greatly enhanced our understanding of evolutionary processes. Ironically, genetics was

Darwin’s greatest failure. Despite devoting an enormous amount of effort to collecting data, he never arrived at a clear, unambiguous interpretation of the phenomena of inheritance and variation, although he observed Mendelian ratios in several crosses in his work on plants (Charlesworth & Charlesworth 2009; Howard 2009). In contrast to Gregor Mendel, his contemporary, he did not formulate a model of inheritance that made quantitative, testable predictions of the outcomes of controlled crosses, and so failed to grasp the significance of his ratios. Nevertheless, his work showed clearly that there was extensive heritable variation in domestic animals and plants; selection practised by humans on this variation is extremely effective, as Darwin discussed in the first chapter of the *Origin*. He could, therefore, be confident that natural selection was a mechanistically feasible cause of evolution.

This did not, however, fully convince his contemporaries or immediate successors. It took the rediscovery of Mendelian inheritance in 1900 (the year that also saw the birth of quantum theory), to put the study of inheritance on a sound scientific basis. It took a further three decades for genetic knowledge to be firmly incorporated into theoretical models of evolution that could be tested against data on natural and human populations, leading to the Modern Evolutionary Synthesis of the 1930s and 1940s. This work showed that variability is conserved by the mechanisms of heredity, that selection can be extremely effective both in changing the composition of a population and maintaining variation, and that random mutations are the source of variability on which selection and other evolutionary forces act. It also showed that neutral or very weakly selected variants can spread through a population, through the random sampling effects of finite population size. In the 1940s and 1950s, the field of ecological genetics was highly successful in documenting the effects of selection on genetic variants found in nature.

From the 1960s onwards, genetic models have greatly influenced thinking in other areas of evolutionary biology, such as the study of social behaviour and plant and animal mating systems. There has also been a steadily increasing influence of molecular biology on the methods used to study natural variation and evolution, as well as in framing new questions to be answered. In return, methods based on evolutionary genetics principles, such as genome-wide association studies of complex trait inheritance

One contribution of 18 to a Discussion Meeting Issue ‘Genetics and the causes of evolution: 150 years of progress since Darwin’.

(Donnelly 2008), are increasingly being applied to problems of practical importance in medical and agricultural research. It is no exaggeration to say that we may well be at the beginning of the most exciting period in the history of evolutionary genetics, with the prospect of a huge increase in the amount of data, coupled with ever-more complex statistical genetic models for interpreting them.

The papers presented at our meeting described genetic approaches to studying evolution that span the range from theoretical modelling to the analysis of massive datasets on variation in DNA sequences and gene expression. Pemberton (2010) initiated the meeting with an account of the complexities of interpreting long-term studies of the genetics and evolution of quantitative traits in wild populations of large mammals. Manceau *et al.* (2010) presented an overview of studies of the molecular genetic basis of variation in pigmentation in the field mouse *Peromyscus polionotus*, together with the ecological factors causing selection for colour differences between populations. Modern approaches to human evolution, using large datasets on DNA sequence divergence between primate species and on variation within the human population, were described by Kim *et al.* (2010) and Hancock *et al.* (2010). These studies show that Darwin's insight that we are descended from an ancestral species closely related to chimpanzees and gorillas has been amply confirmed by modern studies, and that the DNA of human populations provides evidence of changes reflecting adaptation to local environments.

Despite the title of Darwin's great work, he never arrived at a fully satisfactory understanding of how reproductive isolation between species evolves. Much progress has been made on this by the application of genetics to both the theory of speciation and the empirical analysis of its causes. It is generally agreed that some degree of spatial isolation between populations increases the likelihood that they will diverge sufficiently that they become incapable of interbreeding. Martin & Willis (2010) presented an analysis of the genetic basis of adaptation to local conditions in geographically isolated populations of the monkey-flower *Mimulus guttatus* and partial reproductive isolation between them. Schluter *et al.* (2010) described work on the genetics of adaptation of sticklebacks to freshwater habitats, again documenting how natural selection to local conditions can drive populations apart.

Little was known about bacteria at the time of the *Origin*, and nothing about viruses, but their use in genetics was fundamentally important for the molecular revolution of the twentieth century. The interactions between pathogens and their hosts has long been recognized as important drivers of evolutionary change in both parties (Haldane 1949), and form a major research topic in modern evolutionary biology. The power of molecular sequence data to illuminate the patterns and processes of evolution in viruses was brought out by the contributions of Sharp & Hahn (2010) and Wichman & Brown (2010), on HIV and a bacterial virus, respectively. The important role of population structure in modulating the evolution of the level of virulence of pathogens was emphasized by

Eshelman *et al.* (2010), who showed that, while bacterial pathogen life-history evolution has important epidemiological and ecological effects, it is underpinned by a simple genetic basis. The intricate factors affecting the infectiousness of bacterial pathogens, involving the combination of kin selection, mutation and local demography, were discussed by Frank (2010).

Darwin had little direct evidence for natural selection, and relied heavily on the evidence from domestic animals and plants to demonstrate the effectiveness of selection. Modern genetics has played an important part in the development of efficient methods of artificial selection, and in revealing the history of farm animals and plants. Brown (2010) described how the diversity generated by traditional breeders, to which Darwin frequently referred, is being eroded by modern farming practices, with possible negative consequences for farming communities in the developing world. Dan Bradley further elaborated on this theme of domestication with results from the study of DNA sequence polymorphisms in cattle (Murray *et al.* 2010). It turns out that cattle domestication is more diffuse than originally thought, probably involving multiple events and introgression from wild aurochs.

Darwin also pioneered the concept of sexual selection, according to which traits limited to males have evolved because they confer greater mating success, despite their negative effects on survival. After being neglected for nearly 100 years, this has become a major theme in evolutionary biology. Edward *et al.* (2010) reviewed work on an extension of sexual selection: traits selected in males may also harm females with which the males mate, and the females may evolve ways of resistance. Barrett *et al.* (2010) described work on the evolution of the great diversity of sexual systems in plants. This is another a topic that was pioneered by Darwin, and which has received an enormous impetus from genetic approaches, leading to much better understanding of the evolutionary causes of phenomena such as separate sexes. The question of the evolutionary causes and consequences of sexual reproduction itself was discussed by Barton (2010), who described advances in our theoretical understanding of the population genetic processes that can create an evolutionary advantage for genetic recombination. Under some circumstances, recombination can, however, come with a cost. Ratnakumar *et al.* (2010) argued that there is evidence from sequence comparisons of humans with related species that regions of the human genome that have unusually high rates of genetic recombination may be vulnerable to the effects of biased gene conversion, so that amino-acid changes with harmful fitness effects can be driven through the population.

Finally, Emerson & Li (2010) gave the Mendel Lecture of the Genetics Society, on the theme of evolution and variation in levels of gene expression. This showed how concepts from population genetics can be combined with sophisticated methods of measuring gene expression levels, yielding an understanding of the processes controlling their evolution.

We hope that the papers in this issue of *Phil. Trans. R. Soc. B* convey a sense of the diversity and richness of research in modern evolutionary genetics, and

how the last 150 years has built on, and sometimes radically modified, the foundations laid by Charles Darwin.

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April 2010

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