Evolution: History

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The modern theory of evolution was founded by Charles Darwin, but an overview of the history of evolutionism shows that ideas of the transformation of species predated Darwin, and that even following the publication of Darwin’s Origin of Species in 1859, a complex series of developments was needed to create the genetic theory of natural selection accepted by most biologists today.

Introduction

The history of evolutionism has been widely studied, and Darwin’s role, in particular, has been intensively discussed. The fact that Darwin’s theory of natural selection has emerged as the dominant modern paradigm has encouraged the notion of a ‘Darwinian revolution’ in which old-fashioned creationism was suddenly swept away following the publication of Darwin’s theory. But modern research shows that the basic idea of evolution was widely discussed by radical thinkers before Darwin’s time. The Origin of Species certainly persuaded the scientific community to accept the general idea of evolution, but the selection theory did not at first gain the support of most biologists. During the ‘eclipse of Darwinism’ in the decades around 1900, rival theories of evolution were widely accepted. Only with the coming of genetics were these theories marginalized, paving the way for the synthesis of selectionism and genetics that prevails today.

The eclipse of Darwinism forces us to ask more careful questions about why evolutionism was accepted in the late nineteenth century. If scientists did not at first believe that Darwin had got the right explanation, why was his book so effective in converting them to evolutionism? What changes made the selection theory seem more plausible in the early twentieth century? The modern history of evolutionism seeks to answer these more complex questions, accepting that science does not advance via a series of ‘discoveries’ which command immediate support. The process by which theories are developed and then accepted and refined is a complex one, involving a constant interaction between observation, interpretation and persuasion. The situation is complicated by the fact that attitudes toward Darwinism differ. Outside science, there is still much opposition to the selection theory, and historians writing from an anti-Darwinian perspective will tell a very different story in which the theory is the product of an aggressive materialism distorting scientific objectivity. Even those who regard Darwinism as one of the key ideas of modern science disagree over important aspects of how the theory was developed, especially over the possibility that ideological factors may have affected scientists’ thinking.

Early Ideas

Darwin was accused by his critics of concealing the fact that he was not the first scientist to propose a theory of evolution. In fact he was well aware of earlier attempts, although convinced that his own approach was superior. If we define the concept of ‘evolution’ very generally to mean any non-miraculous process by which new forms of life are produced, then the first such theories were proposed by the ancient Greeks. But because the Christian Church discouraged materialist speculations, such ideas were ignored for many centuries. Only in the eighteenth century were the first comprehensive ideas of the transmutation of species developed, and these often differed markedly from our modern perspective. By the early nineteenth century, theories developed by J. B. Lamarck and others were being widely discussed by radical thinkers, although they were still rejected by the conservative scientific community of the time.

The Greek philosopher Empedocles and the Roman poet Lucretius both proposed that complex living things could be produced by ‘spontaneous generation’, i.e. directly from the activity of nonliving matter. In principle, there was no reason why the forms produced by such a process should conserve their structure over many generations. But the philosophers Plato and Aristotle both argued that the form of each species of life was absolutely fixed – for Plato each species had an ideal form or pattern which was conserved at a transcendental level, the individual members being merely copies of this eternally fixed pattern. On this ‘typological’ view of species, the world of life was divided into a number of absolutely fixed species which maintained their structure through time by reproduction, and which could not blend by hybridization. Individual variations were by definition trivial and transitory. It was widely supposed that the species were arranged in a ‘chain of being’ – a linear pattern stretching from the lowest form of life up to the human race. No species could become extinct because this would break the continuity of the chain and leave a gap in creation.

For Christian thinkers, the ideal form of the species could be seen as the blueprint in the mind of God the Creator, while the chain of being represented the overall
Darwin

Charles Darwin was born in 1809 and originally trained in medicine. Turning his back on this, he took a BA at Cambridge, expecting to become an Anglican clergyman. At Cambridge, his extracurricular studies in natural history and geology brought him to the attention of the professors of botany and geology, J. S. Henslow and Adam Sedgwick. It was Henslow who obtained for him a position to travel aboard the survey vessel HMS Beagle on her voyage to South America (1831–1835). Here Darwin was converted to Charles Lyell’s uniformitarian geology, finding new evidence that geological changes were slow and gradual rather than catastrophic. Darwin also collected fossils and studied the geographical distribution of species. It was on the Galápagos Islands that he found the evidence which converted him to evolution. The various islands were inhabited by distinct species of finches, which had almost certainly evolved from small populations originally derived from a single original species. Darwin was soon convinced that isolated populations evolved to adapt to their local environment. Generalizing from this, he conceived evolution as an ever-branching tree, some branches becoming extinct while others subdivide and move off on different tracks.

On his return to England, Darwin searched for a mechanism to explain the changes. He studied the work of animal breeders, and learnt that they could modify species by artificial selection. Individuals in the population exhibited random variations, and the breeders selected and bred from those individuals that happened to fit their requirements. He wondered if anything in nature could select adaptive characters in a similar manner, and was then deeply impressed by Thomas Malthus’ ‘principle of population’, according to which the population always tends to outstrip the food supply. This leads to a ‘struggle for existence’ in which many must die, and Darwin realized that those individuals with variations adapting them to the local environment would tend to survive and breed. Over many generations this process of ‘natural selection’ would modify the whole population. Darwin’s reliance on Malthus is seen by many historians as evidence that the theory of natural selection was inspired by the competitive ethos of Victorian capitalism. In the free-enterprise economy, as in nature, competition led to what the philosopher Herbert Spencer called the ‘survival of the fittest’.

Darwin developed his theory in the late 1830s but did not publish. In part, this was because he was afraid of public controversy. But he also realized that he still had much to do if his theory was to answer the questions that would be raised by other naturalists. He opened up a network of correspondence with experts who could help him. Some of these, including the botanists J. D. Hooker and Asa Gray, who helped Darwin on biogeography, were eventually told about the theory. Darwin also studied barnacles, which proved immensely useful to him in highlighting the ways in which his theory could be exploited in taxonomy. The barnacles helped him to see the extent of variation in nature, and showed him the sometimes bizarre effects that natural selection could have on a species. In the 1850s, studies of the fossil record by Richard Owen and others showed him that evolution was a process of constant pattern of creation. It should be noted, though, that the early fathers of the Christian Church were not committed to a literal interpretation of the Genesis creation story. That position only emerged with the Protestant Reformation of the sixteenth century. The claim that the world was created in 4004 bc was first articulated by the Protestant scholar James Ussher in the 1650s. At the same time, scientific naturalists such as John Ray (who pioneered modern ideas on classification) sought a synthesis with religion via natural theology. The study of living things confirmed that each species was carefully adapted to a particular way of life, thereby displaying the Creator’s wisdom and benevolence. This was the ‘argument from design’, intended to prove the existence of a wise and benevolent Creator from the observed nature of His handiwork.

This viewpoint (which resembles that of modern creationism) was challenged by the philosophers of the eighteenth century. Materialists such as Denis Diderot claimed that matter could produce life by spontaneous generation, and that the appearance of monstrosities confirmed the instability of species. Georges Leclerc, comte de Buffon, argued that species could be modified by exposure to new environments. But Buffon still thought that complex species could be generated directly from nonliving matter, at least during the earth’s early history. The first comprehensive ideas of evolution were developed by two thinkers: Erasmus Darwin (grandfather of Charles) and J. B. Lamarck. Lamarck’s Zoological Philosophy of 1809 proposed that simple organisms are generated spontaneously and then become more complex in successive generations. Meanwhile they adapt to changes in the environment by the ‘inheritance of acquired characteristics’. The giraffe got its long neck because its ancestors stretched their necks to reach the leaves of trees. The acquired modifications were inherited and thus accumulated over many generations.

In the early nineteenth century, Lamarck’s theory was widely discussed by radical thinkers but was suppressed by the scientific community. In 1844, the Edinburgh publisher Robert Chambers wrote a popular book, Vestiges of the Natural History of Creation, which led middle-class readers to accept that the progressive evolution of life was part of the divine plan of creation. Although treated with suspicion by academic scientists, Vestiges made the idea of evolution respectable by incorporating it into the increasingly popular theory of social progress.

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divergence and specialization: even in a stable environment, there would still be pressure on a species to adapt more closely to its own specialist way of life. By this time, Darwin was finding it increasingly difficult to believe that natural selection was a process ordained by a wise and benevolent God.

In the mid-1850s Darwin began to write up his theory for publication. He was interrupted in 1858 by the arrival of a paper by Alfred Russel Wallace outlining what appeared to be a theory very close to his own. Wallace, who was earning his living as a collector of exotic species in what is now Indonesia, had studied biogeography and the clues it offered toward an evolutionary explanation. He had also read Malthus. There has been much controversy over the relationship between Darwin and Wallace, some partisans of the latter accusing Darwin of deliberately sidelinin the independent discovery. Others note significant differences between Wallace’s outline and Darwin’s theory (Wallace had no interest in artificial selection) and point out that Wallace’s theory was developed 20 years after Darwin’s. Darwin himself certainly believed that he had been anticipated. Lyell and Hooker arranged for extracts of Darwin’s writings along with Wallace’s paper to be read to the Linnean Society, and Darwin began to write the ‘abstract’ of his theory which became the Origin of Species.

The Origin sparked an intense debate among scientists, religious thinkers and the general public. The religious and philosophical objections to what became known as ‘Darwinism’ are important because they shaped the reactions of the scientists themselves. Within a decade, the Darwinians had succeeded in converting the scientific community and the general public to evolutionism. Yet Darwin’s mechanism of natural selection remained highly controversial, and in the later nineteenth century a variety of non-Darwinian processes was invoked, including Lamarck’s inheritance of acquired characteristics. This situation can be explained by setting the scientific debate against its cultural background. Herbert Spencer linked Darwinism to his philosophy of universal progress, presenting social evolution as an inevitable continuation of the universal trend. And although Spencer wrote of the ‘survival of the fittest’, it is clear that for every individual who was eliminated, there were others who improved themselves in response to the stimulus of competition. Spencer himself was as much a Lamarckian as a Darwinian, and his philosophy helps us to see how evolutionism itself became successful, while a rigid application of Darwin’s selection theory was unacceptable.

**Morphology, Palaeontology and Evolution**

We can map these general concerns onto the scientific debate if we put the arguments into their nineteenth-century perspective. Modern accounts of the ‘Darwinian revolution’ tend to focus on the debate over the selection mechanism, even when they explore the limitations of Darwin’s rather conventional views on heredity. We are told that the one factor that held back acceptance of natural selection was his failure to appreciate Mendel’s idea that heredity is particulate. This view of the debate is a product of hindsight, and obscures rather than illuminates contemporary attitudes towards Darwin’s theory. It marginalizes the role of the non-Darwinian mechanisms popular at the time, and diverts attention from what was, in fact, the main area of evolutionary biology in the late nineteenth century: the reconstruction of the course of evolution. If we dismiss these developments as blind alleys of no real significance, we fail to appreciate what made evolutionism so exciting to the scientists of the time.

Morphology, the study of form or structure, had flourished in early nineteenth-century biology. Comparative anatomists such as Richard Owen sought to unify the main groups of animal life by supposing that they were based on an idealized ‘archetype’ existing in the mind of the Creator. Darwin argued that the archetype was really the common ancestor from which the group had descended by divergent evolution. To many of Darwin’s followers it seemed obvious that the first great task of evolutionary biology would be to reconstruct the tree of life, working out how the branches had separated from one another in the course of the earth’s history. This would be based on comparative anatomy, which would reveal the underlying similarities between superficially distinct types, and on embryology, since early embryos often reveal similarities hidden in adult structures. Ernst Haeckel formulated his ‘recapitulation theory’, declaring that ontogeny (the development of the individual) recapitulated phylogeny (the evolutionary history of the group). Massive efforts were devoted to reconstructing the links between the vertebrate classes. The origin of the vertebrates from an invertebrate ancestor was also studied. In many areas there were no fossils, so anatomical and embryological evidence was all that was available. But evolution was a more complex process than the evolutionary morphologists imagined. Rival theories were formulated and it proved impossible to distinguish between them, leading many scientists to turn away from evolutionary ‘speculations’ in disgust.

Some fossils were available, of course, and more were constantly being discovered. In some cases, they provided evidence for the evolutionists’ claim that distinct modern groups had evolved from a common ancestry. The fossil horses discovered by O. C. Marsh in America were hailed by Huxley as ‘demonstrative evidence of evolution’ because they showed the stages by which the specialized modern form had evolved from a generalized mammalian ancestor. A few key fossils provided links between classes, as when Archaeopteryx showed a combination of reptilian and bird-like features. By the early twentieth century,
palaeontologists were convinced that they had worked out a broad overview of the history of life on earth, although the details of many important transitions still remained obscure.

The morphologists and palaeontologists were seldom interested in the actual process of evolution. They were convinced that the history of life represented a broadly progressive trend, with the tree of life having a main trunk leading to the human species. Few morphologists studied how natural selection would work, and the recapitulation theory was more easily linked to the Lamarckian theory of the inheritance of acquired characters. Palaeontologists also favoured Lamarckism, because with relatively few fossils available it was easy to imagine linear patterns of evolution rather than branching trees. Where a group such as the horses showed an apparently steady increase in specialization, it was assumed that the adoption of a new habit had shaped evolution by the inheritance of the resulting bodily modifications. In some cases, palaeontologists thought that evolutionary trends led toward nonadaptive or even harmful goals, and these were attributed to an inbuilt tendency for organisms to vary in a predetermined direction (orthogenesis).

**Darwinism and Anti-Darwinism**

Many first-generation evolutionists were thus Darwinians in only the loosest sense of the term, and some came out openly against the selection theory. Palaeontologists of the American school of neo-Lamarckism were particularly critical of selectionism. In Britain the novelist Samuel Butler led a campaign to argue that natural selection must be rejected as pure materialism. He claimed that Lamarckism was preferable because it allowed animals to control the direction of their species’ evolution by choosing new habits. Many scientists were influenced by these claims, and Lamarckism formed a major component of what Julian Huxley later called the ‘eclipse of Darwinism’ in the late nineteenth and early twentieth centuries. Lamarckism was weakest, however, in the area of experimental proof that acquired characters could be inherited.

Another point used against the selection theory was the widespread belief that many species possess characters that have no adaptive value. This was one of the points urged by the anatomist George Jackson Mivart, whose *Genesis of Species* of 1871 offered a cornucopia of anti-Darwinian arguments. Another argument centred on the incipient stages of newly formed adaptive structures: a leg that was partly converted into a wing could neither walk nor fly. Mivart himself believed that variation was directed along predetermined lines. Others argued that nonadaptive characters are formed by evolutionary leaps or saltations. This was the position argued by William Bateson in his *Materials for the Study of Variation* of 1894. Significantly, Bateson went on to become one of the founders of genetics, and there can be little doubt that the enthusiasm of the early Mendelians for the idea that characters breed true as units was derived from their belief that the characters are created as units by saltation. Hugo De Vries thought that new species were created by ‘mutations’ (by which he meant evolutionary saltations), not by natural selection. It took some time for geneticists to realize that mutations merely create new genes within the existing population.

Heredity had also become a focus of attention for Darwin and the relatively small number of biologists who took natural selection seriously from the start. Darwin himself was concerned when Fleeming Jenkin argued in 1867 that natural selection could not work if heredity was a process that blended the characters of the two parents together. The effect of a single favourable variation (a sport) would soon be diluted by breeding with unchanged individuals. It was Wallace who pointed out to Darwin that this argument is based on a false assumption. There is always a range of variation within the population, and if one end of the range is favoured, selection will drive the population in that direction. The claim that natural selection will not work unless heredity is conceived to be particulate is thus false, and the selection theory was applied extensively by the biometrical school in Britain. The statistician Karl Pearson and the biologist W. F. R. Weldon showed how the range of variation in a population could be shifted by selection in a way that had a small but measurable effect on the species. Yet Pearson’s opposition to Bateson’s saltationism led him also to reject genetics. Their mutual hostility held back the wider recognition that genetics and Darwinism were in fact compatible. Pearson believed that most of an organism’s characters are rigidly determined by heredity, a view shared by the German biologist August Weismann. The latter’s concept of the ‘germ plasm’ enshrined the notion of a material substance in the cell nucleus that transmits characters from one generation to the next. Weismann insisted that the germ plasm could not be affected by changes in the parents’ bodies, so Lamarckism was theoretically impossible. This view was taken up by the geneticists of the twentieth century.

**Genetics and the Evolutionary Synthesis**

Mendelian genetics was far more than a new theory of heredity; it reflected a wider rejection of the whole world view of Lamarckism and the recapitulation theory, in which evolution was modelled on the development of the individual organism. Mendel’s laws of particulate inheritance were rediscovered in 1900 by De Vries and others, and soon Bateson had coined the term ‘genetics’ for the new science. Bateson also led an effective campaign against the limited experimental evidence offered in support of
Lamarckism. Evolution must now be based only on the production of new genetic characters by mutation. But most early geneticists saw no role for natural selection: they assumed that mutation produced new characters which would be reproduced even if they offered no selective advantage. New species were still thought to be produced by saltations. It was only gradually that geneticists such as Thomas Hunt Morgan realized that most mutations produce only small modifications (large ones are mostly lethal), and so mutation by itself can at best only extend the range of variation in the population. Originally a staunch antiselectionist like Bateson, Morgan eventually conceded that harmful characters produced by mutation would be weeded out of the population, and only beneficial ones would become established. The way was now paved for the reconciliation of genetics and the selection theory.

The first generation of geneticists were laboratory workers who did not think in terms of whole populations. The skills needed to study the variability of wild populations had been developed by the biometricians, who supported the selection theory, but Pearson, a key member of the biometrical school, held out against genetics because of his hostility to Bateson. The science of population genetics was created by biologists who synthesized the techniques of biometry with the new theory of heredity. In Britain, Ronald Aylmer Fisher and J. B. S. Haldane showed how the two approaches could be synthesized, with Fisher’s *Genetical Theory of Natural Selection* of 1930 summarizing the new approach. In America, Sewall Wright used different techniques to produce a similar reconciliation. In the course of the 1930s the tide began to turn strongly in favour of Darwinism.

Some historians have suggested that the emergence of population genetics was the key factor in the creation of modern Darwinism. It was certainly one of the most important, but Ernst Mayr, himself a participant in the emergence of the new synthesis, insists that the field naturalists were independently turning to Darwinism, bringing their own unique insights to bear in the production of the synthetic theory. Fisher’s theory assumed that selection acted on a large, widely distributed population and that its effects would be very slow. Field naturalists like Mayr noted that evolution proceeded best in small, isolated populations, just like those Darwin had studied on the Galápagos Islands. The Russian-born biologist Theodosius Dobzhansky helped to translate the mathematics of the population geneticists into hypotheses that the field naturalists could test. Significantly, he worked with Sewall Wright, whose theory had (unlike Fisher’s) assumed populations to be broken up into smaller, partially isolated, fragments. By the 1940s the new Darwinism was complete, and Julian Huxley’s *Evolution: The Modern Synthesis* of 1942 gave it a name. Since then the modern synthesis of genetics and Darwinism has dominated evolutionary biology. There have been major developments within the theory, including sociobiology, and controversies such as the one surrounding punctuated equilibrium, but few biologists have challenged the overall thrust of the theory.

**Further Reading**


