Natural Selection from the Genetical Standpoint

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Fifty years ago, in the year in which I went to Cambridge as an undergraduate, the fiftieth anniversary of the publication of the *Origin of the Species* was being celebrated, apart from other things, by the publication of Bateson's book *Mendel's Principles of Inheritance,* and in the same year by a remarkable collection of able essays assembled by Professor A. C. Seward under the title of *Darwin and Modern Science.* It was a period of exciting new advances on the genetical front, but it is clear in retrospect that no progress had been made in understanding the bearing of the new knowledge on evolutionary theory, and that the leaders of biological thought had largely lost sight of the cogency of the principle of Natural Selection in supplying the driving force of evolutionary progress, and its detailed guidance. Of the essays I have mentioned, only two were principally concerned with selection theory. The veteran August Weismann contributed a very brilliant paper, which must be among the last of his writings on a subject to which so much of his life's work had been devoted; and Professor E. B. Poulton of Oxford summarized with equal felicity the extremely cogent evidence supplied by coloration, especially in the mimetic butterflies. But these two were clearly in a minority whose views were regarded with much scepticism, for, strange as it must seem to the present generation, many were persuaded that the element of discontinuity inherent in a particulate theory of inheritance implied a corresponding discontinuity in the evolution of one specific type from another.

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When the matter is examined from the point of view of Population Genetics, it is apparent that the difference due to substituting the particulate theory of Mendel for the traditional blending theory lies centrally in the fact that, under any particulate theory the heritable variance is well conserved, whereas with a blending theory it is rapidly dissipated. The mutation rates needed to maintain an observable amount of variation differ at least by a factor of ten thousand, for with a particulate theory only minor causes of loss such as the chances of random sampling, and the elimination of genes by selection, have to be made good, Darwin conceived that new variation, such as he thought could be produced by change of environmental conditions, had to be snapped up by selection, within a few generations, before it had time to die away. He was, therefore, led into unnecessary speculation as to how new variability could be generated. However, although he believed that almost every individual must be, to use a later term, a mutant, and indeed a multiple mutant, he showed a deep understanding in resisting the easy notion that evolutionary progress was, so to speak, *worked* by mutation.

A letter published later, which bears the critically important date 1856, is evidence of his attitude shortly before the Linnaean Society discussion, and the appearance of the *Origin,* He says "But at present, after drawing up a rough copy on this subject, my conclusion is that external conditions do extremely little, except in causing mere variability. This mere variability (causing the child *not* closely to resemble its parent) I look at as very different from the formation of a marked variety or new species".

The alternative theories of evolution, which have from time to time gained some degree of popular support all indeed use mutation as the mainspring. With Lamarck the *sentiment interieure*, or the emotional state and desires of an animal were supposed to act in such a way as to modify the inherited nature of its offspring, and by this means to induce progressive change in the direction of the satisfaction of these desires, a fairy-story wish fulfilment. A similar mutagenic power was attributed to the Use or Disuse of muscles and other organs. The orthogeneticists believed that by an inherited tendency to mutate in certain directions large and elaborate progressive changes could be brought about over millions of years. Others have ascribed to the environment or "landscape" a power controlling evolutionary change, *not* through the selective process, but by the induction of the appropriate mutations. The challenge to all such "mutation theories", offered by the fact of particulate inheritance, is that even if the special causes on which they rely were really capable of producing mutations, any mutation-rates consistent with particulate inheritance would be totally insufficient to bring about any direct evolutionary change whatever, being easily neutralised even by quite trifling counter-selection. The vast number of deleterious mutations, which must constantly take place in wild populations, have for this reason no direct evolutionary effect; though slighter changes, of a harmless, or even conditionally beneficial character, may be long conserved in the species, and serve to maintain that pool of heritable variation, on which depends the possibility of future progress. The steps from mutation to evolutionary change are thus conditional and indirect. Darwin writing in ignorance of particulate inheritance, could scarcely have hit the nail more squarely on the head.

When Gregor Mendel, shortly after his return from University studies in Vienna, began to experiment with the garden pea, *the Origin of Species,* and even the celebrated Darwin-Wallace joint communication to the Linnaean Society in 1858, were still in the future. It is possible, but not very probable, that he had heard of Charles Darwin, as an explorer perhaps, or a geologist. He had certainly not heard of Natural Selection. Though the possibility of organic evolution had long been discussed in general terms, Mendel's work was not designed to throw light on this question. On the contrary it was designed, and designed in meticulous detail, to elucidate the nature of hereditary transmission, and it is undoubtedly due to this concentration of aim that his success was so thorough and complete, at least for the cultivated varieties of *Pisum sativum.*

By the time he read his long paper to the Brunn Natural History Society in February and March 1865, the situation had changed greatly. Everyone had heard of Darwin, and everyone was talking of evolution.

Mendel himself had probably already read the *Origin* . It is not unnatural, therefore, that he alludes to evolution, and indeed uses terms of unquestioning acceptance, in the first and the last sections of his paper.

In the former he says simply "It requires indeed some courage to undertake a labour of such far-reaching extent; it appears, however, to be the only right way by which we can finally reach the solution of a question the importance of which cannot be overestimated in connection with the history of the evolution of organic forms. The paper now presented records the results of such a detailed experiment"; that is to say that his business is with the nature of inheritance, but that a clear understanding of this should help to clarify the process of evolution - as indeed it surely has!

It has been largely overlooked that in the latter he points out, though somewhat obscurely, and perhaps diffidently, that the system of inheritance he had discovered, at least if it were generally applicable, would remove one of the difficulties that had troubled Darwin; namely that the most anciently cultivated species showed more rather than less variation, than others brought more recently into culture.

To the series of accidents which prevented the appreciation of Mendel's work, one more must therefore be added. The two men above all others to whom Mendel's discovery would have been all-important, August Weismann and Francis Galton, both lived indeed to hear of the discovery, 35 years later, in the eighth or ninth decades of their lives. Even when in 1900 attention was called to Mendel's paper and it was widely reprinted and translated, the sense of his own allusions to evolution theory was overlooked, and neither Weismann nor Galton came to know how fully these forgotten researches justified the point of view for which each in his own way had fought.

The early Mendelians could scarcely have misapprehended more thoroughly the bearings of Mendel's discovery, and of their own advances, on the process of evolution. They regarded species as passively awaiting the next favourable mutation, instead of recognizing them as abundantly supplied with heritable variation, prepared in advance for changes in all directions, and sensitively poised to respond to every kind of selective influence. They confused the discontinuity of particulate trans mission with discontinuity in the genealogy of new species. They thought of Mendelism as having dealt a death blow to selection theory, whereas in reality it had swept the field of all its competitors.

A centenary celebration is an occasion for retrospect, yet I submit, though the view is an old-fashioned one, that the purpose of retrospect is to prepare ourselves for the future, by avoiding the unnecessary repetition of the errors of the past. In England the teaching of biology had been neglected, and towards the end of the nineteenth century continental influence was predominant. Whether for this reason, or for others, it Is certain that In the generation following Darwin's death, his theory of Natural Selection was almost totally misunderstood by teachers and writers. Nearly everyone thought he knew what was in the *Origin*, and that it contained nothing new for him, but he did not open the book to make sure. Many were quite willing to celebrate the anniversary of its publication as a great event in the history of human understanding, even though the book had actually contributed nothing to their own understanding.

The efflorescence of so-called theories of evolution, of a fanciful nature, such as that of Samuel Butler or Willis's *Age and Area*, would indeed not have been possible had Darwin's theory been understood in academic circles; but these theories show in another way what may still be a weakness in biological education—I mean the confusion between a Scientific Theory and a Bright Idea. There is, I submit, no reason why biological students, as well as those in physics and chemistry, should not acquire with their courses a clear notion of what is meant by an intellectual discipline, or an awareness that confirmation and verification are rational and objective processes, appropriate to a mental age getting too mature for the fairy-stories of simple wish-fulfilment. At a time when competition is severe for any competent university teacher, it may seem hard to stress any further requirement, yet it is obvious that many junior teachers have been quite adequately equipped with *knowledge,* without having acquired any sufficient understanding of scientific reasoning, and still harbouring the very simple faith that the newest is the truest.

It would not be easy to find a formula for producing a Charles Darwin, or his equivalent, every two hundred years or so. The simpler task I suggest for our reflection at a centenary celebration is that of conserving the gains made, at least in the major advances in human understanding. In particular, as we are so fortunate in the middle third of the twentieth century to have recovered an understanding of Darwin's theory, our task is to prevent it from being obliterated by the very process of university education, which might be used to consolidate it and other advances as bases for further progressive extension. More attention to the History of Science is needed, as much by scientists as by historians, and especially by biologists, and this should mean a deliberate attempt to understand the thoughts of the great masters of the past, to see in what circumstances or intellectual *milieu* their ideas were formed, where they took the wrong turning or stopped short on the right track. A sense of the *continuity* and the progressive and cumulative character of an advancing science is the best prophylactic I can suggest against the manic-depressive alternations of the cult of *vogue* and *boost,* which threatens to smother the scientific efforts, gigantic as they are, of at least one great nation.

COMMENT

This paper, which was Fisher's contribution to a Centennial Symposium on the Origin of Species, held in Canberra, 1959, includes several paragraphs inadvertently omitted from the original publication.