Jonathan Slack

GENES

A Very Short Introduction

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Genes before 1944

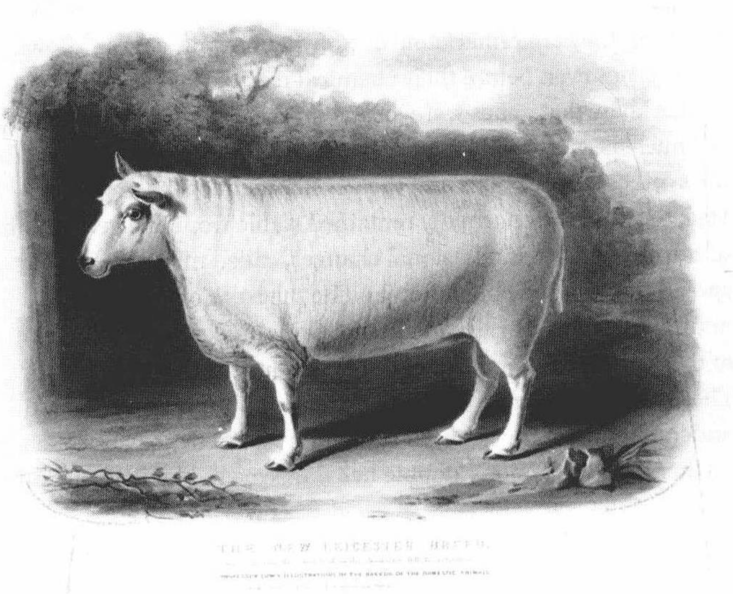
In 1938 a remarkable pair of articles was published in the *Quarterly Review of Biology*. They were by an American biology professor from the University of Missouri, Addison Gulick, and they were about the nature of the gene. These articles are rarely consulted today since they were written shortly before it was discovered that genes consisted of deoxyribonucleic acid (DNA). However, they are remarkable in showing how much was known about genes even before their chemical nature was established. Gulick knew that genes were located in the chromosomes of the cell nucleus, and were complex structures that somehow directed the synthesis of enzymes and the development of the organism. He knew that they normally remained stable from one generation to the next, and that occasional changes, called mutations, could spread through the population and be the basis of evolution by natural selection. He also made surprisingly accurate estimates of the sizes and numbers of genes in various types of organism. These articles illustrate that to appreciate how our current understanding of the gene came about we need to go back much further than the famous 'double helix', discovered by Watson and Crick in 1953.

Two completely separate lines of work led to our modern view, and they came together shortly after the appearance of Addison Gulick's articles to create the new science of molecular biology.

One was the study of heredity by biological experimentation and the other was the study of the chemistry of DNA.

Biology of heredity

Before the 18th century there was little informed speculation about heredity. Even the word did not exist ('heredité' first appeared in France, 'genetic' in England, both about 1830). Before then there was plenty of animal breeding and vague ideas of 'blood lines', but this was uninformed by much understanding of reproduction. In the 18th century the first systematic breeding of agricultural animals had begun. Robert Bakewell, a sheep breeder from Dishley, near Loughborough, England, bred a line of New Leicester sheep that grew faster and produced more meat than before (Figure 1). This was done by mating the best males and females to create a self-reproducing population (breed) that



1. New Leicester sheep. From David Low's *The Breeds of Domestic Animals of the British Islands*, London, 1842

maintained the new characteristics in a stable way. The experience of animal breeding conveyed the idea that heredity involved the blending, or averaging, of the distinct characters, also known as traits, of the parents. It was quite understandable that animal breeders should have believed in the blending of traits since this is what you see when animals are mated and characters such as height or weight or growth rate are measured. But the blending theory of inheritance was to become a serious problem for Darwin's theory of natural selection.

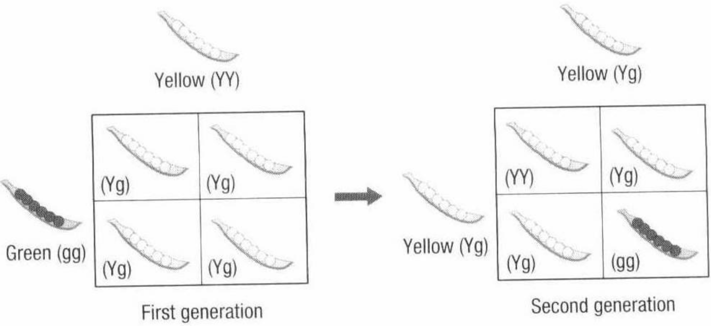
By the time of Darwin's work in the mid-19th century, the fact that biological evolution had occurred was reasonably well accepted by scientists, mostly on the basis of the changes seen in the fossil record. The real impact of Darwin's work, and that of his contemporary Alfred Wallace, was to provide an actual and credible mechanism for the changes seen in living organisms over evolutionary time. This mechanism was natural selection, and the case for it is simply stated. If a population of animals or plants varies with regard to some traits, if those traits are heritable, and if they affect the likelihood of reproduction, then the composition of the population will inevitably shift between each generation. The traits associated with more reproduction will become more common, and will eventually displace the alternatives. The direction and speed of the shift will be determined by the selective conditions that cause the differential reproduction of the individuals with the different traits. The theory of natural selection seems very compelling, and it is especially compelling as presented by Darwin in *The Origin of Species* (1859), which contains a huge array of examples drawn from natural history to support the case. At the time, the main opposition to the theory was from religious groups who realized that the principle of natural selection undermined the 'argument from design', an important argument for the existence of God, and also from those offended by the idea of a biological kinship between humans and animals. However, there was also some scientific opposition, and the most serious was that which focused on the difficulty of reconciling natural selection with blending inheritance.

Supposing that one individual is slightly better suited to reproduction than others due to the possession of a particular trait. Because the favourable trait is rare, he or she will most likely mate with an individual lacking it and their offspring will then have it in a diluted form. After three or four generations the hereditary factors responsible for the trait will be diluted out almost completely. So selection has only a few generations to operate and this will not be enough to change the whole breeding population unless the reproductive advantage conferred by the new trait is very large indeed. Darwin himself was well aware of the problem but he was also opposed to the idea of large jumps in evolution and favoured the idea that evolution progressed in a smooth and imperceptible manner via many small changes.

Some thinkers followed this argument to its logical conclusion and concluded that the hereditary factors responsible for evolution must have large effects, such that substantial selection could occur before they became diluted out. In this way the trait might become common enough for some matings to occur between parents who both possessed it and it would no longer be diluted in their offspring. Among these thinkers was William Bateson who collected in his book *Materials for the Study of Variation* (1894) a remarkable set of examples of discontinuous and qualitative variation within animal and plant populations. More direct evidence for the existence of large heritable changes came from observation of spontaneously occurring 'mutations'. In particular the Dutch botanist Hugo de Vries in 1886 observed the *de novo* appearance of dramatically new forms of the Evening Primrose, which bred true in subsequent generations. Nonetheless, blending inheritance remained a serious problem for the theory of natural selection.

In fact the solution to the problem had been provided as early as 1866 by Gregor Mendel, a monk at the Abbey of St Thomas in

Brno, now in the Czech Republic. In the early 19th century, Brno was a centre of textile manufacture and of sheep breeding, and the Abbey already had a two-hectare experimental garden. Mendel had received education about animal and plant breeding in the course of his studies of philosophy at the University of Olomouc, and he was encouraged to continue his work at Brno by the Abbot. Between 1856 and 1863, Mendel conducted a number of experiments with peas. He was fortunate enough to choose simple characters, which we would now call characters determined by single Mendelian genes, rather than complex characters determined by many genes. Among these characters were a round or wrinkled appearance, and a green or yellow colour. Mendel postulated that there were invisible hereditary 'factors' causing each visible character, and showed that there were predictable rules for their inheritance. His breeding experiments indicated that each individual plant contained two factors for each character, one derived from each parent. When reproductive cells (pollen or eggs) are formed, each contains just one factor, randomly selected from the two possibilities available in that plant. In some cases one factor would suppress the other: we should now call this a dominant gene. For example a cross between yellow and green peas gives only yellow offspring. However if these offspring are crossed to each other, then 25 per cent of the next generation are green, indicating that the green factors are still there, but cannot be expressed in the presence of the yellow factors (Figure 2). So, Mendel showed that the hereditary factors behaved as discrete units, such that each parent provided one to each offspring and the appearance of the offspring depended on the specific combination of factors inherited and the dominance rules between them. Mendel published his work in the *Verhandlungen des naturforschenden den Vereines in Brünn* in 1866. But this was what we should now call a 'low-impact journal', and nobody noticed. After he became Abbot in 1868 he was mostly occupied with administrative duties. He died in 1884 with the wider world still being ignorant of the founding principles of genetics that he had discovered.



2. Mendel's peas. When yellow peas are crossed to green peas, the first generation seeds are all yellow. But when members of the first generation are crossed to each other, 25 per cent of the second generation seeds are green. Mendel explained this by postulating factors, here called Y for yellow and g for green, such that the yellow factor is dominant over the green where they occur together

The 20th century

In Western Europe and America, arguments continued over whether natural selection could work through blending inheritance, and whether mutations of large effect were a credible source of variation. Not until 1900 was Mendel's work rediscovered and further developed. Several people were responsible for this including Hugo de Vries of mutation fame and the German botanist Carl Correns. It was immediately apparent that the major contradiction had now been removed. Mendel's factors were stable and persisted from generation to generation and variation in a population existed because of the differences between the factors that were present in each individual. So it was not necessary to postulate new mutations to explain every newly appearing variation. Moreover the more complex characters, whose inheritance appeared to be of a blending nature, could be explained as resulting from the action of several independent Mendelian factors.

In the late 19th century improved microscopes and new stains from the chemical industry had improved visualization of cells and their nuclei. The German anatomist Walther Flemming, working at Kiel, first identified chromosomes, and described the process of cell division, now called mitosis, in which the chromosomes enter the nuclei of both daughter cells. The Belgian cytologist Edouard van Beneden showed that there was a characteristic chromosome number for each species and that this number was found in the various different cell types of an organism. He followed chromosomes of the nematode *Ascaris* through cell division and showed that the number was conserved, but that it halved during the formation of reproductive cells (divisions forming reproductive cells are now called 'meioses'; singular, 'meiosis').

By the beginning of the 20th century, after Mendel's work had been resurrected, Theodor Boveri in Germany and Walter Sutton in the USA independently showed that chromosomes behaved just like Mendel's hereditary factors. From then on most scientists believed that the chromosomes were the hereditary factors or at least contained them. The hereditary factors themselves were named 'Gene' (in German this is plural, equivalent to 'genes' in English) in 1909 by Wilhelm Johannsen, Professor of Plant Physiology at the University of Copenhagen. The term was derived from the Greek *γενεα* (=generation or race). This is an interesting linguistic example of the entity being named after the process, as 'genetic' had been in use since 1830, and 'genetics', as a noun, was introduced by William Bateson in 1905.

The centre of gravity then moved to the USA where Thomas Hunt Morgan, at Columbia University, effectively established modern genetics through his studies of the fruit fly *Drosophila*. *Drosophila* is a small insect with a short generation time. Large numbers can be kept in small tubes, many crosses can be carried out in a reasonable time scale, and insects have a lot of complex anatomy on the surface that it easy to observe by simple visual examination. *Drosophila* is therefore very well suited to genetic work in the laboratory. Despite much effort, no treatments were found that